DISTRIBUTION AND HABITAT ASSOCIATIONS OF DEEP-SEA FISHES IN A MARINE PROTECTED AREA:

THE ECOLOGICAL ROLE OF SOFT-BOTTOM BIOGENIC HABITATS FOR GROUNDFISH POPULATIONS IN THE NORTHWEST ATLANTIC, AND IMPLICATIONS FOR CONSERVATION

by

© Marion Boulard

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Abstract

While many studies have assessed relationships between fishes and large hard-substrate cold-water corals (CWC), relatively few have examined the relationships of fish with habitat provided by smaller corals in soft-bottom environments.

Here, I analyzed data from two *in-situ* benthic surveys, collected in 2017 and 2018 by two underwater video systems (UVS) in the Laurentian Channel Marine Protected Area (MPA), which hosts the largest known sea pen densities and diversity in the Canadian Northwest Atlantic. My objectives were 1) to understand the small-scale linkages between fish, biological and physical habitat features in a soft-sediment deep-sea environment, and 2) to evaluate the bias and relative effectiveness of UVSs to bottom trawls in sampling fish assemblage characteristics.

I found evidence of taxon-specific influence of specific habitat biotic and abiotic features on fish density, especially CWC habitats. Specifically, I suggest that sea pens in the Laurentian Channel MPA may provide nursery habitats for early-life stage fishes dominating the assemblage and that fish undergo ontogenetic shifts in micro-habitat use and specialization.

Most taxa and fish did not react to UVSs or not enough to induce bias in estimating observed abundances, and variability in fish reaction was mostly influenced by fish *in-situ* behavior. In addition to improving UVS assessments, studying fish behavior – both *in-situ* and response – and its variability with ecological factors can improve our knowledge on fish habitat use and ecology. Additionally, I illustrate similar fish diversity and relative abundance (for a similar survey area covered), higher total and specific fish densities and similar fish population size structure assessed by UVS compared to that caught by scientific bottom trawls.

Overall, my results suggest that:

1. Small-scale heterogeneity of specific biotic and abiotic habitat features in a soft-bottom environment has a taxon-specific influence on fish distribution.
2. Sea pens in the Laurentian Channel MPA provide safe resting and feeding grounds for early-life stage fishes that may stay over multiple years to grow before presumably migrating and settling in their adult habitat.
3. However, fish-habitat associations were not as strong as associations found in hard-bottom ecosystems, suggesting a facultative relationship between fish and invertebrates in the MPA.
4. Sea pens in the MPA should be protected as a habitat in addition to as a taxon, and monitoring indicators should include fish-related metrics.
5. UVSs have proven to be an efficient, non-destructive tool to yield *in-situ* small-scale distribution of fish in association with benthic habitat attributes, and *in-situ* imaging can be an effective alternative to scientific bottom-trawl surveys. This approach can meet long-term monitoring objectives of the Laurentian Channel MPA to assess fish populations.

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List of Abbreviations

AIC	Akaike Information Criterion
ANCOVA	Analysis of Covariance
ANOVA	Analysis of Variance
AUV	Autonomous Underwater Vehicle
BRUV	Baited Remote Underwater Video
CCGS	Canadian Coast Guard Ship
CHONe	Canadian Healthy Oceans Network
CT	Conservation Target
CWC	Cold-Water Coral
DFO	Fisheries and Oceans Canada
EBSA	Ecologically and Biologically Significant Area
eDNA	Environmental DNA
EFH	Essential Fish Habitat
FoV	Field of View
GAM	Generalized Additive Model
HOV	Human Operated Vehicle
MCA	Multiple Correspondence Analysis
MPA	Marine Protected Area
MR	Marine Refuge
MSP	Marine Spatial Planning
NMDS	Non-Metric Multidimensional Scaling
PCA	Principal Component Analysis
PERMANOVA	Permutational Multivariate Analysis of Variance
ROPOS	Remotely Operated Platform for Ocean Sciences
ROV	Remotely Operated Vehicle
SAC	Species Accumulation Curves
SBA	Sensitive Benthic Area
SDM	Species Distribution Model
SIMPER	Similarity Percentages
SSDS	Soft-Sediment Deformation Structures
TL	Total Length
ToD	Time of Day
VBGF	Von Bertalanffy Growth Function
VIF	Variance Inflation Factor
VME	Vulnerable Marine Ecosystem
UVS	Underwater Video System

Co-authorship Statement

I, Marion Boulard, led most of the research questions, methodologies and data analysis, and wrote this thesis manuscript under the supervision of Drs. Peter Lawton and Evan Edinger. I participated in the two cruises to collect data in the study area in 2017 and 2018. In addition, I benefited from the collaboration of Dr. Krista Baker, a co-author to three of my chapters submitted for publication, as well as my supervisory committee, composed of Drs. Krista Baker, Jonathan Fisher and Paul Snelgrove, whose guidance helped to define research areas and improve this manuscript.

The following table presents the co-authorship statement for each chapter using the CRediT classification. MB: Marion Boulard, KB: Krista Baker, PL: Peter Lawton, EE: Evan Edinger, JF: Jonathan Fisher.

Co-author contribution	**Chapter 1**	**Chapter 2**	**Chapter 3**	**Chapter 4**	**Chapter 5**	**Chapter 6**
Conceptualization	MB	MB	MB	MB	MB	MB
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Software		MB KB	MB KB	MB KB	MB KB	
Validation		KB	KB	KB	KB	
Formal analysis		MB	MB	MB	MB	
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Writing - Review & Editing	MB KB PL EE	MB KB PL EE JF	MB KB PL EE	MB KB PL EE JF	MB KB PL	MB KB PL EE
Visualization	MB	MB	MB	MB	MB	MB
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Publications Arising

The following publications were produced as part of this dissertation:

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Legrand E., **Boulard M.**, O'Connor J., Kutti T. (2024). Identifying priorities for the protection of deep-sea species and habitats in the Nordic Seas. *IMR technical report for the Norwegian Environment Agency*.

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General Introduction

The deep sea – or everything that lies below the photic zone (200 m) or beyond continental shelves – is the largest yet least explored and least studied ecosystem on Earth. The ocean covers about 70% of the Earth's surface, and 90% of that ocean lies in the deep sea. Yet, only 5% of the deep seafloor has been mapped with modern high-resolution technology (*e.g.*, multibeam sonar systems) and less than 1% of it has been studied in detail (**Ramirez-Llodra *et al.*, 2010**).

Once considered to be vast and desolate, recent advances in deep-sea technology have revealed the deep sea to be home to diverse and dynamic habitats, including abyssal plains, submarine canyons, seamounts, hydrothermal vents, mid-ocean ridges, cold seeps and cold-water coral reefs, that support unique species, and diverse and complex communities (**Roberts *et al.*, 2009 | Etnoyer *et al.*, 2010 | German *et al.*, 2011 | Harris & Macmillan-Lawler, 2015 | Georgieva *et al.*, 2021**).

Despite its remoteness, the deep sea is not immune to human influence as we previously thought. Indeed, like many other ecosystems on the planet, deep-sea ecosystems face an unprecedented accumulation of threats due to increasing human activities and demand for natural resources (**Halpern *et al.*, 2008 | Swartz *et al.*, 2010**). Multiple anthropogenic stressors, such as climate change, ocean acidification, habitat loss, deep-sea mining, hydrocarbon exploration and exploitation, overfishing and pollution (**Koslow *et al.*, 2000 | Keeling *et al.*, 2010 | Smith *et al.*, 2013 | Danovaro *et al.*, 2017**), can affect the biological, chemical and physical properties of marine ecosystems, ultimately modifying their functioning and reducing the resources and ecosystem services on which human societies depend (**Worm *et al.*, 2006 | Hewitt *et al.*, 2008 | Cardinale *et al.*, 2012**).

Many studies have brought attention to the vulnerability of deep-sea ecosystems to habitat destruction and biodiversity loss (**Danovaro *et al.*, 2008**). Yet, the remoteness of deep-sea habitats presents a unique challenge to study deep-sea biodiversity, habitat and ecosystem processes, and understand the effects of human activities on them. As a result, our scientific knowledge of deep-sea ecosystems often remains limited or insufficient to provide adequate information to decision makers (**Kennedy *et al*., 2019**). Therefore, there is a crucial need to understand the vulnerability of deep-sea ecosystems, as well as the biology and ecology of deep-sea fauna for effective conservation measures of deep-sea ecosystems and for the sustainable management of marine natural resources. In this context, this thesis aims to assess the distribution and relationships between deep-sea fishes, cold-water corals and other benthic habitats in a marine conservation area.

1-1 | Background overview

1-1.1 | Deep-sea corals

When most people think of corals, they think of colourful reef systems in warm, shallow, tropical waters. In fact, corals are distributed in both shallow and deep-sea environments and create important habitats for many marine species, including fish and invertebrates. Being far out of reach and sight, deep-sea or cold-water corals (CWCs) are not as well-known as their shallow relatives, and only recently received attention from the scientific community (**Mortensen *et al*., 1995 | Roberts *et al*., 2009**). Yet, in the last 50 years, advances in deep-sea technology helped us better understand deep-sea coral distribution, biology, ecology and vulnerability to human activities and climate change.

CWCs can be found all over the world in a wide range of depths, including in the Northwest Atlantic (**Mortensen *et al*., 2006 | Roberts *et al*., 2009**). They live primarily on continental shelves and slopes, submarine canyons, and seamounts in a wide variety of substrates and hydrological conditions (**Gage & Tyler, 1991 | Mortensen & Buhl-Mortensen, 2004 | Bryan & Metaxas, 2006 | Wareham & Edinger, 2007 | Wareham, 2009**). In the Canadian Northwest Atlantic, CWCs are mostly distributed on the edge and slope of the continental shelf (<200-2,000 m deep) (**Mortensen *et al*., 2005 | Wareham & Edinger, 2007 | Wareham, 2009**), with records of corals on the continental rise as deep as 2,200 m (**Baker *et al*., 2012a**).

Deep-sea corals are among the slowest growing and longest-lived marine organisms, with some species reported to be thousands of years in age (**Roark *et al*., 2006 | Roberts *et al*., 2009**). CWCs come in many shapes and sizes, and include a wide range of skeletal cnidarians, such as colonial and solitary scleractinians (hard corals), pennatulaceans (sea pens), alcyonaceans (soft corals and sea fans), antipatharians (black corals) and stylasterine hydrocorals (lace corals) (**Cairns, 2007**). More than 70 species of deep-sea corals have been found in the Canadian Northwest Atlantic (**Wareham-Hayes *et al*., in prep.**). Most CWCs, such as *Paragorgia* sp. and *Paramuricea* sp. gorgonians, or *Desmophyllum pertusum* scleractinians are sessile and require hard-bottom substrates for attachment and strong current conditions that enhance food supply (**Mortensen & Buhl-Mortensen, 2005 | Bryan & Metaxas, 2006 | Mortensen *et al*., 2006 | Roberts *et al*., 2009**). In contrast, other CWCs such as sea pens, some sea fans and some solitary scleractinians inhabit low-current soft-bottom environments where they anchor themselves in soft sediments or rest on soft-bottom substrates (**Williams, 2011**).

About two thirds of the Earth's surface is covered by deep-sea sediments (**Heese & Schacht, 2011**), which makes deep-sea sedimentary habitats the most dominant habitat on the planet, and as a result sea pens the most common and widely distributed group of CWCs. Sea pens are colonial corals that comprise approximately 200 species globally (**Williams, 2011**), of which 14 have been described across the Northwest Atlantic and Eastern Arctic oceans (**Wareham-Hayes *et al*., in prep.**).

Like other deep-sea corals, sea pens come in a wide range of sizes and shapes. Some specimens can be as small as 15 cm (*e.g., Virgularia mirabilis*), while others can be up to 2-m tall (*e.g., Umbellula* spp.); in addition, species can resemble feathers, quill pens, pinwheels, umbrellas, whips or clubs (**Williams, 1995 | Wareham-Hayes *et al*., in prep.**). Sea pens have a unique morphology among deep-sea corals, in that they are composed of a bare peduncle they use to anchor themselves in soft sediments, and of an above-ground rachis which bears functional polyps (**Williams, 1995**). Moreover, while being sedentary, they are not necessarily sessile organisms. Indeed, some species can move around the seabed, and even completely retract into the sediment, presumably as a way to avoid predation (**Musgrave, 1909 | Wyeth & Willows, 2006**).

Sea pens, like other CWCs, are characterized by slow growth rates and a high longevity (**Roberts *et al*., 2009**). Estimates from previous studies conducted in the Canadian Northwest Atlantic suggest that sea pens were 20-30 years old on average, with one specimen recorded to be ~70 years old. Their radial growth rates ranged from 40-230 µm/year, while their linear growth rates ranged from 1-5 cm/year (**Neves *et al*., 2015a, 2018 | Murillo *et al*., 2018 | Greeley, 2022**).

Sea pens are extremely vulnerable to bottom-contact fishing activities as fishing gear is likely to damage or completely remove organisms from their habitat (**Malecha & Stone, 2009 | Rooper *et al*., 2011 | Jørgensen *et al*., 2015**). Sea pen growth rate and longevity have been used as proxies to determine their recovery time, which has been estimated at over 20 years for some species (**Neves *et al*., 2015a**). Despite being the most diverse coral group, sea pens remain widely understudied, and little is known about their biology, and especially about their recruitment. Nonetheless, knowledge of their fundamental biology, in addition to sea pen growth rate and longevity, is essential to assess the sensitivity and resilience of these vulnerable organisms to the potential impacts caused by natural and anthropogenic disturbances, as well as to inform management and conservation strategies.

1-1.2 | Deep-sea corals habitats

Large and dense concentrations of deep-sea corals have been reported in the Canadian Northwest Atlantic and are referred to as coral reefs (*e.g.*, *Desmophyllum pertusum* on the Scotian Shelf), gardens (*e.g.*, *Keratoisis flexibilis* bamboo coral in Disko Fan), forests (*e.g.*, *Primnoa resedaeformis* and *Paragorgia arborea* on the Scotian Shelf) or fields (*e.g.*, sea pens in the Laurentian Channel) (**Costello *et al*., 2005 | Mortensen & Buhl-Mortensen, 2005 | Wareham & Edinger, 2007 | Edinger *et al*., 2009 | Wareham, 2009 | Edinger *et al*., 2011 | Neves *et al*., 2015b | Buhl-Mortensen *et al*., 2017a | Beazley *et al*., 2021 | Coté *et al*., 2023 |**

Williams *et al*., 2023). Like their shallow relatives, CWCs increase habitat heterogeneity on both hard and soft substrates by forming complex three-dimensional structures.

These CWCs are considered deep-sea ecosystem engineers as they locally increase structural and biological complexity in homogeneous deep-sea environments, create micro-habitats used by many benthic species, including invertebrates and groundfish, and support diverse and productive ecosystems (**Robert *et al*., 2009 | Buhl-Mortensen *et al*., 2010**). Deep-sea corals are ecologically important as they provide local feeding, resting, shelter and nursery areas for benthic communities (**Husebø *et al*., 2002 | Auster, 2005 | Buhl-Mortensen & Mortensen, 2005 | Costello *et al*., 2005 | Roberts *et al*., 2006 | Stone, 2006 | Auster, 2007 | Etnoyer & Warrenchuk, 2007 | Ross & Quattrini, 2007 | Moore *et al*., 2008 | Roberts *et al*., 2009 | Buhl-Mortensen *et al*., 2010 | Baillon *et al*., 2012 | Baker *et al*., 2012b | Stone, 2014**). This is especially true for large as well as hard-bottom corals, but little is known in comparison about the functional role and ecological importance of smaller corals growing on soft-bottom substrates, such as sea pens, that are assumed to provide less habitat heterogeneity (**Tissot *et al*., 2006 | Buhl-Mortensen *et al*., 2010 | D'Onghia *et al*., 2011 | Baillon *et al*., 2012 | D'Onghia *et al*., 2012 | Danovaro *et al*., 2014**).

Sea pens are a traditionally overlooked group of CWCs that are typically quite small and can have a relatively sparse distribution compared to dense CWC reefs. While there is evidence that sea pen fields provide important ecological habitat functions to many species, including fish and invertebrates (**Tissot *et al*., 2006 | Buhl-Mortensen *et al*., 2010 | Garcia-Matucheski & Muniain, 2011 | Baillon *et al*., 2012**), it remains unclear to what extent they provide biogenic habitats, which fish species use these habitats and how, and what is the nature of their relationship with different size (and age) classes of demersal fish species.

1-1.3 | Groundfish ecology

Groundfish – or demersal fish – is a diverse group of fish that live and feed on or near the seabed. Groundfish exhibit a wide variety of morphologies, sizes and life history adaptations, which determine their habitat use, dependency and specialization (**Gage &**

Tyler, 1991 | Bergstad, 2009 | Priede, 2017). Groundfish species distribution and, further, community composition are driven by species preference for certain environmental conditions including bottom currents, water temperature, substrate type and quality, depth range, presence and type of benthic invertebrate community, as well as by ecological processes such as prey-predator relationships and competition for resources (**Bergstad, 2009**).

In the Canadian Northwest Atlantic, the mixing of warm waters coming from the Gulf Stream with the cold waters from the Labrador Current creates a key area of high productivity on the Southern Shoal and tail of the Grand Banks of Newfoundland. The meeting of these two flows generates favorable conditions to sustain large populations of groundfish species (**DFO, 2000**). Groundfish co-occur at all depths and in all bottom habitats of the continental shelf, and can be found in deeper waters along the continental slope and rise (**Bergstad, 2009**). They are often found in a wide variety of substrates, ranging from sand and mud to coarser substrates such as gravel (**Moyle & Cech, 2004**), and tend to prefer productive benthic ecosystems where invertebrate communities are established (**Juan-Jorda *et al*., 2009**).

There are two types of groundfish: benthic and benthopelagic fish (**Moyle & Cech, 2004**), which are generally categorized as either rockfish (*e.g.*, redfish), flatfish (*e.g.*, flounders), roundfish (*e.g.*, gadiforms), or elasmobranchs (*e.g.*, skates). Benthic fish are exclusively distributed on the seafloor where they commonly rest in low-current environments as an energy-efficient feeding strategy. They are ambush predators that employ a sit-and-wait foraging strategy to hunt near-bottom prey, relying on their camouflage and burrowing to avoid detection by prey and predators (**Auster, 1985 | Krieger, 1993 | Koslow, 1996 | Uiblein *et al*., 2003 | Lorance & Trenkel, 2006 | Ryer, 2008 | Devine *et al*., 2020**). Conversely, benthopelagic fish are large active swimmers and foraging predators that can be found in the water column just above the seafloor.

Most groundfish species are carnivorous and are often grouped as either zooplanktivores, benthophages or piscivores, feeding on a wide variety of prey including zooplankton, epiand infaunal invertebrates, and benthopelagic fish found close to the seabed (**Sedberry & Musick, 1978 | Mauchline & Gordon, 1986 | Bergstad, 2009**).

As multiple habitats can offer different resources, it is common for groundfish to settle – and rest – in different areas than their feeding or breeding areas. As a result, most groundfish species can undergo multiple migration cycles that vary both spatially and temporally. For instance, demersal fish may undertake frequent daily small-scale foraging journeys. They can move horizontally between resource patches or vertically in the water column, following nictemeral cycles (**Isaacs *et al.,* 1974**). During diurnal migrations, groundfish tend to be more active around and during the night as a way to maximize their feeding and minimize predation from larger predators (**Beamish, 1966**). At a broader scale, demersal fish may undertake less frequent seasonal migrations (once a year to once in a lifetime), for breeding, spawning or overwintering (**Bergstad, 2009**).

As groundfish individuals age and develop, they require different resources for growth, reproduction and survival. Therefore, fish undergo many ontogenetic shifts associated with increase in body size over their lifespan (**Saborido–Rey & Kjesbu, 2005**). These shifts tend to occur in fish as larvae metamorphose into small juveniles and before they reach their final adult morphology and sexual maturity (**Pittman & McAlpine, 2003 | Bergstad, 2009**). Size-specific shifts are often associated with changes in fishes' morphology, species interactions, diet, position in the trophic chain, swimming abilities, vulnerability to predation, habitat selection and specialization (**Warner & Schultz, 1992 | Persson *et al.*, 1996**).

1-1.4 | Deep-sea groundfish and CWC habitats

Due to the relative inaccessibility and remoteness of their habitats, deep-sea groundfish have been less studied than their shallow-water relatives and are poorly understood. Deep-sea fish generally live long, mature late and can have a low fecundity rate (*e.g.*, Redfish, elasmobranchs) (**Merrett & Haedrich, 1997**). These life-history characteristics render deep-sea fish vulnerable to ecological, environmental and anthropogenic pressures. Moreover, the survival of deep-sea fish is highly dependent on their habitats.

This is especially true for early-life stage fishes whose small size often restricts them to structurally complex micro-habitats that provide small prey availability, protection from predation and shelter from strong bottom currents (**Auster *et al*., 2005 | Costello *et al*., 2005 | Etnoyer & Warrenchuck, 2007 | Moore *et al*., 2008 | Roberts *et al*., 2009**). Conversely, certain larger, older individuals can be less specialized as they have greater mobility and capacity to cover large distances, and can therefore take advantage of a wider range of habitats than small fish (**Bergstad, 2009**). In any case, micro-habitats provide fish with access to a variety of resources, drive their recruitment, maximize their growth rates and reduce mortality risks (**Olson, 1996 | Grober-Dunsmore *et al.,* 2009 | Sheaves, 2009**). Yet, very few studies have aimed to compare fish occurrence in relation to developmental stage, small-scale habitat selection and CWCs (**Diaz *et al*., 2003 | Baillon *et al*., 2012 | Henderson *et al*., 2020**).

Deep-sea groundfish have been reported to use dense aggregations of CWCs as shelters against near-bottom currents, foraging and resting areas, or shelters against predation (**Auster *et al*., 2005 | Costello *et al*., 2005 | Etnoyer & Warrenchuk, 2007 | Moore *et al*., 2008 | Roberts *et al*., 2009**). Yet, little is known about the small-scale habitat requirements of deep-sea fish, and even less about groundfish distribution in relation to soft-bottom CWC habitats. Fish-habitat relationships have been broadly studied in hard-bottom CWC environments (**Edinger *et al*., 2007 | Biber *et al*., 2014 | Ross *et al*., 2015 | Arnaud-Haond *et al*., 2017 | D'Onghia, 2019 | Devine *et al*., 2020**), while only a few studies have investigated small-scale fish distribution in relation to habitats in soft-sediment environments (**D'Onghia *et al*., 2011 | Baillon *et al*., 2012 | D'Onghia *et al*., 2012**). One proposed reason for this disparity is the general assumption that muddy ocean floors are homogeneous and stable (**Danovaro *et al*., 2014**). This assumption is valid for very large scales (~100 km^2), but is not necessarily true at the smaller spatial scale at which most marine organisms respond to their environment (1-100s of m) (**Thistle, 2003**).

The nature of the relationship between fish and CWC habitats is not fully understood and functional connections are still unclear. Specific influence of benthic habitat structures on fish has been advanced by several authors in both soft- (**Baillon *et al*., 2012**) and hard-bottom environments (**Fosså *et al*., 2002 | D'Onghia, 2019 | Henderson *et al*., 2020**). Conversely, other studies have suggested a coincidental co-occurrence of habitat-forming species and fishes, primarily influenced by abiotic variables such as depth (**Baker *et al*., 2012b | Biber *et al*., 2014 | Milligan *et al*., 2016 | Devine *et al*., 2020**), substratum (**Auster, 2005 | Ross *et al*., 2015**), or as a result of shared habitat preferences and overlapping distributions (**Stone, 2006**).

1-1.5 | Monitoring the deep sea

The study of deep-sea groundfish, CWCs and their small-scale associations is still a relatively young field, largely due to the difficulty in accessing their remote habitats. Prior to the 21st century, knowledge of these species and their ecology was primarily obtained through bottom fisheries and scientific trawl surveys, coming at the cost of the benthic individuals being collected or their habitats (**Jennings & Kaiser, 1998**).

In the Canadian Northwest Atlantic, data on commercial and non-commercial fish and invertebrate species are collected during Fisheries and Oceans Canada (DFO) multispecies annual trawl surveys, yielding information on faunal distribution, biomass, diversity and relative abundance, as well as fish population dynamics, community structure and habitat associations (**Stoner *et al*., 2008 | DFO, 2015a**). Scientific bottom trawl surveys have the advantage of covering relatively large areas (*e.g*., 1.5 km per tow in the Northwest Atlantic) and of enabling the collection of biological samples, allowing for post-survey data collection including studies of genetics, gut contents and fish aging. Yet, because trawls cover a large spatial scale, small-scale processes to which fish respond (~1-100-m scale) are often masked (**Edinger *et al*., 2007 | Baker *et al*., 2012b**), which can lead to knowledge gaps or misinterpretation. Moreover, although this approach provides valuable data, its use is controversial due to its impacts on benthic communities and habitats (*e.g*., habitat destruction, resuspended sediment, and fauna removal) (**Auster, 2005**).

With advances in ocean technology over recent decades, imaging and acoustic underwater systems are increasingly used as an alternative to scientific bottom trawls to conduct deep-sea benthic surveys (**Sward *et al*., 2019**). These systems are effective, non-destructive and non-extractive monitoring tools that can be deployed in both trawlable and non-trawlable areas (*i.e*., rocky-bottom substrates and protected areas), and assist in reducing knowledge gaps associated with scientific bottom-trawl surveys (**Lorance *et al*., 2000 | Stoner *et al*., 2008 | Sward *et al*., 2019**). For instance, video-based surveys can provide additional and complementary valuable *in-situ* data that were previously impossible to collect in the deep sea, in structurally complex habitats and at a finer spatial scale (**Ross & Quattrini, 2007 | Laidig *et al*., 2013 | Clark *et al*., 2016**). This enables the assessment of variables including faunal density, small-scale habitat association of fish and habitat attributes, fish habitat use, community composition, interactions of fish in their natural environment and fish population size structure (**Adams *et al*., 1995 | Lorance *et al*., 2000 | Lorance *et al*., 2002 | Uiblein *et al*., 2002, 2003 | Trenkel *et al*., 2004 | Lorance & Trenkel, 2006 | Ross & Quattrini, 2007 | Stoner *et al*., 2008** | **Ryer *et al*., 2009 | D'Onghia *et al*., 2011 | Clark *et al*., 2016**).

A wide range of underwater video systems (UVS) are used to observe benthic species in their natural environment, including drop-cameras (**Rooper *et al*., 2010, 2015**), remotely operated vehicles (ROV) (**Lorance & Trenkel, 2006 | Stone, 2006 | Adams *et al*., 1995**), underwater towed vehicles (**Clarke *et al*., 2009 | Lembke *et al*., 2013**), human operated vehicles (HOV) (**Krieger, 1993 | Laidig & Yolavich, 2016**), baited cameras (**Widder *et al*., 2005 | Devine *et al*., 2019**) and autonomous underwater vehicles (AUV) (**Clarke *et al*., 2009 | Meyer *et al*., 2019**). However, these systems are relatively new and the technology is still improving.

As with any survey gear type, there are limitations in using UVSs to record mobile fauna. For example, fish are known to react to UVSs which can potentially induce *in-situ* bias in observations and results. Documented behavioral responses include avoidance and attraction, which can respectively lead to the under or overestimation of fish abundances, as well as to missed or erroneous identifications of habitat associations (**Trenkel *et al*., 2004 | Stoner *et al*., 2008 | Ryer *et al*., 2009 | Laidig *et al*., 2013** | **Sward *et al*., 2019**). Fish natural behaviour may be altered due to a number of influences from UVSs or from the survey vessel at the surface (**Trenkel *et al*., 2004 | Lorance & Trenkel, 2006 | Stoner *et al*., 2008 | Sward *et al*., 2019**). Additionally, the type and intensity of fish reactions to UVSs can be influenced by many variables including fish-specific biology and ecology, as well as environmental conditions such as habitat, substrate, temperature or current speed (**Engås, 1994 | Trenkel *et al*., 2004**).

Yet, the influence of video systems on fish behaviour is rarely measured during dedicated fish surveys (**Stoner *et al*., 2008**) and, when it is, measurements are often limited to anecdotal or qualitative reports (**Pacunski *et al*., 2008 | Rountree & Juanes, 2010 | Smith *et al*., 2010 | Consoli *et al*., 2016 | Thomson *et al*., 2018 | Dunlop *et al*., 2020 | Wetz *et al*., 2020 | Vigo *et al*., 2023**). There is a need to quantitatively study fish reactions to UVSs during surveys, as well as the nature and magnitude of these reactions. Doing so will inform more accurate fish assessments and improve our understanding of UVS limitations, while providing insight into fish habitat utilization (**Stoner *et al*., 2008 | Laidig *et al*., 2013**).

Some of DFO's monitoring programs are either gradually transitioning from existing large-scale research bottom trawls to less-destructive small-scale *in-situ* UVSs to assess vulnerable benthic environments, or have taken a more inclusive approach and incorporated both gear types within their monitoring strategies. In any case, as part of this transition or as part of a multi-tool approach, a comparative analysis of benthic community characteristics is essential to ensure the continuity of long-term data series, and the ability to track changes in benthic ecosystems while excluding potential bias related to gear selectivity. Indeed, detecting changes in species abundance, diversity or size structure between survey tools could reflect differences in catchability. Therefore, there is a crucial need to compare faunal assemblage characteristics assessed by different survey tools within a given study area to create local baselines and calibrate assessments.

1-1.6 | Vulnerability of deep-sea benthic communities

Until recently, due to the remote and inaccessible nature of the deep seas, human activities had limited impacts on deep-sea benthic habitats and communities compared to shallower ecosystems. Yet, recent technological advances and increasing worldwide demand for resources have pushed marine industries, such as oil and gas exploration and extraction, deep-sea mining and bottom fisheries, further and deeper into the ocean (**Koslow *et al*., 2000**). The cumulative impacts caused by these activities, combined with potential impacts from climate change and ocean acidification, are a major threat to the biodiversity, structure, function, productivity and resilience of deep-sea ecosystems (**Simeoni *et al*., 2023**). The high-longevity and slow-growing nature of deep-sea corals and deep-sea groundfish render them vulnerable to physical and chemical disturbances resulting from direct and indirect human activities, deep-sea fisheries being one of the most notable of these (**Fosså *et al*., 2002 | Halpern *et al*., 2008 | DFO, 2010a | Rooper *et al*., 2011 | Clark *et al*., 2016 | Yoklavich *et al*., 2018 | Pham *et al*., 2019 | González-Irusta *et al*., 2022**)**.**

The Northwest Atlantic is known for its large populations of commercial groundfish (*e.g*., Atlantic cod (*Gadus morhua*), Witch flounder (*Glyptocephalus cynoglossus*), Greenland Halibut (*Reinhardtius hippoglossoides*), Redfish (*Sebastes* spp.)) and for its rich fishing history. Beginning in the late 1500s, the commercial ground fishery grew radically through the late 19th century, driven by increasing global demand and technological advances (*e.g*., bigger fleets, improvement of fishing gear) (**NAFO Secretariat, 2009**). Over time, intensive fisheries shifted to deeper waters and led to dramatic declines of demersal fish stocks, the destruction of benthic habitats, the decrease of habitat complexity, as well as the removal of non-target taxa as bycatch (*e.g*., habitat-forming sessile organisms) (**Auster *et al*., 1996 | Loder *et al*., 1998 | Koslow *et al*., 2000 | Templeman & Davis, 2006**).

The resilience and recovery rates of deep-sea ecosystems after intense near-bottom fishing activities are poorly known due to a lack of data on organism biology and ecology. It has been estimated that it could take decades to centuries for impacted deep-sea benthic communities to recover, if they recover at all (**Rice, 2005 | Templeman & Davis, 2006 | Edinger *et al*., 2007 | Sherwood & Edinger, 2009 | Gwladys *et al*., 2014 | Clark *et al*., 2019 | Morrison *et al*., 2020**).

Adequate protection of commercial groundfish and their habitats is necessary for maintaining fish biodiversity, healthy populations, ecosystem stability, as well as for ensuring the long-term sustainable management of fisheries (**Meinam *et al.*, 2023**). Thus, understanding deep-sea CWC and groundfish biology and ecology is an important step toward effective management and conservation strategies.

1-2 | Context of the study

1-2.1 | Canadian marine protected and conserved areas

Several species of CWCs have been internationally recognized as vulnerable marine ecosystems (VMEs), for their uniqueness or rarity, fragility, functional significance as habitat provider, and for their life-history traits that render recovery difficult (**FAO, 2009**). Their vulnerability in addition to the role they play as deep-sea ecosystem engineers have established CWCs as key conservation targets in Canadian waters (**DFO, 2010b, 2015b**).

In an effort to protect CWCs, CWC habitats and associated biodiversity – including groundfish – marine conservation strategies in Canada led to the designation of several marine conservation areas. In Canadian waters, DFO holds exclusive authority to implement, manage and monitor Marine Protected Areas (MPAs) under the Canadian Oceans Act (**1997**). Notably, no-take MPAs, or MPAs where harmful human activities are restricted or entirely prohibited, have proven to be one of the most effective adaptive management tools to protect and restore biodiversity, healthy habitats and ecosystems functions (**Edgar *et al.*, 2014**). In addition, MPAs are a key regulatory component to fisheries management, as they contribute to fish stock recruitment (**Edgar *et al.*, 2014 | Gonçalves, 2023**). Among the 14 Canadian MPAs protecting coastal and marine ecosystems, the Laurentian Channel MPA was designated in 2019 to protect an ecologically important area with relatively intact habitats and complex oceanographic conditions (**Templeman, 2007**).

1-2.2 | Study area: the Laurentian Channel MPA

1-2.2.1 | The Laurentian Channel

- **Location and extent**

The Laurentian Channel is a deep submarine valley of glacial origin in eastern Canada. It is 80-90 km wide on average and extends over 1500 km from the St. Lawrence estuary and Saguenay River to the edge of the continental shelf between Nova Scotia and the southwest coast of Newfoundland (**Fig. 1-1**). Its depth ranges from 100 m at the banks to 500 m at its central basin. The channel is delimited by continental shelf banks on each side, whose edges vary between 100 to 200 m deep (**Fig. 1-1**) (**DFO, 2011a**).

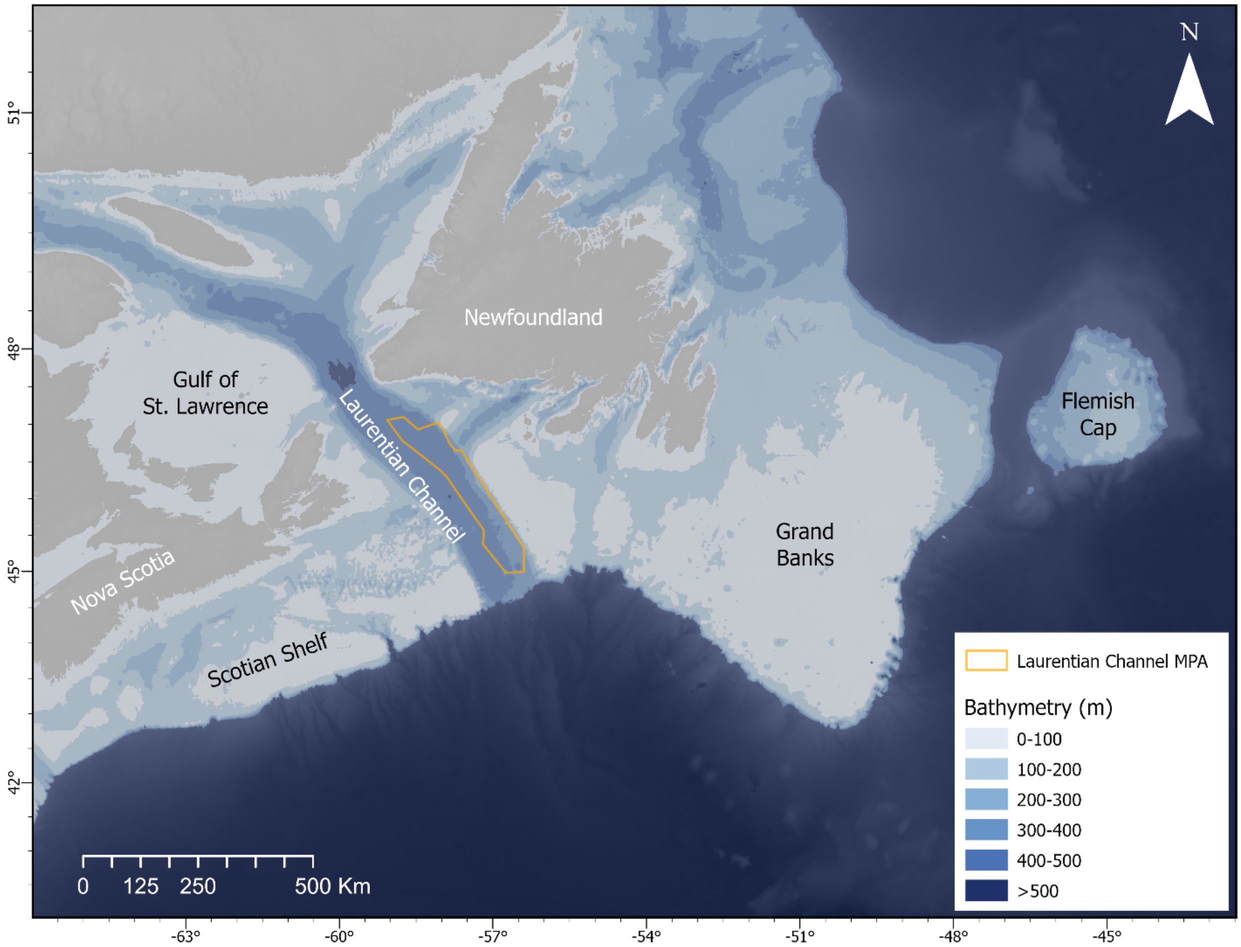

Fig.1-1 | Bathymetry of the Canadian Northwest Atlantic continental shelf and location of the Laurentian Channel MPA.

- **Substrate**

Past glacial processes have carved the bedrock across most of the channel and blanketed the seafloor with sediments. The seabed consists mostly of glacial and post-glacial mud and clay mainly present in the deepest areas of the channel, while post-glacial coarser sediments (*e.g.*, sand, gravel, shell debris and boulders) mixed with glacial till (*e.g.*, sandy clay matrix with gravel, cobble, and boulders) occur mostly on the shallower bank flanks (**DFO, 2011a | Lacharité *et al.*, 2020**). Additional impacts of glaciation can be found in the presence of underlying bedrock geomorphic features. These include iceberg scours, iceberg pits or pockmarks, generally caused by the grounding movements of icebergs (**Fader, 1991**). Those geomorphic features were used to classify the MPA into different benthoscapes. Benthoscapes are broad biophysical features of the seafloor derived from surficial geomorphological features and geology (**Brown *et al.*, 2012**). Eight benthoscapes were defined within the Laurentian Channel according to depth, slope and density of iceberg scours and pockmarks (**Fig. 1-2 & Appendix 1-1**) (**Lacharité *et al.*, 2020**).

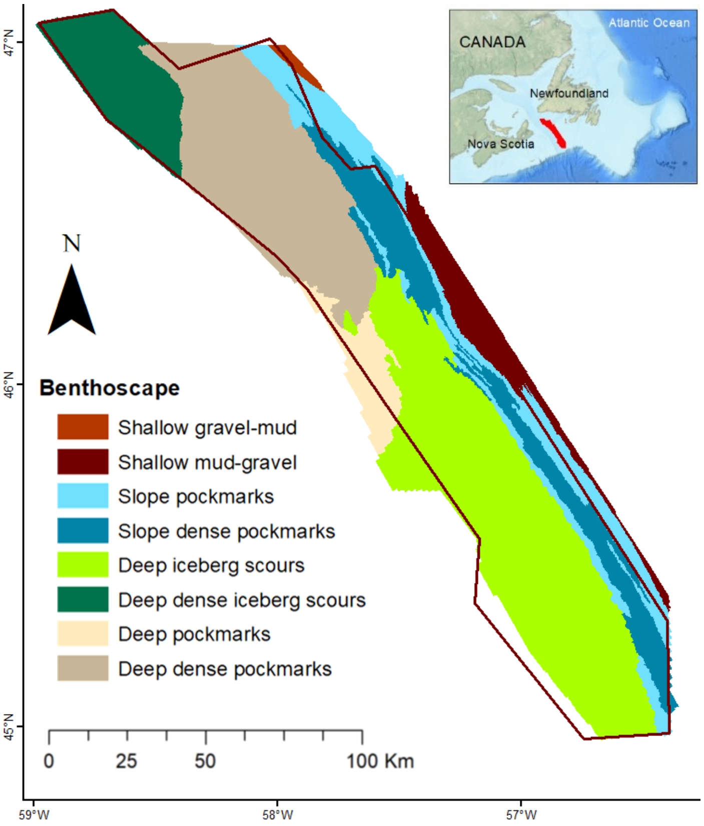

Fig.1-2 | Distribution of benthoscapes in the Laurentian Channel MPA, adapted from Lacharité *et al*. (2020). ‘Mixed sediment’ was the dominant sediment type of the ‘Slope’ benthoscapes, ‘Sandy’ and Bioturbated mud’ were the dominant sediment types of the ‘Iceberg scours’ benthoscapes, and ‘Fine sediment’ was the dominant sediment type of the ‘Pockmarks’ benthoscapes (Appendix 1-1).

- **Oceanographic conditions**

The Laurentian Channel water column is stratified into three distinct thermal layers: a warm surface layer (2-7 °C), a cold intermediate layer (-1 to +1 °C) and a deep warm layer (5 °C on average) (**Lauzier & Trites, 1958 | DFO, 2011a**). Bottom waters in the channel remain relatively warm compared to the surrounding continental banks, shelves and rise, but vary interannually as a result of the mixing of the cold oxygen-rich Labrador Current waters and warm, salty, oxygen-poor Gulf Stream waters, forming the Slope waters at the entrance of the channel on the continental shelf (**Fig. 1-3**) (**Lauzier & Trites, 1958 | DFO, 2011a**). The interface of these flows, in addition to the moderate cold-water upwelling at the head of the Laurentian Channel, supports a high biodiversity, a complex trophic chain and unique benthic habitats (**Templeman, 2007**).

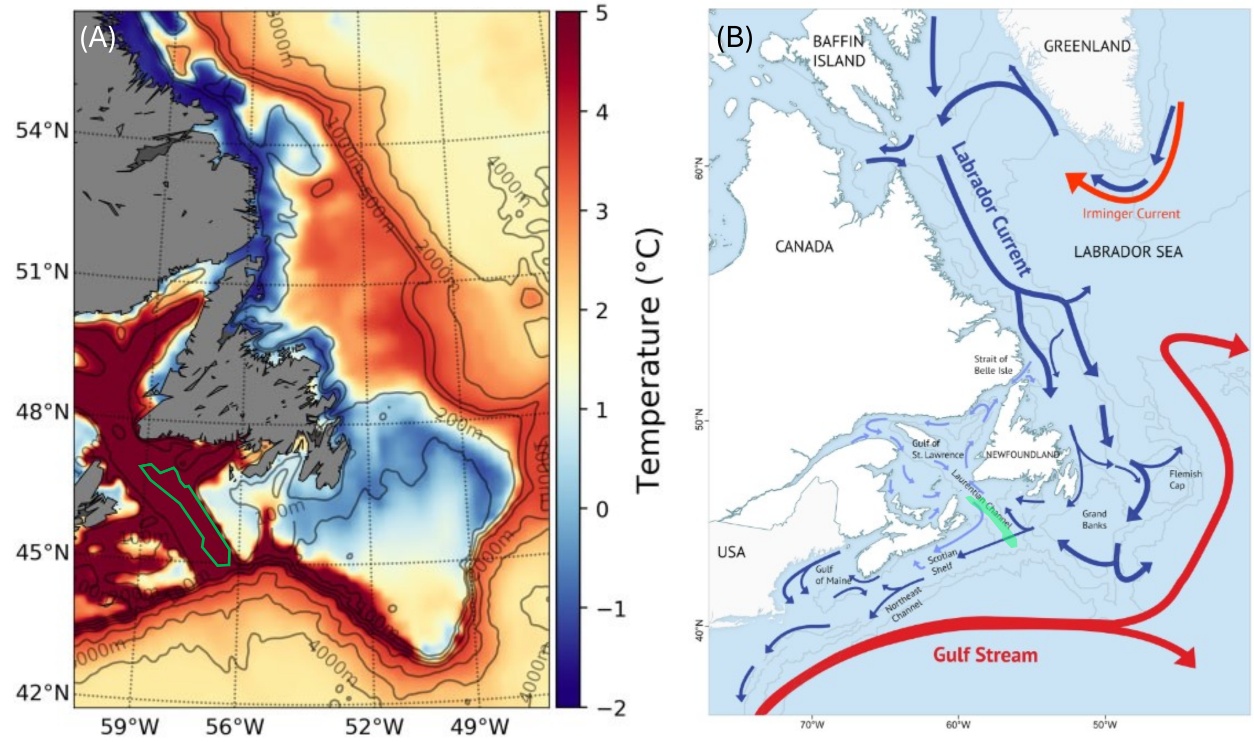

Fig.1-3 | (A) Bottom temperature distribution along the Newfoundland and Labrador Shelf on 1 May 2019, adapted from Mullowney & Baker (2020). (B) Currents of the Canadian Arctic

and Atlantic, adapted from Bernier *et al*. (2018). Two main currents influence eastern Canada, the cold Labrador Current from the Arctic (dark blue) and the warm Gulf Stream from the south (red). In addition, the St. Lawrence River releases freshwater in the Gulf of St. Lawrence that mixes with Atlantic waters (light blue). The Laurentian Channel MPA is shown in green on both maps.

- **Biodiversity**

The Laurentian Channel is an important marine area providing habitat for many commercially, culturally and ecologically important marine species. The highest density of Black Dogfish (*Centroscyllium fabricii*) in Canadian waters is found in the channel, which is a unique and rare area where pupping is known to occur (**Kulka, 2006 | DFO, 2012**). It is an important feeding, spawning, nursery and rearing area for many species including Porbeagle Shark (*Lamna nasus*) and Smooth Skate (*Malacoraja senta*) (**DFO, 2012**). The channel is also a critical seasonal migration corridor for a variety of marine taxa (*e.g*., fish, cetaceans, pinnipeds) between the Gulf of St Lawrence and the Atlantic Ocean. The Northern Wolffish (*Anarhichas denticulatus*) and Leatherback Sea Turtle (*Dermochelys coriacea*) are two Species at Risk that can be found in the area (**DFO, 2011a, 2012, 2024**). As a result, the channel was identified as an ecologically and biologically significant area (EBSA) (**Fig. 1-4**) (**Templeman, 2007 | Wells *et al*., 2019**). EBSAs are unique areas that provide important habitats to diverse, threatened and vulnerable species, and support productive ecosystems.

The channel hosts the highest-known sea pen densities and species richness in the Newfoundland and Labrador Shelves bioregion, which has led to the designation of Significant Benthic Areas (SiBAs) in the area (**Fig. 1-4**) (**Kenchington *et al*., 2016 | Lewis *et al*., 2016**). SiBAs are defined as 'significant areas of cold-water corals and sponge dominated communities' (**Kenchington *et al*., 2016**). Sea pen fields have been recognized as Vulnerable Marine Ecosystems (VME) (**FAO, 2009 | Murillo *et al*., 2010 | Kenchington *et al*., 2013**) due to their low resilience in facing anthropogenic habitat destruction, increased sedimentation in the water column and biomass removal (**Koslow *et al*., 2000 | DFO, 2011a | Ramirez-Llodra *et al*., 2011**).

One of the earliest studies of the associations between fish and soft-bottom invertebrates in the Laurentian Channel reported a strong association between Redfish larvae and diverse sea pens, which were assumed to be used as spawning areas, and also as shelters by early-life stage fishes (**Baillon *et al.*, 2012**). However, no study since then has further investigated the ecological relationships between fish and CWCs in this area.

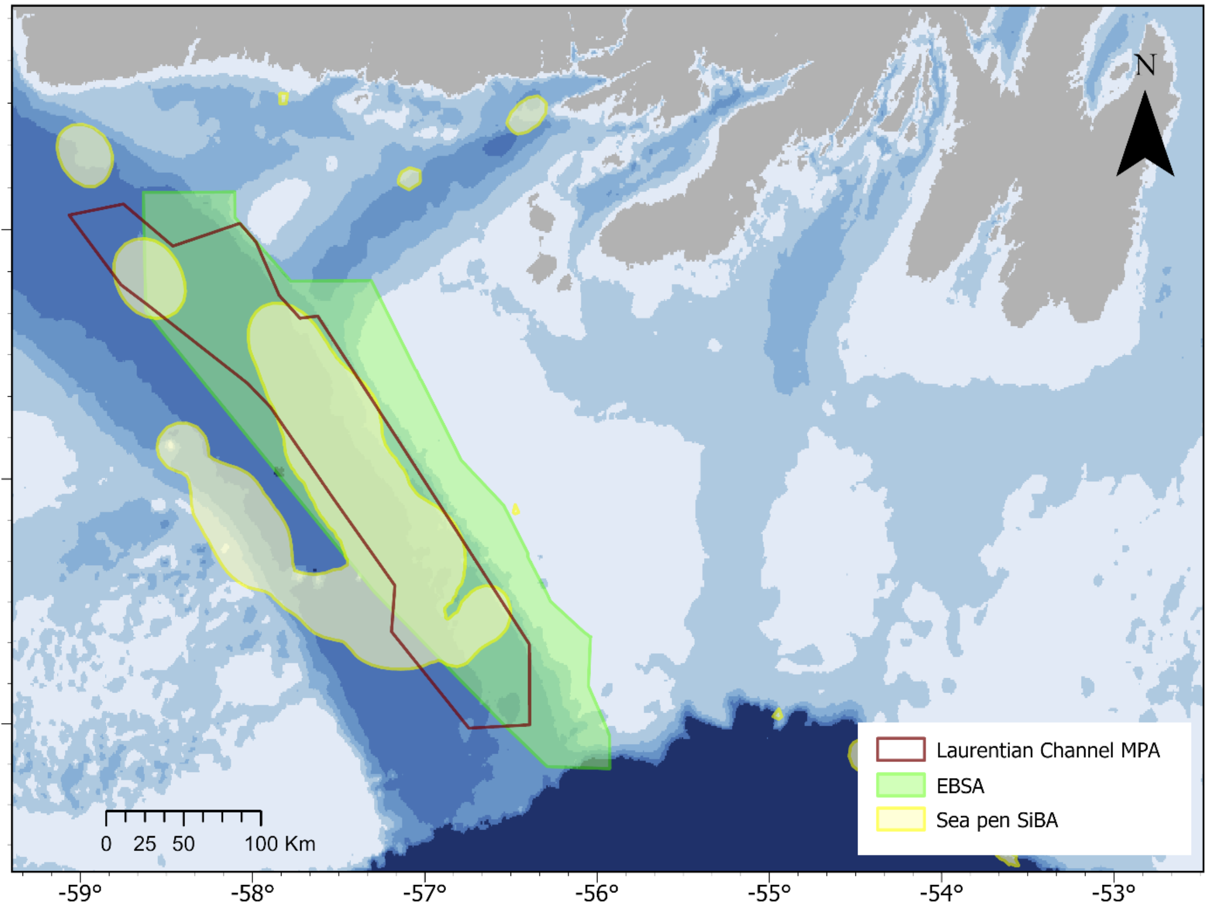

Fig.1-4 | Location of the Laurentian Channel EBSA, sea pen SiBA and MPA. EBSA and SiBA layers were retrieved from Wells *et al.*, 2019 and Kenchington *et al.*, 2016.

- **Threats**

Many human activities occurring in the channel have been identified as major threats to the temporal and spatial stability of the Laurentian Channel ecosystem, the most significant of these being commercial bottom-fishing (**DFO, 2012**). Though bottom trawling has occurred for decades in the channel, most of the efforts was concentrated along the eastern slope of the channel and the thalweg (**DFO, 2012 | Muntoni *et al*., 2019**). Other threats identified in the area include oil and gas exploration, marine traffic, submarine cables, marine pollution and climate change (**DFO, 2012**). Potential impacts resulting from human activities in the channel are habitat destruction, biomass removal, increased sedimentation in the water column, spills, the introduction of invasive species, dredging, collisions, noise disturbance, presence of marine debris, release of sewage water and contaminants (**Templeman & Davis, 2006 | Lewis *et al*., 2016**).

1-2.2.2 | The Laurentian Channel MPA

The Laurentian Channel MPA is located at the mouth of the channel, near the continental slope and covers a third of the channel (11,580 km^2), including parts of the existing EBSA and SiBA. Depths in the MPA range from 139 to 485 m (**Fig. 1-4**). The main objective of the MPA is to 'conserve biodiversity in the Laurentian Channel MPA through protection of key species and habitats, ecosystem structure and function and through scientific research (**Lewis *et al*., 2016**).

Six taxa were selected as key conservation targets based on the designation of the EBSA and SiBA in the channel: sea pens, Black Dogfish, Porbeagle Shark, Smooth Skate, Northern Wolffish and Leatherback Sea Turtle, for which specific conservation objectives and monitoring indicators were developed. In addition to those six taxa of interest, the MPA is also expected to contribute to the conservation and protection of commercial and non-commercial fish species, unique habitats and other associated biodiversity (**Templeman, 2007 | Kenchington *et al*., 2016 | Lewis *et al*., 2016 | Warren *et al*., in prep.**).

The Laurentian Channel MPA is considered a 'no-take' MPA, where 'any activity that disturbs, damages, destroys or removes […] any living marine organism or any part of its habitat' is prohibited (**DFO, 2019**). Thus, all commercial or recreational fishing, and oil and gas activities are not allowed in the area. However, certain activities such as marine navigation, aboriginal fisheries, installation, maintenance and repair of submarine cables, scientific research and monitoring, educational activities, or any activities pertaining with emergency, safety, security, and sovereignty activity are allowed as they are not considered incompatible with the MPA conservation objectives (**DFO, 2019**). The MPA was characterized as minimally disturbed by fishing activities compared to surrounding areas, such as the eastern banks, where fishing efforts were historically more intense (**Koen-Alonso *et al*., 2018 | Muntoni *et al*., 2019**).

The Laurentian Channel MPA remains an understudied area where persistent knowledge gaps related to the function, structure and processes of its ecosystem should be addressed to inform an adaptive monitoring strategy. Notably, proposed research objectives related to the MPA include advancing understanding of the distribution, abundance, life history, biology, ecology and resilience to impacts of the taxa of interest, as well as of the identification of benthic habitats and associated biodiversity (**Lewis *et al*., 2016**). Addressing those research objectives is fundamental for the development of baseline knowledge, monitoring indicators and protocols, the assessment of MPA effectiveness, and the achievement of the MPA conservation objectives.

An important component of a successful long-term monitoring program is the development of a robust study design. An important step in the design of the scientific monitoring approach is the selection of appropriate survey tools, techniques and methodologies to fill data gaps, and assess the status and ecological trends of the specific conservation objectives (**Neves *et al*., in prep. | Warren *et al*., in prep.**). As part of the multi-tool approach adopted for the long-term monitoring program of the MPA, both multispecies bottom trawls and UVSs will be used to measure some of the conservation objective indicators. For instance, these indicators include faunal abundance, biodiversity and distribution (both tools), faunal biomass (bottom trawl), faunal size distribution, and epi- and infaunal species composition (UVS). While both tools can collect complementary or comparable data, they do not operate at the same spatial scale. Moreover, in a strategy to prioritize the use of less destructive and less invasive monitoring tools in a conservation area over traditional approaches, there is a need to assess the potential of UVSs to become the primary monitoring tool in the MPA.

1-3 | Thesis overview

In this context, this dissertation aims to investigate deep-sea groundfish-habitat associations in a soft-sediment environment in a marine conservation area of the Northwest Atlantic using data collected by UVSs. The objectives of this research are 1) to fill knowledge gaps associated with overlooked soft-sediment habitats, 2) to assess the ecological role of CWCs, notably sea pens, for groundfish taxa and 3) to evaluate the potential of UVSs to conduct small-scale benthic surveys targeting mobile fish taxa. Finally, this study will inform the monitoring strategy of the Laurentian Channel MPA.

1-3.1 | Common methodology to all research chapters

For all research chapters (**2-5**), I analyzed video data collected *in situ* during two benthic habitat surveys conducted by a remotely operated vehicle (ROV) and a near-seabed drift-camera system in the Laurentian Channel MPA.

1-3.1.1 | Survey design and data collection

A total of 17 underwater video transects were recorded at 14 survey stations within the Laurentian Channel MPA during two collaborative research cruises between the Canadian Healthy Oceans Network (CHONe) and Fisheries and Oceans Canada (DFO) (**Fig. 1-5**). The first cruise took place in September 2017 on the Canadian Coast Guard Ship (CCGS) *Martha L. Black*, using the ROV ROPOS (Remotely Operated Platform for Ocean Sciences) (**Fig. 1-6A**). The second cruise was conducted in July 2018 on the CCGS *Hudson*, using the DFO near-seabed drift-camera system CAMPOD (**Fig. 1-6B**). Of the 14 stations visited, 3 of these were surveyed by both ROPOS and CAMPOD, comprising 6 of 17 transects (**Fig. 1-5 & Table 1-1**). The surveys had multiple objectives, including the *in-situ* study of infaunal processes, benthic macro-invertebrates and demersal fish community attributes, and fish-habitat associations in the area. The study design aimed to sample a wide range of habitats, while also targeting areas with the highest-known sea pen abundance. The stations were selected according to sea pen diversity and bycatch weight sampled in surrounding areas during previous bottom-trawl surveys led by DFO from 2005 to 2016 (**Table 1-1**).

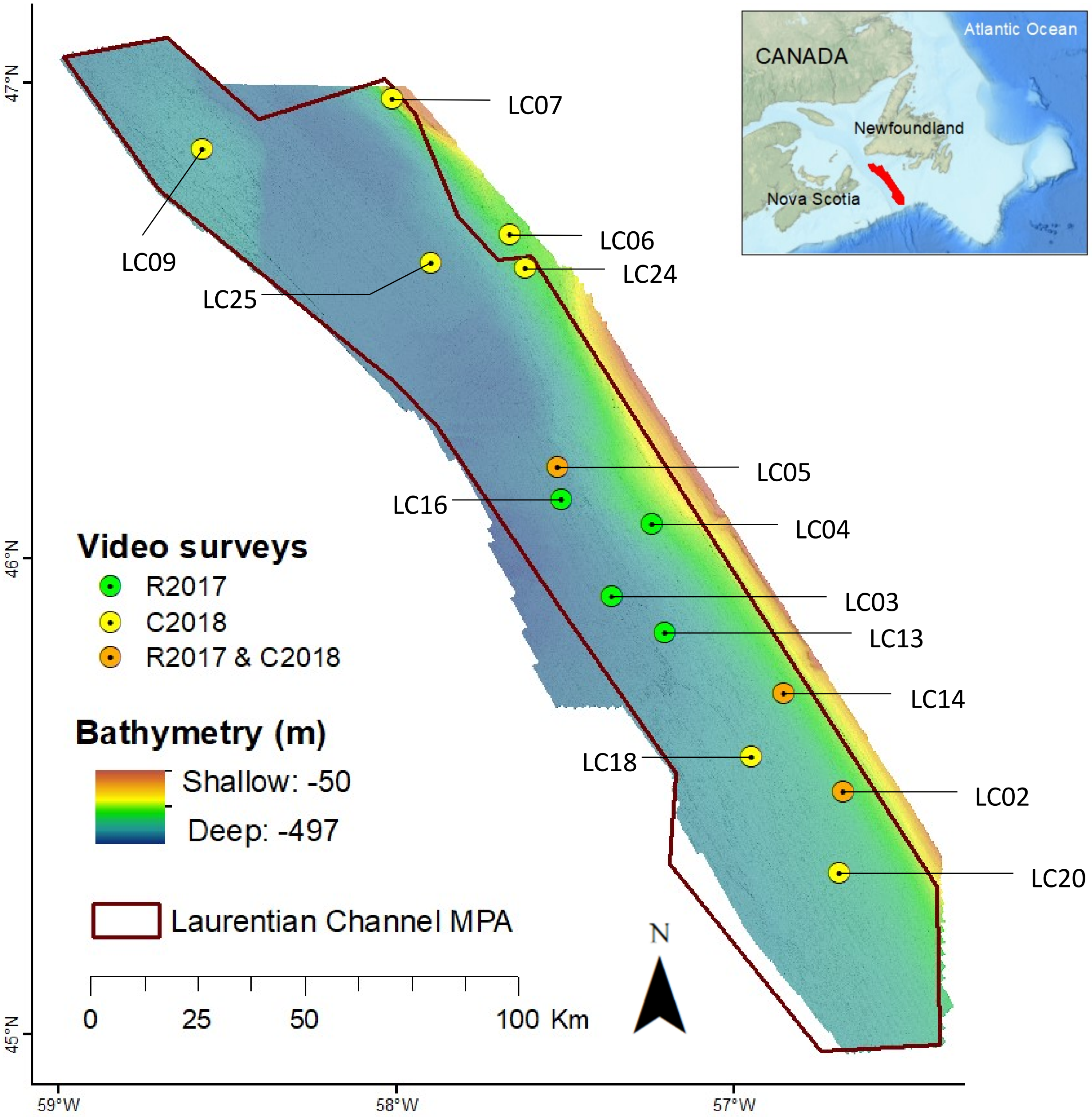

Fig. 1-5 | Location of stations surveyed in 2017 and 2018 using the ROV ROPOS (green), the near-seabed drift-camera system CAMPOD (yellow) or both systems (orange).

ROPOS and CAMPOD were each equipped with two zoom-capable high-definition video cameras in both survey orientations (forward- and downward-looking), each with a wide and uniform high-intensity video lighting field, allowing for customized survey set-up. In part due to a primary design priority to capture downward high-resolution digital still imagery, CAMPOD had more variable video imaging specifications between its cameras at the time of the survey. In particular, the lighting field and imaging quality from the forward-facing video camera on CAMPOD in the 2018 survey was of much lower quality than that available with ROPOS in 2017. Both ROPOS cameras and the CAMPOD downward camera were paired with lasers placed 10 cm apart, used as a scale. Multiple sensors were mounted on the two underwater video systems (UVSs), recording time, depth, UVS position, altitude and speed at 1-second intervals. In addition, ROPOS was equipped with multiple sampling tools (*e.g.*, two robotic arms, storage boxes, core tubes) to enable the collection of biological and physical samples during surveys. Both UVSs were maintained at a slow speed (0.6 m.s^{-1}) and at a low altitude (~1.3 m above seafloor). In keeping with the multiple survey objectives, the UVS transect sampling strategies were originally designed to investigate spatial patterns in sessile epibenthic fauna (**de Mendonça & Metaxas, 2023, 2024**).

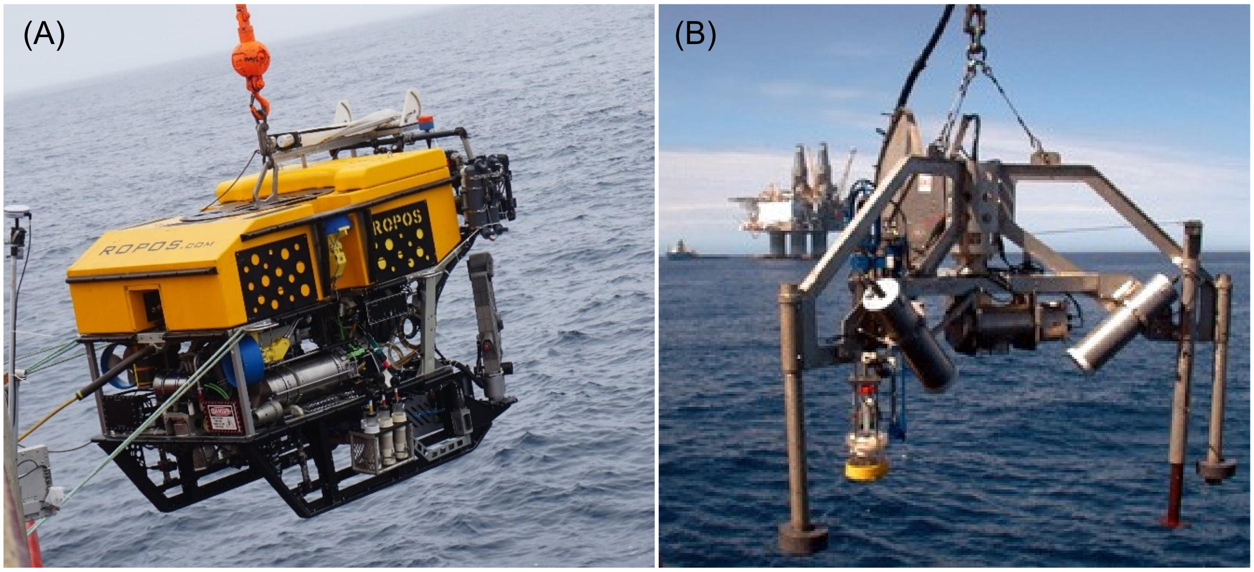

Fig. 1-6 | (A) ROV ROPOS and (B) near-seabed drift-camera system CAMPOD being deployed before an *in-situ* survey.

Table 1-1 | ROPOS and CAMPOD (UVS) survey depth range, temperature range, time on bottom, distance, and area covered at each station. Cold-water coral (CWC) diversity and weight were estimated from multi-species trawl surveys conducted by Fisheries and Oceans Canada from 2005 to 2016. CWC diversity ranges from 1 (low), 3 (medium) to 4-5 (high) coral species. CWC cumulated weight in trawl ranges from 0-4 kg (low) to >9 kg (high). Three stations were sampled during both UVS surveys: LC02, LC05 and LC14.

Survey	UVS	Station	Period	Depth range (m)	Temperature (°C)	Time (h)	Distance (km)	Area (ha)	Criteria of interest		
									CWC Diversity	CWC Weight	Other
R2017	ROPOS	LC02	Sept. 2017	343-356	5.8-7.4	11.1	8.7	4.9	Medium	High	-
R2017	ROPOS	LC03	Sept. 2017	444-450	5.6-6.9	9.6	5.7	2.7	High	High	-
R2017	ROPOS	LC04	Sept. 2017	339-350	6.1-7.1	11.7	7.6	4.1	0	0	Past fishing pressure
R2017	ROPOS	LC05	Sept. 2017	435-441	5.4-6.4	11.3	9.8	5	Low	High	-
R2017	ROPOS	LC13	Sept. 2017	427-436	5.5-6.7	8	6.1	2.7	0	0	-
R2017	ROPOS	LC14	Sept. 2017	330-349	5.9-8.9	10.3	5.3	2.7	High	Low	-
R2017	ROPOS	LC16	Sept. 2017	441-449	5.7-7.3	8.3	6.2	3.3	Low	High	-
Total R2017				**330-450**	**5.4-8.9**	**69.5**	**49.4**	**25.4**			
C2018	CAMPOD	LC02	July 2018	264-358	6.8-7.8	4	6.2	2.9	Medium	High	Previous video-surveyed
C2018	CAMPOD	LC05	July 2018	407-444	5.7	1.2	1.5	0.7	Low	High	Previous video-surveyed
C2018	CAMPOD	LC06	July 2018	315-320	6.9	2.6	3.6	1.7	Medium	High	Past fishing pressure
C2018	CAMPOD	LC07	July 2018	179-272	3.6-7.4	1.8	2.5	1.2	Low	Low	Past fishing pressure
C2018	CAMPOD	LC09	July 2018	418-425	6	2.2	3.2	1.5	Low	High	-
C2018	CAMPOD	LC14	July 2018	305-365	6.2-7.4	2.6	3.5	1.7	High	Low	Previous video-surveyed
C2018	CAMPOD	LC18	July 2018	341-408	5.8-6.6	3.6	4.5	2.1	Low	High	-
C2018	CAMPOD	LC20	July 2018	386-394	5.8	2.2	4.8	2.2	High	Low	-
C2018	CAMPOD	LC24	July 2018	451-455	5.8	3.1	4	1.9	Medium	Low	Past fishing pressure
C2018	CAMPOD	LC25	July 2018	318-344	6.4-6.9	2.6	3.6	1.7	Low	Medium	Past fishing pressure
Total C2018				**179-455**	**3.6-7.8**	**25.8**	**37.3**	**17.5**			
Combined R2017 & C2018				**179-455**	**3.6-8.9**	**95.3**	**86.7**	**43.6**			

The ROPOS transect design consisted of four sets of two parallel transects (**Fig. 1-7A**). Each transect was 400 m; the four sets were 200 m apart; and the parallel transects were 10 m apart. A suitable and common sampling strategy to survey mobile fish species is to follow long strip transects (>500 m) across depth and substrate strata (**Sward *et al.*, 2019**). We thus amended the original survey design with one additional linear transect. The CAMPOD transect design consisted of three 1-km parallel transects with a 200-m spacing (**Fig. 1-7B**).

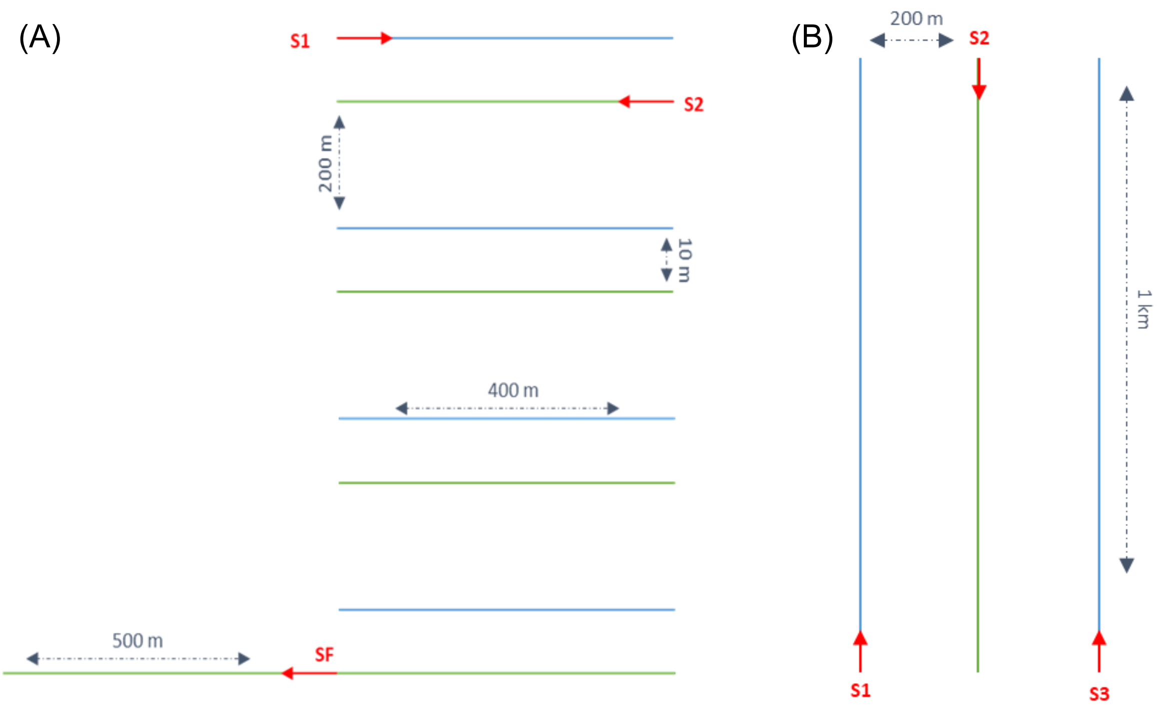

Fig. 1-7 | Multispecies video survey strategy designed for (A) ROPOS and (B) CAMPOD dives. Each ROPOS dive consisted of four primary sets of two 400 m long parallel transects (blue lines). Each double set was designated 200 m apart and the two parallel transects of each set were 10 m apart. Blue segments represent the first segment sampled of each pair and green segment the second segment sampled. Additional 500 m transect sections were added following the end as operational situations permitted. CAMPOD transect design consisted of three 1-km parallel transects with a 200-m spacing. Red arrows indicate ROPOS and CAMPOD direction of movement. (S1) First transect start point, (S2) Second transect start point, (S3) Third transect start point, (SF) ROPOS Fish transect start point.

1-3.1.2 | Video analysis

For both UVS surveys we used the annotation software AdélieVidéo (Adélie, IFREMER) to analyze videos from both cameras simultaneously. AdélieVidéo enables the synchronization of both camera recordings with the UVS navigation data and allows users to visualize and comment on video footage. Georeferenced data were recorded continuously on fish, epibenthic invertebrates and substrates observed in the video analysis, as well as on survey operations at 1-second resolution (**Table 1-2**). Invertebrates and fish were identified to the lowest possible taxonomic rank. When taxonomic identification to the genus or species level was not possible, we grouped organisms to a higher taxonomic rank based on visual assessment of morphological characteristics. In these instances, organisms were classified as morphotypes (**Howell *et al.*, 2019**). Fish abundance, total length, *in-situ* behavior (*i.e.*, fish behavior presumably natural and undisturbed at the time of first observation, and defined by their altitude, activity and locomotion) and response behavior (*i.e.*, fish reaction to UVS defined as either attraction, no reaction or avoidance) were recorded from both surveys. To characterize benthic habitat type, invertebrate abundances were recorded from the ROPOS survey while, due to time constraints, only the presence/absence of invertebrate taxa was recorded from the CAMPOD survey. To characterize bottom type, four unique substrates (mud, shell debris, gravel and boulders) and three micro-habitat features (burrows, depressions and dunes) were recorded each second of video footage form both surveys.

Table 1-2 | Video survey and type of data recorded in the video analysis and chapters they were used in.

Data acquisition	Chapter 2	Chapter 3	Chapter 4	Chapter 5
Video survey	R2017	R2017 & C2018	R2017 & C2018	R2017 & C2018
Type of data				
Invertebrate taxonomic identification	✓	✓	✓	
Invertebrate abundance	✓			
Invertebrate presence		✓	✓	
Fish taxonomic identification	✓	✓	✓	✓
Fish abundance	✓	✓	✓	✓
Fish total length		✓	✓	✓
Fish behavior			✓	
Substrate	✓	✓	✓	
Survey operation			✓	

Data were recorded continuously during both transect and transit (between transect) modes for the ROPOS survey (**Fig. 1-7A**) and only during transect mode for the CAMPOD survey (**Fig. 1-7B**). Multiple snapshots were taken along the survey track from the ROPOS forward-looking camera video recordings to assess the width of the field of view (FoV). As the CAMPOD forward camera was not paired with lasers, we could not calculate the FoV of this system from the videos. Video sections where the field of view was obstructed (*e.g.*, resuspended sediment, close-up on a specimen or feature during investigation, or UVS too high in water column) were removed from the dataset. Sections where UVSs were maneuvering from transect to transit or transit to transect, as well as sections off-transects with multiple crossings were also removed.

1-3.2 | Research objectives and thesis outline

In addition to the introductory chapter (**1**), this thesis contains four research chapters (**2-5**) and a conclusion chapter (**6**). All references and appendices are presented at the end of the thesis. The general introduction provides a broad presentation of deep-sea corals and deep-sea fish, deep-sea coral habitats, knowledge gaps on fish-coral habitat associations at a small spatial scale, approaches to monitor groundfish, as well as a presentation of the conservation context of my study. Chapters 2 and 3 aim to assess the influence of biological and physical habitat features on the small-scale distribution of abundant groundfish taxa in a low-heterogeneity soft-bottom deep-sea ecosystem. Chapters 4 and 5 aim to explore the bias and relative effectiveness of UVSs to bottom trawls in sampling fish assemblage characteristics.

While many studies have assessed relationships between fishes and large features in hard-substrate environments, relatively few have examined the relationships of fish with habitat provided by smaller features in soft-bottom environments. In Chapter 2, I characterize fish communities across a range of benthic habitats in the MPA and identify the biotic and abiotic factors that may drive deep-sea groundfish distribution in a soft-bottom environment. In particular, I assess the influence of depth, and biological and physical micro-habitat features on fish taxon-specific density.

In Chapter 3, I describe the local size structure of four deep-sea groundfish taxa in the MPA, I assess the influence of fish body size and benthic habitats on fish distribution and I identify abiotic drivers of size for each taxon. This chapter aims to highlight fish habitat use variability, as well as the importance of sea pen habitats for specific fish life stages.

UVSs are gradually replacing scientific bottom trawls as the primary tool to conduct *in-situ* multispecies benthic surveys, especially in deep-sea environments. It is crucial then to assess induced bias when surveying mobile fish taxa as well as to evaluate the relative effectiveness of survey gear in sampling fish assemblage characteristics in order to standardize fish video surveys. In Chapter 4, I describe fish *in-situ* behavior according to their altitude, activity and locomotion and assess its variability at a taxon-specific level in relation to environmental and fish biological factors. In addition, I describe fish response behavior to two UVSs and assess fish reaction variability at a taxon-specific level in relation to environmental and technical factors, as well as to fish biology and ecology attributes.

In Chapter 5, I compare fish diversity, abundance and local size structure assessed by bottom trawls, and two UVSs. This chapter aims to determine the extent to which UVSs can be substituted for bottom trawls and yield comparable results to those currently provided by scientific trawl surveys.

The conclusion of this thesis summarizes the main findings of this research, their contribution to the empirical knowledge of fish-habitat relationships in deep-sea low-heterogeneity soft-bottom ecosystems, and their implications for *in-situ* benthic surveys and conservation efforts/strategy (monitoring, management). I conclude this dissertation with providing several recommendations for future dedicated research.

Chapter 2

The effect of small-scale habitat features on groundfish density in deep-sea soft-bottom ecosystems[1]

Abstract

In the deep-sea, cold-water corals (CWCs) and other structure-forming fauna locally increase habitat complexity and are host to many fish species. While many studies have focused on hard-bottom CWCs, very little is known about fish associations with soft-bottom CWC habitats.

To understand the small-scale linkages between fish, benthic and non-bio-structural habitats in a soft-sediment deep-sea environment, we analyzed remotely operated vehicle (ROV) survey videos and recorded the occurrence of fish, invertebrate habitat-forming species and substratum along transects, in the Laurentian Channel Marine Protected Area (MPA) in the Canadian Northwest Atlantic.

Almost 13,300 individual fish were recorded, of which all but 65 specimens were identified to family or lower taxonomic rank. The five numerically dominant fish taxa were Redfish (*Sebastes* spp.), Witch Flounder (*Glyptocephalus cynoglossus*), Marlin-Spike Grenadier (*Nezumia bairdii*), Longfin Hake (*Phycis chesteri*) and one Teleostei morphotype. Teleostei sp1 represents three fish genera (Sandlance (*Ammodytes* sp.), and two Barracudinas (*Arctozenus* sp. and *Paralepis* spp.)) morphologically difficult to differentiate on video footage.

Multivariate analysis revealed four habitats based on epibenthic invertebrate densities and diversity. These were dominated by various combinations of sea anemones (Actiniaria), nephtheid soft coral, solitary cup corals (Scleractinia) and three taxa of sea pen (*Pennatula* spp., *Kophobelemnon* sp. and *Anthoptilum* spp.). Univariate analyses performed on dominant fish densities revealed the local influence of hard-bottom substrates and the common influence of soft-sediment micro-features for three fish taxa.

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[1] A modified version of this chapter was published as: **Boulard M., Lawton P., Baker K., Edinger E.** (2023). 'The effect of small-scale habitat features on groundfish density in deep-sea soft-bottom ecosystems'. *Deepsea Research I*. Vol. 193.

All fish densities were correlated with invertebrate density, negatively for Redfish and positively for all other taxa. Our models also predicted the association of four fish taxa with one to two benthic habitat types within their preferred depth range.

Our results suggest that small-scale habitat heterogeneity in a low relief soft-sediment environment, provided by both physical and biological structures, has a measurable species-specific influence on fish communities. This influence was weaker than typical fish-habitat relationships found in hard-bottom systems, suggesting fish-invertebrate relationships are not obligate. Additionally, we provided evidence that Redfish continue occupying sea pen habitats months after spawning. Our study supports the necessity to continue monitoring the MPA using *in-situ* video systems to understand the links between fish and habitats in the Laurentian Channel.

2-1 | Introduction

Spatial heterogeneity is a key factor influencing ecological assemblages and processes at various scales (**Dutilleul & Legendre, 1993**). Greater heterogeneity contributes to more complex and diverse assemblages, and can influence the structure and community composition of populations, as well as ecosystem functions (**Griffin *et al.*, 2009**). Deep-sea environments (below 200 m) can be shaped by a high habitat heterogeneity, characterized by variations in bottom type, currents or gradients of environmental variables (*e.g.*, bathymetry, temperature, salinity). At local scales, variation in sediment type and topography can provide habitats to many benthic species, such as habitat-forming invertebrates. Biogenic structures formed by epibenthic species such as cold-water corals (CWCs) are influenced by environmental heterogeneity but also contribute to increased habitat complexity and heterogeneity for other species.

CWCs include a wide range of skeletal cnidarians, such as colonial and solitary scleractinians (hard corals), pennatulaceans (sea pens), alcyonaceans (soft corals and sea fans), antipatharians (black corals) and stylasterine hydrocorals (lace corals) (**Cairns, 2007**). CWCs increase habitat heterogeneity on both hard and soft substrates by forming complex three-dimensional structures that locally increase biodiversity and biomass of benthic communities (**Roberts *et al*., 2006 | Auster, 2007 | Buhl-Mortensen *et al*., 2010**). CWCs are ecologically valuable as they provide shelters from predation and serve as feeding, resting and nursery areas for many benthic invertebrates and groundfish species (**Costello *et al*., 2005 | Stone, 2006 | Roberts *et al*., 2009 | Stone, 2014**). While most CWCs and other epifaunal suspension feeders settle on rocky substrates, other CWCs (*e.g*., sea pens, some sea fans and some solitary scleractinians) anchor themselves in soft sediments or rest on soft-bottom substrates.

The nature of the relationship between fish and biogenic habitat is quite ambiguous and functional connections are still unclear. Specific influence of benthic habitat structures on fish has been advanced by several authors in both soft (**Baillon *et al*., 2012**) and hard-bottom environments (**Fosså *et al*., 2002 | D'Onghia, 2019 | Henderson *et al*., 2020**). Conversely, other studies have suggested a coincidental co-occurrence of habitat-forming species and fishes, primarily influenced by abiotic variables such as depth (**Baker *et al*., 2012a | Biber *et al*., 2014 | Milligan *et al*., 2016 | Devine *et al*., 2020**), substratum (**Auster, 2005 | Ross *et al*., 2015**), or as a result of shared habitat preferences and overlapping distributions (**Stone, 2006**).

Fish-habitat relationships have been broadly studied in hard-bottom CWC environments (**Edinger *et al*., 2007 | Biber *et al*., 2014 | Ross *et al*., 2015 | Arnaud-Haond *et al*., 2017 | D'Onghia, 2019 | Devine *et al*., 2020**), while only a few investigated small-scale fish distribution in relation to habitat in soft-sediment environments (**D'Onghia *et al*., 2011 | Baillon *et al*., 2012 | D'Onghia *et al*., 2012**). One proposed reason for this disparity is the general assumption that muddy ocean floors are homogeneous and stable (**Danovaro *et al*., 2014**). This assumption is valid for very large scales (~100 km^2), but is not necessarily true at the spatial scale at which most marine organisms respond to their environment (1-100s of m) (**Thistle, 2003**). Local micro-features in soft sediments, defined as soft-sediment deformation structures (SSDS) can take many forms (**Shanmugam, 2017**) and can have a significant influence on benthic fauna (**Snelgrove, 1994 | Passchier & Kleinhans, 2005 | Zeiler *et al*., 2008**). SSDS can result from physical (*e.g*., sand waves and ripples shaped by bottom currents), geological (*e.g*., iceberg scours), chemical (*e.g*., pockmarks) or biological processes (*e.g.*, bioturbation and burrows). Differences in macro-benthic community composition, found between SSDS such as sandbanks, sand waves and ripples likely influence ecosystems and ecosystem processes (**Mestdagh *et al.*, 2020**), and therefore could influence the distribution of groundfish species.

Our objectives were 1) to characterize fish communities across a range of benthic habitats in the Laurentian Channel MPA, 2) to identify the small-scale habitat attributes that may drive groundfish distribution in a soft-bottom environment and 3) to produce fish distribution maps. We tested the influence of bottom types, invertebrate size classes, invertebrate density and CWC habitats on fish assemblages.

2-2 | Methodology

2-2.1 | Data preparation

For this study, we used the data collected during the 2017 ROPOS survey only. Following recommendations from Baker *et al*. (**2012a**) and Miles (**2018**), we elected to divide the video data into 10-m segments, which were used as sample units to match with the small-scale distribution of habitat attributes. Both studies suggested that small spatial scale was more appropriate to highlight fine-scale heterogeneity and run species distribution models (**Baker *et al.*, 2012a | Miles, 2018**). For each snapshot extracted, the field of view was measured in ImageJ (**Schneider *et al.*, 2012**) using the lasers as a scale to estimate the width covered (total of 5,200 snapshots, 1 to 5 per segment, with an average width of 5.3 m). The surface area of each segment was estimated as the segment length multiplied by the average field of view. Fish and invertebrate densities (ind./m^2) were calculated in each segment, by dividing abundances by segment area.

Each segment was assigned a bottom type according to the presence or absence of substrates and soft-sediment micro-habitat features: 1) ‘Flat’: mud only, absence of SSDS and hard-bottom substrate (**Fig. 2-1A**), 2) ‘Soft negative’ relief: presence of SSDS such as depressions and burrows, absence of hard-bottom substrate (**Fig. 2-1B**), 3) ‘Soft positive’ relief: presence of SSDS such as dunes, absence of hard-bottom substrate (**Fig.**

2-1C), 4) ‘Soft mixed’ relief: presence of both positive and negative relief SSDS, absence of hard-bottom substrate (**Fig. 2-1B & 2-1C**) and 5) Hard-bottom substrate: presence of hard substrate, presence of SSDS possible (**Fig. 2-1D**).

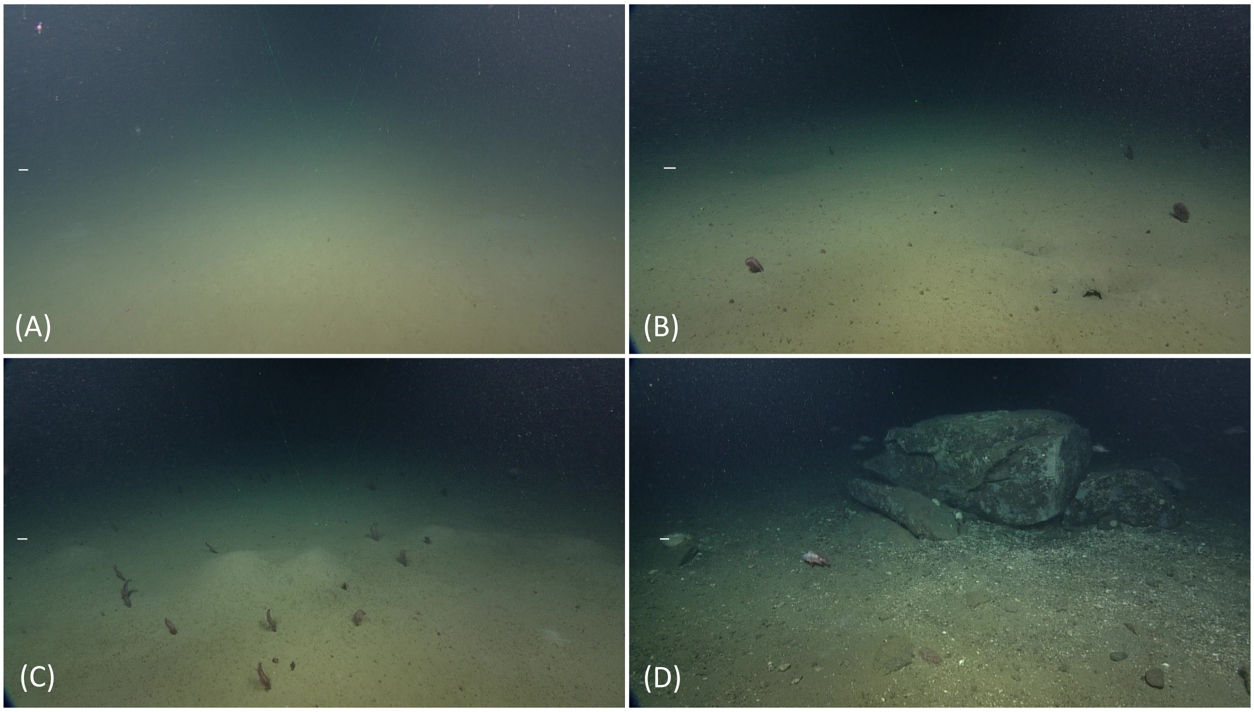

Fig. 2-1 | Frame captures from underwater video recordings of the main substrates and soft-sediment micro-habitat features observed in the Laurentian Channel MPA used to define bottom types. (A) ‘Flat’: no-relief muddy sediment, (B) ‘Soft negative’: depressions and burrows in soft sediment, (C) ‘Soft positive’: small soft-sediment dunes, (D) ‘Hard’: hard substrate comprised of boulders, gravels and shell debris. ‘Soft mixed’ was a fifth bottom type characterized by the presence of soft negative and soft positive relief features. Scale bar: 10 cm.

Fish assemblages were defined by fish species richness and fish densities. Invertebrate assemblages were defined by species richness, invertebrate densities and invertebrate height. Invertebrate height could not be measured from the videos. Data on invertebrate dimensions were found in two identification guides of epibenthic megafauna observed in the North Atlantic region (**Beazley & Kenchington, 2015 | Kenchington *et al*., 2015**). Based on these guides, we grouped invertebrate morphotypes into three categories, based on characteristic height estimates of each taxon in literature descriptions: small (<5 cm tall), medium (5-25 cm tall) and tall (25-100 cm tall) (**Appendix 2-1**).

2-2.2 | Statistical analysis

2-2.2.1 | Benthic habitat types characterized by invertebrate assemblages

All data analyses were performed using R (**R Core Team, 2019**). We determined benthic habitat types by conducting multivariate analyses on the Hellinger-transformed invertebrate densities per 10-m segment (**Legendre & Gallagher, 2001**). We used the Hellinger transformation as it is adapted to multivariate analyses dealing with species abundances with many zeros. First, we used the Gap statistic analysis, using the function ‘clusGap’ from the ’cluster’ package, to estimate the optimal number of clusters necessary to describe benthic habitat types (**Tibshirani *et al*., 2001 | Maechler *et al*., 2021**). In order to identify and extract the clusters in the dataset, we measured the dissimilarity between the Hellinger-transformed invertebrate densities using the Euclidean distance (‘dist’ function from the ‘cluster’ package) and used the dissimilarity matrix to perform a Hierarchical Clustering Analysis using Ward’s method (‘hclust’ function from the ‘cluster’ package), accounting for the optimal number of clusters identified by the Gap statistic method. Then, we used the ‘cutree’ function (‘cluster’ package) to add each segment to the cluster they belong to. Finally, we conducted a Principal Component Analysis (PCA) on the Hellinger-transformed invertebrate densities, including clusters as factors. We performed the PCA using the package ‘ade4’ then used the package ‘Factoextra’ to visualize both the distribution of clusters and the predominant invertebrate species in each assemblage (**Thioulouse *et al*., 2018 | Kassambara & Mundt, 2020**). It should be noted that we use the term ‘benthic habitat type’ herein to describe the clusters defined by the statistical analysis; this usage does not imply these are fully representative invertebrate community types.

2-2.2.2 | Quantification of physical and biological habitat attributes

To quantify habitat heterogeneity in the study area, we grouped the five bottom types into three physical categories: ‘Flat’ (mud), ‘Soft’ (soft negative, positive and mixed reliefs) and ‘Hard’. We also identified two biological categories: absence or presence of epibenthic invertebrates (‘No Invertebrates’ and ‘Invertebrates’). We calculated the relative contribution (percentage of 10-m segments) of the six following physical-biological combinations: ‘Flat-No invertebrates’, ‘Flat-Invertebrates’, ‘Soft-No invertebrates’, ‘Soft-Invertebrates’, ‘Hard-No Invertebrates’ and ‘Hard-Invertebrates’.

2-2.2.3 | Biotic and abiotic drivers of fish distribution

2-2.2.3.1 | Influence of benthic habitat types on fish diversity

In order to compare the diversity of fish assemblages between benthic habitat types, we calculated the Shannon-Wiener index (H) in each habitat, using fish abundance per taxa and a logarithm base of exp(1). Hutcheson t-tests were then performed to calculate pairwise comparisons between diversity indices (**Hutcheson, 1970**).

2-2.2.3.2 | Influence of benthic habitat types on total and specific fish densities

We ran analyses of variances (ANOVA) on the square-root transformed fish densities to test for significant differences between benthic habitat types. We used the square-root transformation to reduce the weight of abundant species in the analysis. We verified data independence, homoscedasticity and normality to ensure compatibility with the assumptions of ANOVA analyses by plotting the model diagnostics. Then, we performed Tukey tests as a *post-hoc* analysis to run pairwise mean comparisons between benthic habitat types when significant differences were found.

2-2.2.3.3 | Ecological covariates of fish specific densities

In order to identify small-scale ecological predictors of fish densities, we performed generalized additive models (GAMs) for the five most dominant taxa of the fish assemblage, using the ‘mgcv’ package (**Wood, 2011**). GAMs are an adaptation of generalized linear models in which the beta coefficient from standard linear regressions is replaced by several non-linear smoothing functions (or splines) to model linear and non-linear relationships between predictors and the response variables.

Potential biotic and abiotic covariates included in the models were mean depth, mean bottom temperature, invertebrate total density, invertebrate taxon-specific density (of the most contributing taxa to the assemblages identified by the cluster analysis) per segment, as well as benthic habitat type (as defined by the cluster analysis) and bottom type. Prior to running the models, we checked for collinearity among predictors using Variance Inflation Factor analysis (VIF) and kept variables with a VIF lower than 3 (**Zuur *et al.*, 2010**). Based on this analysis, it was concluded that both depth and bottom temperature could not be included in the same model because they were highly correlated. We decided to test the influence of dominant invertebrate taxa in a separate model. Comparing the influence of specific invertebrate taxa will help us assess 1) the influence of invertebrate size 2) the influence of CWC taxa *vs.* other potentially habitat-forming invertebrate taxa and 3) the influence of sea pen taxa *vs*. other CWCs on fish density.

To determine if we should account for spatial autocorrelation to run our models, we included the 'corSpatial' function ('nlme' package), following a gaussian distribution, to all models (**Pinheiro *et al.*, 2022**). We performed *a posteriori* residual diagnostics on the model outputs using the package 'DHARMa' to ensure assumptions were met (**Hartig, 2022**). We tested if there was a relationship between residuals and specific predictors. We also tested for outliers, overdispersion, zero inflation and spatial autocorrelation (using functions 'simulateResiduals', 'testDispersion', 'testZeroInflation' and 'testSpatialAutocorrelation'). We extracted predicted fish densities using the 'predict_gam' function from the 'tidymv' package (**Coretta, 2021**) and created partial dependence plots to visualize fish response to the different variables tested.

The best fitting models (those that explained the most variance and had the lowest Akaike information criterion (AIC)) for predicting fish density were the same for each fish taxon:

Eq. 1: *Fish density* ~ s(Depth) + s(Invertebrate density) + Benthic habitat type + Bottom type + s(Station, bs = "re")
Eq. 2: *Fish density* ~ s(Invertebrate taxon$_1$ density) + … + s(Invertebrate taxon$_n$ density) + s(Station, bs = "re")

Where,

Fish density = mean density of one of a given fish taxon recorded in a 10-m segment
Depth = mean depth (m) of the 10-m segment
Invertebrate density = average invertebrate total density per 10-m segment
Benthic habitat type = factor representing the benthic habitat type the 10-m segment was attributed to according to the cluster analysis
Bottom type = factor that identifies the dominant substrate type in each 10-m segment
Invertebrate taxon density = average density of one dominant invertebrate taxon.

We added as many invertebrate taxa in Eq. 2 as identified by the PCA ($taxon_1$ to $taxon_n$). Stations were added as a random term (bs = “re”) in both models. *s* represents the smoothing functions of the given covariates. A Tweedie distribution family (tw) was used because it can handle continuous data containing zeros.

2-2.2.4 | Fish specific distribution maps and Getis-Ord hot-spot analysis

To investigate how the five dominant taxa of the fish assemblage were spatially distributed at each survey location, we determined the local spatial Getis-Ord Gi* statistic using ArcGIS (**Ord & Getis, 1995 | Esri Inc., 2020**). We used this method to test for local spatial patterns in fish distribution. The hot-spot analysis identifies the locations of statistically significant ‘hot-spot’ and ‘cold-spot’ clusters, by calculating the Gi* statistic for each segment, based on fish densities. The Gi* index returns for each segment a z-score and a p-value that indicate locations of either high or low value spatial clusters. Hot spots are defined as statistically significant clusters of high fish density values (positive z-score) compared to expected values given by a random distribution model, while cold spots are defined as significant clusters of lower values (negative z-score). We produced distribution maps for the five most dominant fish species and represented the percentage of 10-m segments that presented either an aggregation pattern (hot spots or clusters of high fish densities), a dispersion pattern (cold spots or clusters of low fish densities) or a random distribution at each station. The Getis-Ord hot-spot analysis is a robust statistical method that allows for an easy visual identification and location of significant fish associations in relation to habitat physical and/or biological attributes, between and within habitats.

2-3 | Results

2-3.1 | Data summary

The ROV captured 57h of video footage at depth from 331 to 450 m (**Table 1-1**). The survey covered 38.6 km in total linear extent and an area of approximately 19.4 ha within the study area. The surveys were clustered within two discrete depth ranges, 331-356 m (three stations) and 429-450 m (four stations). Recorded bottom temperatures ranged from 5.4 to 7.3 °C. The average bottom temperature was 6.7 °C at the shallowest station and 5.9 °C at the deepest station.

2-3.2 | Quantification of physical and biological habitat attributes

Mud was found in all segments, and was always the most dominant substrate (**Table 2-1**). The bottom types most observed in the survey were 'Flat' (55%, **Fig. 2-1A**) and soft bottom with negative relief (41%, **Fig. 2-2B**). Soft bottom with mixed relief (3%, **Fig. 2-1B & 2-1C**), soft bottom with positive relief (<1%, **Fig. 2-1C**) and hard-bottom substrate (<1%, **Fig. 2-1D**) were the least encountered bottom types (**Table 2-1**). A distribution map of bottom types across stations is presented in Fig. 2-2A.

Table 2-1 | Frequency of occurrence (number of 10-m segments) of the different substrates and soft-sediment micro-habitat features per bottom type.

Bottom type	**Substrate and soft-sediment micro-habitat feature**							**Total bottom type**
	Mud	Depression	Burrow	Dune	Boulder	Gravel	Shell debris	
Flat	1909	0	0	0	0	0	0	1909
Soft negative	1452	899	1154	0	0	0	0	1452
Soft positive	56	0	0	56	0	0	0	56
Soft mixed	123	95	100	123	0	0	0	123
Hard	20	10	6	0	16	3	8	20
Total substrate	3560	1004	1260	179	16	3	8	3560

Invertebrates were present in 95% of the area surveyed. They contributed to habitat heterogeneity in flat areas ('Flat-Invertebrates') in 52% of the segments, and in soft-bottom areas with micro-relief ('Soft-Invertebrates') in 43% of the segments (**Table 2-2**). Only 3% of the area covered was considered as homogeneous, defined as 'Flat-No Invertebrates', less then 1% was considered as 'high heterogeneity' ('Hard-Invertebrates'). No segment was identified as 'Hard-No invertebrates'. A distribution map of physical and biological attributes across stations is presented in Fig. 2-2B.

Table 2-2 | Frequency of occurrence (number of 10-m segments) of different combinations of physical substratum types and epibenthic invertebrate faunal representation. 'Flat' corresponds to muddy substrate with no relief. 'Soft' corresponds to the grouped soft negative, positive and mixed relief bottom types. 'Hard' corresponds to boulders, gravels and shell debris.

Bottom type	**Benthic habitat**		**Total**
	No invertebrates	Invertebrates	
Flat	105	1847	1952
Soft	70	1518	1588
Hard	0	20	20
Total	175	3385	3560

We also quantified habitat heterogeneity based on invertebrate sizes. The most dominant group of invertebrates was medium (5-25 cm tall), representing 65.5% of all the invertebrates, and comprised mostly *Pennatula* (53%) and smaller *Kophobelemnon* (7%) sea pens. The second most dominant group of invertebrates was small (<5 cm tall), representing 30% of all observed invertebrates and consisting mostly of solitary scleractinian corals, such as *Flabellum* sp. (27%). Tall invertebrates (25-100 cm) represented only 4% of all the invertebrates and were mostly *Anthoptilum* sea pens. A distribution map of invertebrates by size classes across stations is presented in Fig. 2-4C.

2-3.3 | Benthic habitat types characterized by invertebrate assemblage composition

The Gap statistic analysis identified five clusters, based on invertebrate densities, to best describe the different fauna assemblages (**Appendix 2-2**). The PCA performed on invertebrate densities in relation to the clusters identified five benthic habitat types defined largely by depth (Dim. 1 (41% of variance)) and ten dominant invertebrate taxa (**Appendix 2-3**). Clusters distributed to the right of the plot (positive range of Dim1) corresponded to benthic habitat types found in the 331-356 m depth range (clusters C2 'Penna-Flab' and C3 'Sclerac-Penna'), while clusters distributed to the left of the Dim1 axis were benthic habitat types found in the 429-450 m depth range (clusters C1 'Barren', C4 'Sclerac-Anthop-Kopho' and C5 'Kopho-Acti'). None of the other environmental variables assessed seemed to drive the distribution of the benthic clusters along Dim. 2 (*e.g.*, latitude, longitude, bottom temperature and bottom types).

'Penna-Flab' and 'Sclerac-Penna' were sea pen fields distributed near the eastern bank (**Fig. 2-2D**) and dominated by *Pennatula* spp. and two solitary scleractinian taxa, showing the highest total densities of all habitats. Total invertebrate densities ranged from 0 to 7 ind./m^2 (**Appendix 2-4**). We ranked invertebrate densities as very low (≤0.1 ind./m^2), low (0.1-0.3 ind./m^2), medium (0.3-1 ind./m^2) and high (>1 ind./m^2). 'Penna-Flab' was dominated by *Pennatula* spp. (75% of the abundance of the assemblage, high density) and *Flabellum* spp. (17%, low density). 'Sclerac-Penna' was dominated by Scleractinia sp1 (59%) and *Pennatula* spp. (37%), with both taxa presenting medium densities (**Fig. 2-3**).

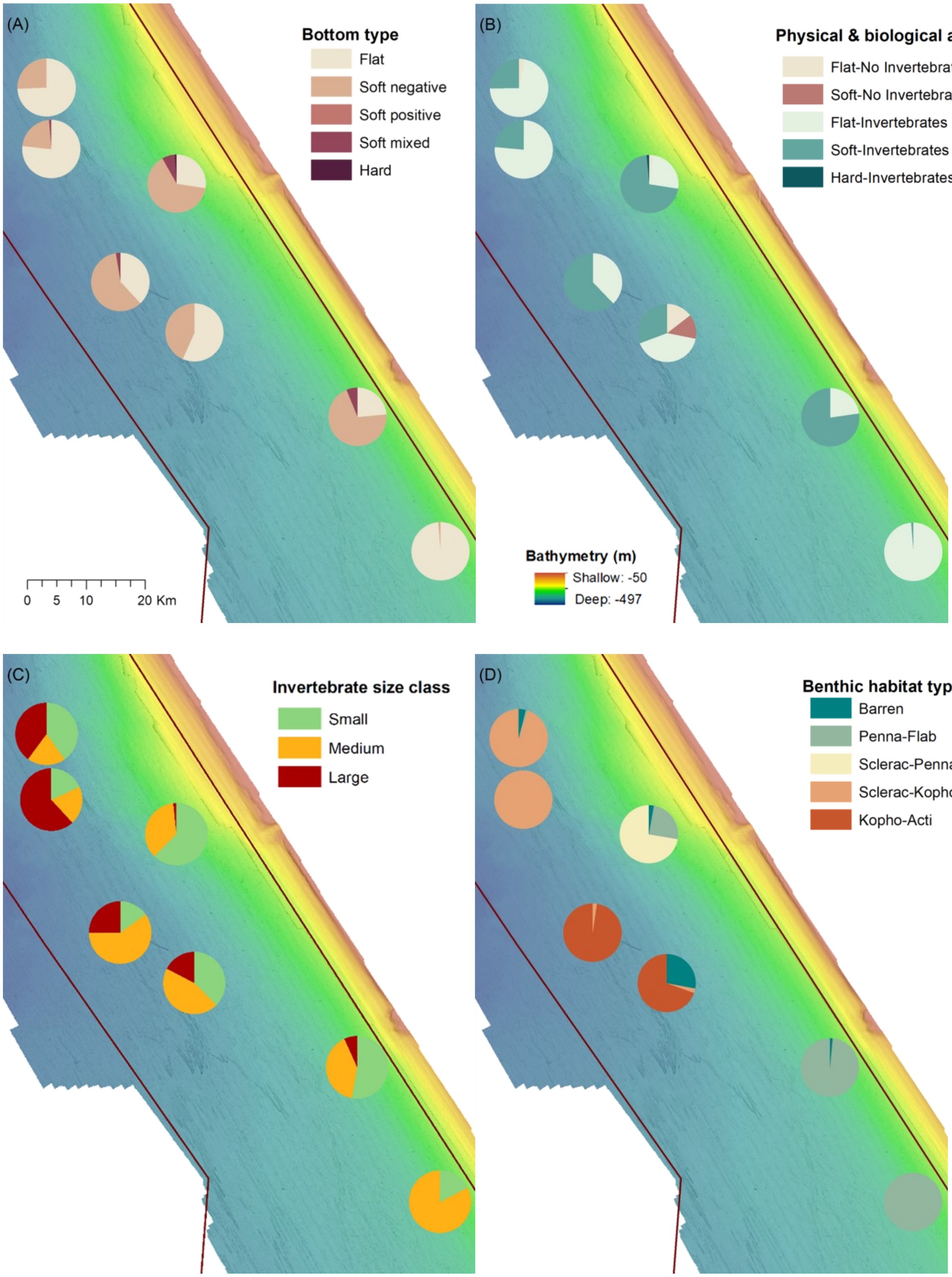

Fig. 2-2 | Characterization of habitat heterogeneity according to (A) bottom types, (B) physical and biological attributes, (C) invertebrate size classes, (D) benthic habitat types defined by the cluster analysis across stations. Pie charts show the proportion of each category found at each station.

Two invertebrate clusters showed the lowest invertebrate total densities (medium), but a higher invertebrate diversity compared to the two *Pennatula*-dominated habitats. ‘Sclerac-Kopho-Anthop’ was found in the deep upstream section of the channel (**Fig. 2-2**) and was dominated by Scleractinia sp4 (26%), *Kophobelemnon* sp. (21%) and *Anthoptilum* spp. (21%), all presenting medium densities (**Fig. 2-3**). ‘Kopho-Acti’ was found in the deep central section of the channel (**Fig. 2-2**) and was dominated by *Kophobelemnon* sp. (36%) and *Actinoscyphia* sp. (29%), with both taxa presenting low densities (**Fig. 2-3**). Actiniaria sp6, Cerianthid sp1 and nephtheid soft coral were mostly present in those two benthic habitat types, but each represented less than 10% of the abundance of each assemblage. The ‘Barren’ habitat was the only cluster with no epibenthic fauna and was mostly found close to one ‘Kopho-Acti’ habitat (**Fig. 2-2**).

Small and medium were the two dominant invertebrate size classes in all invertebrate clusters (**Appendix 2-4**). They represented more than 90% of the invertebrate assemblages in ‘Penna-Flab’, ‘Sclerac-Penna’ and ‘Kopho-Acti’, and 75% in ‘Sclerac-Kopho-Anthop’. The tall invertebrate size class was mostly present in ‘Sclerac-Kopho-Anthop’ and represented 25% of the assemblage. We did not find any relation between benthic habitat types and bottom types, as more than 90% of each cluster was dominated by ‘Flat’ and ‘Soft negative’ bottom types (**Appendix 2-4**).

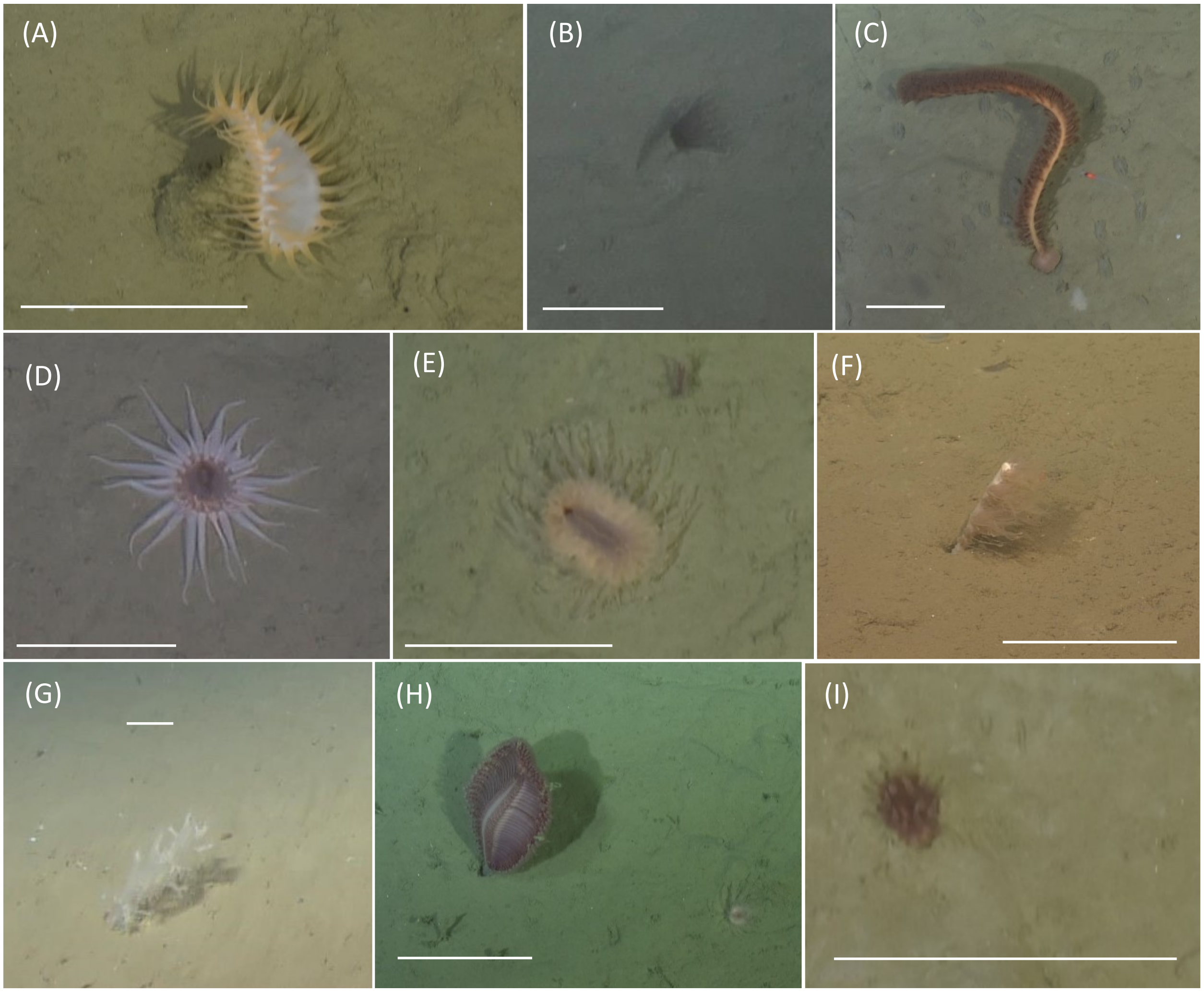

Fig. 2-3 | Frame captures from underwater video recordings of the invertebrate taxa contributing to invertebrate assemblages defined by the cluster and PCA analyses. (A) *Actinauge cristata*, (B) Actiniaria sp6. (C) *Anthoptilum* spp., (D) Cerianthid sp1., (E) *Flabellum (Ulocyathus) alabastrum*, (F) *Kophobelemnon* sp., (G) Nephteidae sp., (H, left) *Pennatula aculeata*, (H, right) *F. alabastrum*, (I) *Flabellum (Ulocyathus) angulare*. All pictures were taken from the downward-looking camera except pictures F and G that were taken from the forward-looking camera. Scale bar: 10 cm.

2-3.4 | Fish occurrence and community composition

2-3.4.1 | Fish occurrence

A total of 13,297 fishes were observed, comprising 23 morphotypes (**Table 2-3**). Most of them were identified to 18 species (5,500 specimens) and 5 genera (7,705 specimens). Only 65 individuals could not be identified at or below family level. Five taxa represented 90% of all specimens observed and were present at all stations (**Fig. 2-4**).

Table 2-3 | Number of fish individuals observed and their relative contribution (% of total abundance) sorted in descending percentage of total abundance.

Family	Scientific name	Common name/Taxon	Total number observed	Percentage of total abundance
Sebastidae	*Sebastes* spp.	Redfish	6685	50
Phycidae	*Phycis chesteri*	Longfin Hake	1868	14
Pleuronectidae	*Glyptocephalus cynoglossus*	Witch Flounder	1322	10
Macrouridae	*Nezumia bairdii*	Marlin-Spike Grenadier	1222	10
Teleostei[1]	Teleostei spp.	Teleostei sp1	1017	8
Zoarcidae	*Lycenchelys verrillii*	Wolf Eelpout	509	4
Rajidae	Rajidae spp.	Skate sp1	170	1
Myxinidae	*Myxine glutinosa*	Atlantic Hagfish	129	1
Zoarcidae	*Enchelyopus cimbrius*	Fourbeard Rockling	110	1
Gadidae	*Merluccius bilinearis*	Silver Hake	81	1
Actinopterygii[2]	Actino sp. indet.	Actino sp1	61	1
Zoarcidae	*Argentina silus*	Greater Argentine	31	< 1
Phycidae	*Urophycis tenuis*	White Hake	26	< 1
Liparidae	Liparidae sp. indet.	Snailfish sp1	16	< 1
Gadidae	*Pollachius virens*	Pollock	14	< 1
Gadidae	*Gadus morhua*	Atlantic Cod	12	< 1
Lophiidae	*Lophius americanus*	American anglerfish	6	< 1
Zoarcidae	Zoarcidae sp. indet	Zoarcidae sp1	6	< 1
Actinopterygii[2]	Unidentified fish	Actino spp	4	< 1
Ogcocephalidae	*Dibranchus* sp. indet.	Batfish sp1	3	< 1
Pleuronectidae	*Hippoglossus hippoglossus*	Atlantic Halibut	2	< 1
Etmopteridae	*Centroscyllium fabricii*	Black Dogfish	1	< 1
Lamnidae	*Lamna nasus*	Porbeagle shark	1	< 1
Cryptacanthodidae	*Cryptacanthodes maculata*	Wrymouth	1	< 1

[1] Subclass
[2] Class

Redfish (*Sebastes* spp.) was the most abundant taxon, representing almost 50% of total fish observed. Three *Sebastes* species are common to the area: *Sebastes mentella*, *S. fasciatus* and *S. norvegicus*. As they are difficult to differentiate without physical specimens of each individual, we grouped them as one Redfish taxon. The remainder comprised of Longfin Hake (*Phycis chesteri*) at 15%, Witch Flounder (*Glyptocephalus cynoglossus*) and Marlin-Spike Grenadier (*Nezumia bairdii*) at 10% each, and three undistinguishable genera grouped as one morphotype (Teleostei sp1) at 8%.

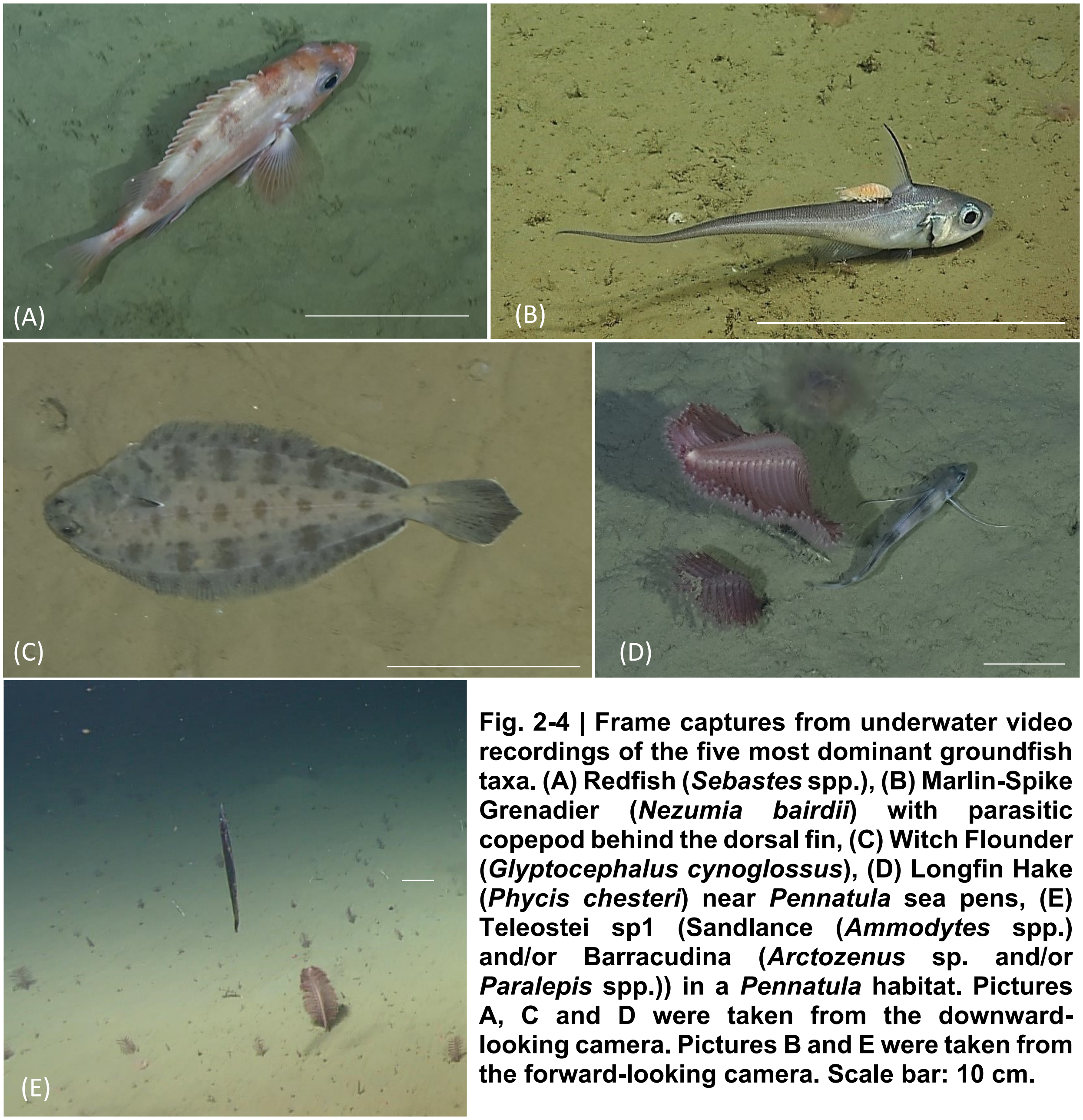

Fig. 2-4 | Frame captures from underwater video recordings of the five most dominant groundfish taxa. (A) Redfish (*Sebastes* spp.), (B) Marlin-Spike Grenadier (*Nezumia bairdii*) with parasitic copepod behind the dorsal fin, (C) Witch Flounder (*Glyptocephalus cynoglossus*), (D) Longfin Hake (*Phycis chesteri*) near *Pennatula* sea pens, (E) Teleostei sp1 (Sandlance (*Ammodytes* spp.) and/or Barracudina (*Arctozenus* sp. and/or *Paralepis* spp.)) in a *Pennatula* habitat. Pictures A, C and D were taken from the downward-looking camera. Pictures B and E were taken from the forward-looking camera. Scale bar: 10 cm.

Teleostei sp1 could represent either Sandlance (*Ammodytes* spp.) or two genera of Barracudina (*Arctozenus* sp. and *Paralepis* spp.). All three taxa are known to occur in the channel, but were difficult to reliably differentiate without detailed views or physical specimens of each individual. Five other taxa were observed at all stations (7% of total abundance), in much lower abundance: Wolf Eelpout (*Lycenchelys vyerrillii*), two species of skates (Rajidae sp.), Atlantic Hagfish (*Myxine glutinosa*) and Fourbeard Rockling

(*Enchelyopus cimbrius*) (**Appendix 2-5**). Thorny Skate (*Amblyraja radiata*) and Smooth Skate (*Malacoraja senta*) were the two species of skates we observed, but were difficult to differentiate without physical specimens of each individual.

2-3.4.2 | Fish diversity per benthic habitat type

Higher diversity indices for fish were identified in the two *Pennatula*-dominated habitats (H = 1.94 and 1.71 respectively), followed by the ‘Barren’ habitat (H = 1.55). Smaller diversity indices were found in the ‘Kopho-Acti’ and ‘Sclerac-Kopho-Anthop’ habitats (H = 1.32 and 1.1 respectively) (**Table 2-4**).

Table 2-4 | Shannon-Wiener diversity index calculated for fish per benthic habitat type and p-values estimated by running Hutcheson t-tests pairwise comparisons on diversity indices.

Benthic habitat type	**Shannon-Wiener index (H)**	Barren	Penna-Flab	Sclerac-Penna	Sclerac-Kopho-Anthop	Kopho-Acti
Barren	1.55	-				
Penna-Flab	1.94	< 0.001	-			
Sclerac-Penna	1.71	< 0.001	< 0.001	-		
Sclerac-Kopho-Anthop	1.1	< 0.001	< 0.001	< 0.001	-	
Kopho-Acti	1.32	< 0.001	< 0.001	< 0.001	< 0.001	-

2-3.4.3 | Fish total and specific densities per benthic habitat type

Total fish densities ranged from 0 to 1.75 ind./m^2. We arbitrarily ranked fish densities as very low (≤0.002 ind./m^2), low (0.002-0.01 ind./m^2), medium (0.01-0.05 ind./m^2), high (0.05-0.07 ind./m^2) and very high (≥0.07 ind./m^2). Based on the ANOVA analyses we ran on fish density per benthic habitat types, total fish densities were highest in ‘Sclerac-Kopho-Anthop’ and ‘Sclerac-Penna’ (high densities), followed by ‘Kopho-Acti’ (medium densities) and lowest in the ‘Penna-Flab’ and ‘Barren’ habitats (medium densities) (**Table 2-5 & Appendix 2-6**). Only 10 of 23 fish taxa had densities higher than 0.001 ind./m^2 associated with at least one benthic habitat type, and differences in fish densities between habitats were observed for eight of them (**Appendix 2-6**). For six of eight fish taxa, densities associated with the ‘Barren’ habitat were the lowest. For three fish taxa, densities were higher in one of the two *Pennatula* habitats than in all the other habitats (Silver Hake, Wolf Eelpout and Teleostei sp1). Marlin-Spike Grenadier and Longfin Hake densities associated with both *Pennatula* habitats were the highest. Conversely, Redfish densities were the lowest in the *Pennatula* and ‘Barren’ habitats, and the highest in ‘Sclerac-Kopho-Anthop’ and ‘Kopho-Acti’. Marlin-Spike Grenadier and Longfin Hake densities associated with ‘Sclerac-Kopho-Anthop’ and ‘Kopho-Acti’ were higher than in the ‘Barren’ habitat. Witch Flounder presented higher densities in ‘Sclerac-Kopho-Anthop’ than in ‘Sclerac-Penna’, yet there was not any difference in density between the other benthic habitat types.

Table 2-5 | Average total densities (ind./m^2) and densities of the most dominant fish taxa per benthic habitat type (± standard error). Only taxa that presented densities ≥ 0.001 in ind./m^2 in at least one benthic habitat type are shown. Densities in bold represent the highest fish densities when compared between benthic habitat types ($p < 0.05$).

	Benthic habitat type					
	Barren	Penna-Flab	Sclerac-Penna	Sclerac-Kopho-Anthop	Kopho-Acti	
Total habitat type	0.0544 (± 0.0062)	0.0632 (± 0.002)	**0.084** (± 0.0027)	**0.0973** (± 0.0047)	0.0693 (± 0.0028)	
Fish taxon						**Total taxon**
Redfish	0.0286 (± 0.0059)	0.0165 (± 0.0015)	0.0232 (± 0.0018)	**0.0689** (± 0.0046)	0.0434 (± 0.0027)	0.0375 (± 0.0015)
Longfin Hake	0.0039 (± < 0.001)	0.01 (± < 0.001)	**0.0296** (± 0.0012)	0.0071 (± < 0.001)	0.0053 (± < 0.001)	0.0107 (± < 0.001)
Witch Flounder	**0.0088** (± 0.0011)	0.0073 (± < 0.001)	0.0061 (± < 0.001)	0.0083 (± < 0.001)	0.0082 (± < 0.001)	0.0077 (± < 0.001)
Marlin-Spike Grenadier	0.0037 (± < 0.001)	0.0066 (± < 0.001)	**0.0136** (± < 0.001)	0.0064 (± < 0.001)	0.0058 (± < 0.001)	0.0072 (± < 0.001)
Teleostei sp1	0.0035 (± 0.001)	**0.0139** (± < 0.001)	0.0029 (± < 0.001)	< 0.001 (± < 0.001)	0.0018 (± < 0.001)	0.0057 (± < 0.001)
Wolf Eelpout	0.0023 (± < 0.001)	**0.005** (± < 0.001)	0.003 (± < 0.001)	0.0018 (± < 0.001)	0.0019 (± < 0.001)	0.0031 (± < 0.001)
Skate sp1	< 0.001 (± < 0.001)	< 0.001 (± < 0.001)	**0.0012** (± < 0.001)	**0.0016** (± < 0.001)	< 0.001 (± < 0.001)	0.001 (± < 0.001)
Hagfish	**0.0012** (± < 0.001)	**0.001** (± < 0.001)	< 0.001 (± < 0.001)	< 0.001 (± < 0.001)	< 0.001 (± < 0.001)	< 0.001 (± < 0.001)
Fourbeard Rockling	0	**0.0013** (± < 0.001)	< 0.001 (± < 0.001)	< 0.001 (± < 0.001)	< 0.001 (± < 0.001)	< 0.001 (± < 0.001)

Silver Hake	< 0.001 (± < 0.001)	< 0.001 (± < 0.001)	**0.0025** (± < 0.001)	0	0	< 0.001 (± < 0.001)

2-3.4.4 | Biotic and abiotic drivers of dominant fish taxa densities

In order to identify ecological predictors of fish densities, we performed GAMs for the five most dominant taxa of the fish assemblage: Redfish, Marlin-Spike Grenadier, Longfin Hake and Teleostei sp1. Following Model 1 (Eq. 1 using average invertebrate density and environmental predictors while accounting for station) we tested the influence of bottom temperature, instead of depth, on fish density. The models explained less variance and had a higher AIC, compared to Model 1. Moreover, bottom temperature did not appear as a significant predictor of fish density for any of the five taxa considered. We also tested the influence of benthic habitat types and bottom types independently, but did not find any difference than when they were included in Model 1. No difference was found between models including and excluding spatial autocorrelation for any fish taxon considered.

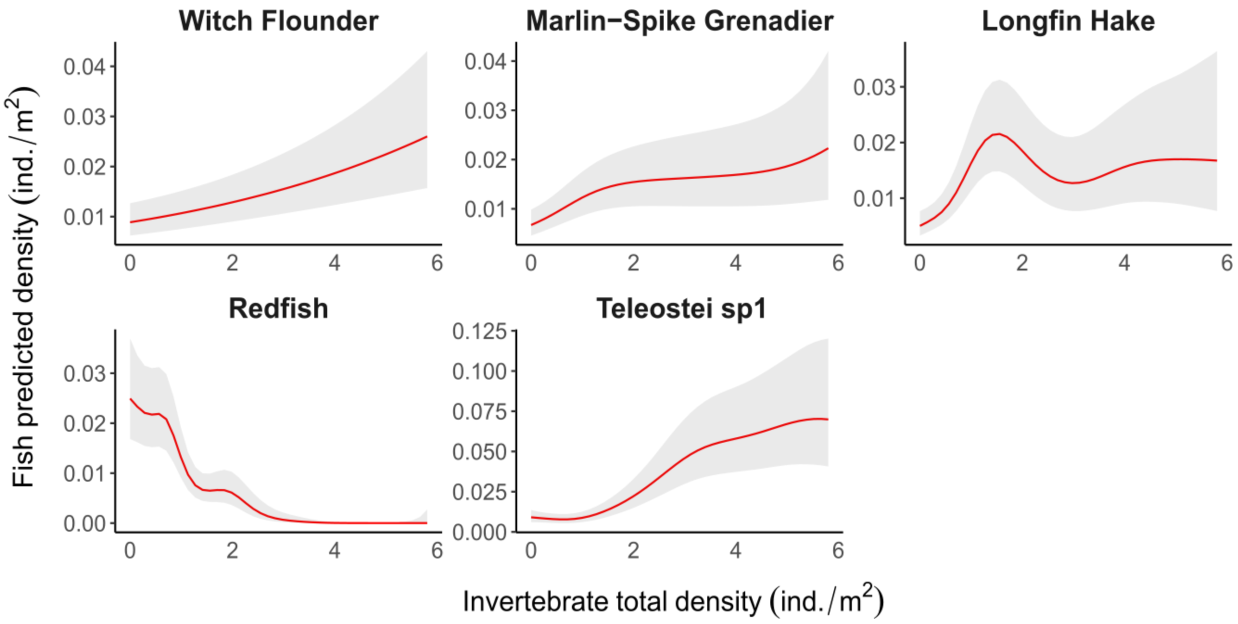

Fig. 2-5 | Model 1 (Eq. 1) partial dependence plots of fish predicted densities in relation to invertebrate total density. Grey areas correspond to the 95% confidence interval.

Model 1 for Witch Flounder explained 2.7% of variance and model 2 explained 1.9% (**Appendices 2-8 & 2-9**). A positive correlation was found between Witch Flounder density and depth, as well as invertebrate total density (**Appendix 2-7 & Fig. 2-5**). Highest densities were associated with the 'Barren' habitat (**Fig. 2-6**). No influence of bottom type was found (**Fig. 2-7**). In addition, Witch Flounder density was positively correlated with the densities of three invertebrate taxa (**Table 2-6**). Witch Flounder was associated with one actiniaria taxon, one scleracinian coral and one medium-size sea pen taxon (**Table 2-6 & Appendix 2-10**).

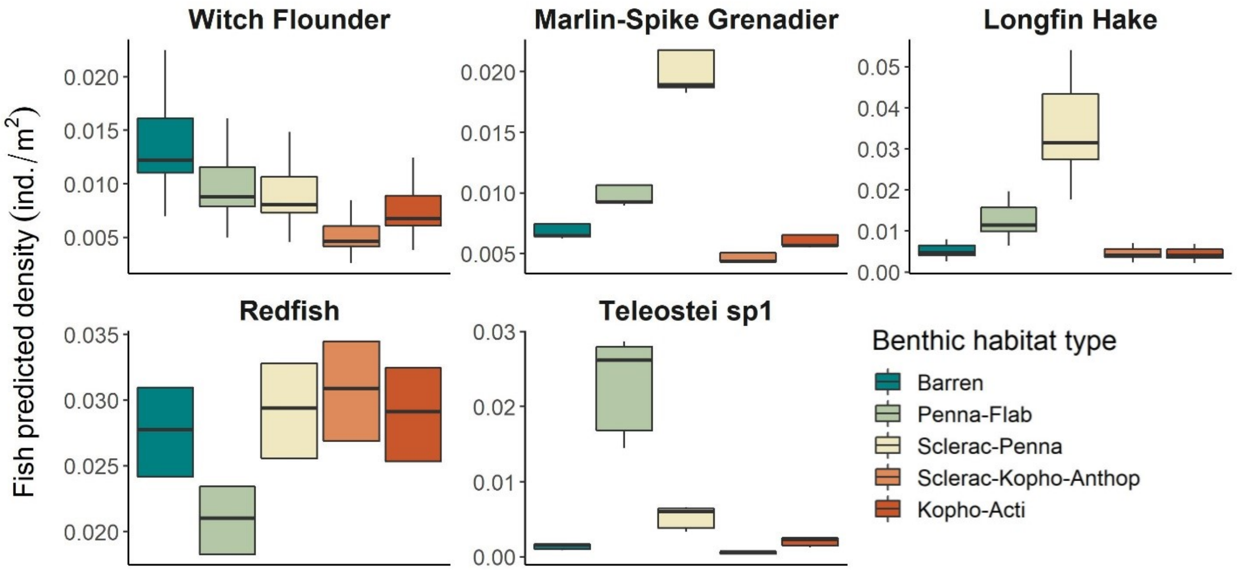

Fig. 2-6 | Model 1 (Eq. 1) partial dependence plots of fish predicted densities in relation to benthic habitat types. The lower and upper boundaries of the box plots correspond to the first and third quartiles (25th and 75th percentiles). The black line within the box plots indicates the median. The upper and lower whiskers indicate the 10th and 90th percentiles.

Model 1 for Marlin-Spike Grenadier explained 8% of variance and model 2 explained 7.4% (**Appendices 2-11 & 2-12**). A negative correlation was found between Marlin-Spike Grenadier density and depth (**Appendix 2-7**), but a positive correlation was found with invertebrate total density (**Fig. 2-5**). Highest predicted densities were associated with one *Pennatula*-dominated habitat (**Fig. 2-6**). The model also revealed highest predicted densities associated with soft positive bottom type (**Fig. 2-7**). In addition, Marlin-Spike Grenadier density was positively correlated with the densities of three invertebrate taxa dominating the *Pennatula* habitats as well as one actiniaria, one scleractinia coral and one *Anthoptilum* sea pen all dominant in the 'Sclerac-Kopho-Anhop' habitat (**Table 2-6 & Appendix 2-13**).

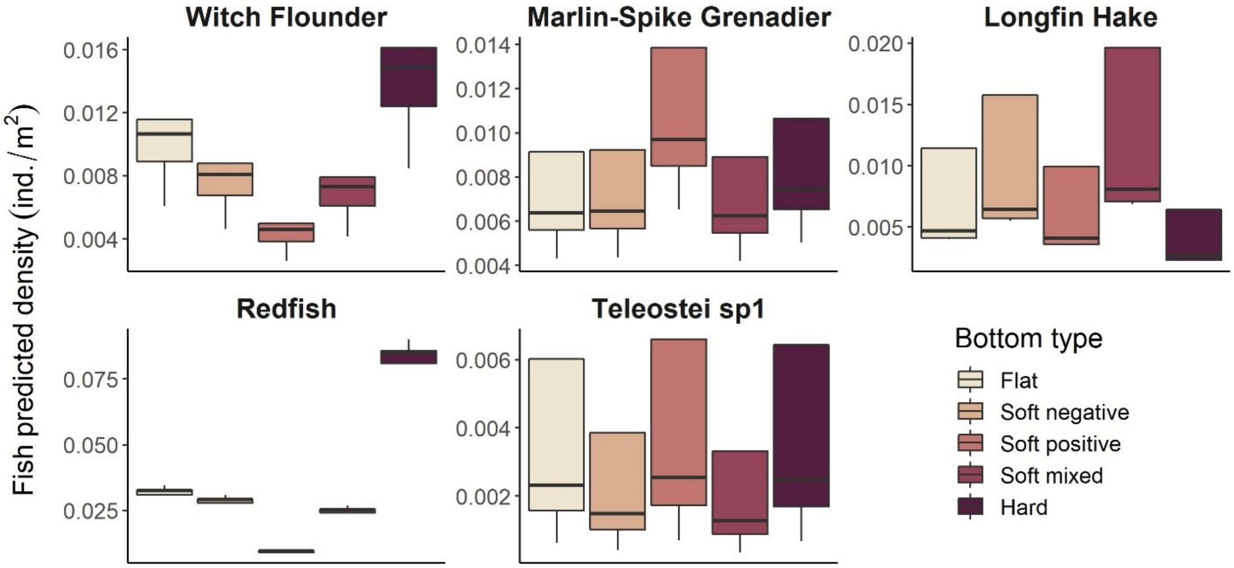

Fig. 2-7 | Model 1 (Eq. 1) partial dependence plots of fish predicted densities in relation to bottom types. The lower and upper boundaries of the box plots correspond to the first and third quartiles (25th and 75th percentiles). The black line within the box plots indicates the median. The upper and lower whiskers indicate the 10th and 90th percentiles.

Model 1 for Longfin Hake explained 21.5% of variance and model 2 explained 26.1% (**Appendices 2-14 & 2-15**). A negative correlation was found between Longfin Hake density and depth (**Appendix 2-7**), but a positive correlation was found with invertebrate total density (**Fig. 2-5**). Highest predicted densities were found associated with the two *Pennatula*-dominated habitats (**Fig. 2-6**). The model revealed highest densities associated with soft negative and soft mixed reliefs (**Fig. 2-7**). In addition, Longfin Hake density was positively correlated with the densities of the three dominant taxa of the *Pennatula* habitats as well as one scleractinia coral and one actiniaria taxon dominant in 'Sclerac-Kopho-Anthop' (**Table 2-6 & Appendix 2-16**).

Model 1 for Redfish explained 21.5% of variance and model 2 explained 19.9% (**Appendices 2-17 & 2-18**). A positive correlation was found between Redfish density and depth (**Appendix 2-7**), but a negative correlation was found with invertebrate total density (**Fig. 2-5**). Highest predicted densities were associated with 'Sclerac-Kopho-Anthop', 'Kopho-Acti' and 'Sclerac-Penna' (**Fig. 2-6**). The model revealed highest predicted densities associated with hard-bottom substrate (**Fig. 2-7**). In addition, Redfish density was positively correlated with the densities of one tall *Anthoptilum* sea pen and one medium-size actiniaria, and negatively with *Pennatula* and one solitary scleractinia coral (**Table 2-6 & Appendix 2-19**).

Table 2-6 | Most dominant fish-invertebrate specific density relationships extracted from Model 2 (Eq. 2). + corresponds to a significant positive correlation between fish density and invertebrate density. – corresponds to a significant negative correlation between fish density and invertebrate density ($p < 0.05$). NS: Not significant. Statistics summary for all models are presented in the appendices.

Invertebrate taxon	Fish taxon				
	Witch Flounder	Marlin-Spike Grenadier	Longfin Hake	Redfish	Teleostei sp1
Pennatula spp.	NS	+	+	-	+
Flabellum spp.	NS	+	+	NS	+
Scleractinia sp1	NS	+	+	NS	+
Kophobelemnon sp.	+	NS	NS	NS	NS
Actinoscyphia sp.	NS	NS	NS	NS	NS
Scleractinia sp 4	+	NS	NS	-	NS
Anthoptilum spp.	NS	+	NS	+	NS
Cerianthid sp1	NS	NS	NS	NS	NS
Actiniaria sp6	+	+	+	+	NS
Nephteidae sp.	NS	NS	NS	NS	NS

Model 1 for Teleostei sp1 explained 42.5% of variance and model 2 (Eq. 2 using dominant invertebrate taxon densities as predictors, while accounting for station) explained 40.6% (**Appendices 2-20 & 2-21**). A non-linear relationship was found between Teleostei sp1 density and depth (**Appendix 2-7**). Higher predicted densities were associated within the 331-356 m depth range. Teleostei sp1 density was positively correlated with invertebrate total density (**Fig. 2-5**). Highest density was associated with one *Pennatula*-dominated habitat (**Fig. 2-6**). No influence of bottom type was found (**Fig. 2-7**). In addition, Teleostei sp1 density was positively correlated with the densities of three dominant invertebrate taxa of the *Pennatula* habitats (**Table 2-6 & Appendix 2-22**).

Overall, invertebrate taxon-specific densities were identified as the strongest predictors of fish densities for all taxa (higher predicted fish density), with additional influence of invertebrate total density for three fish taxa (Teleostei sp1, Marlin-Spike Grenadier and Witch Flounder), benthic habitat type for two fish taxa (Longfin Hake and Marlin-Spike Grenadier), and depth and bottom type for only one fish taxon (Redfish).

2-3.5 | Distribution maps and Getis-Ord hot-spot analysis

Using the Gi* statistic calculated on fish densities per 10-m segment for the five most dominant fish taxa, we compared the percentage of segments that presented significant positive and negative z-scores per benthic habitat type. Clusters of segments with a positive z-score formed hot-spot clusters, representative of an aggregation pattern (high densities), and clusters of segments with a negative z-score formed cold-spot clusters, representative of a dispersion pattern (low densities) (**Fig. 2-8**). Distribution maps of fish density frequency per station are presented in Appendix 2-23.

Witch Flounder presented a medium percentage of aggregation within the ‘Barren’ habitat (39%) and low percentages within ‘Sclerac-Kopho-Anthop’ and ‘Kopho-Acti’ (11 and 16% respectively). Witch Flounder also presented a medium percentage of dispersion within ‘Sclerac-Penna’ and low percentages of dispersion in all the other habitats (7 to 14%) (**Fig. 2-8A**).

Marlin-Spike Grenadier and Longfin Hake presented a high percentage of aggregation (71 and 95%) and no dispersion pattern within the ‘Sclerac-Penna’ habitat (**Fig. 2-8B & 2-8C**). Both taxa also presented a low percentage of aggregation within ‘Penna-Flab’ and ‘Sclerac-Kopho-Anthop’ (8 to 16%). Marlin-Spike Grenadier presented medium percentages of dispersion within all habitats except ‘Sclerac-Penna’ (19 to 34%). Longfin Hake presented high percentages of dispersion within the ‘Barren’ habitat and ‘Kopho-Acti’ (70 and 73%), and medium percentages of dispersion within ‘Penna-Flab’ and ‘Sclerac-Kopho-Anthop’ (40 and 53%).

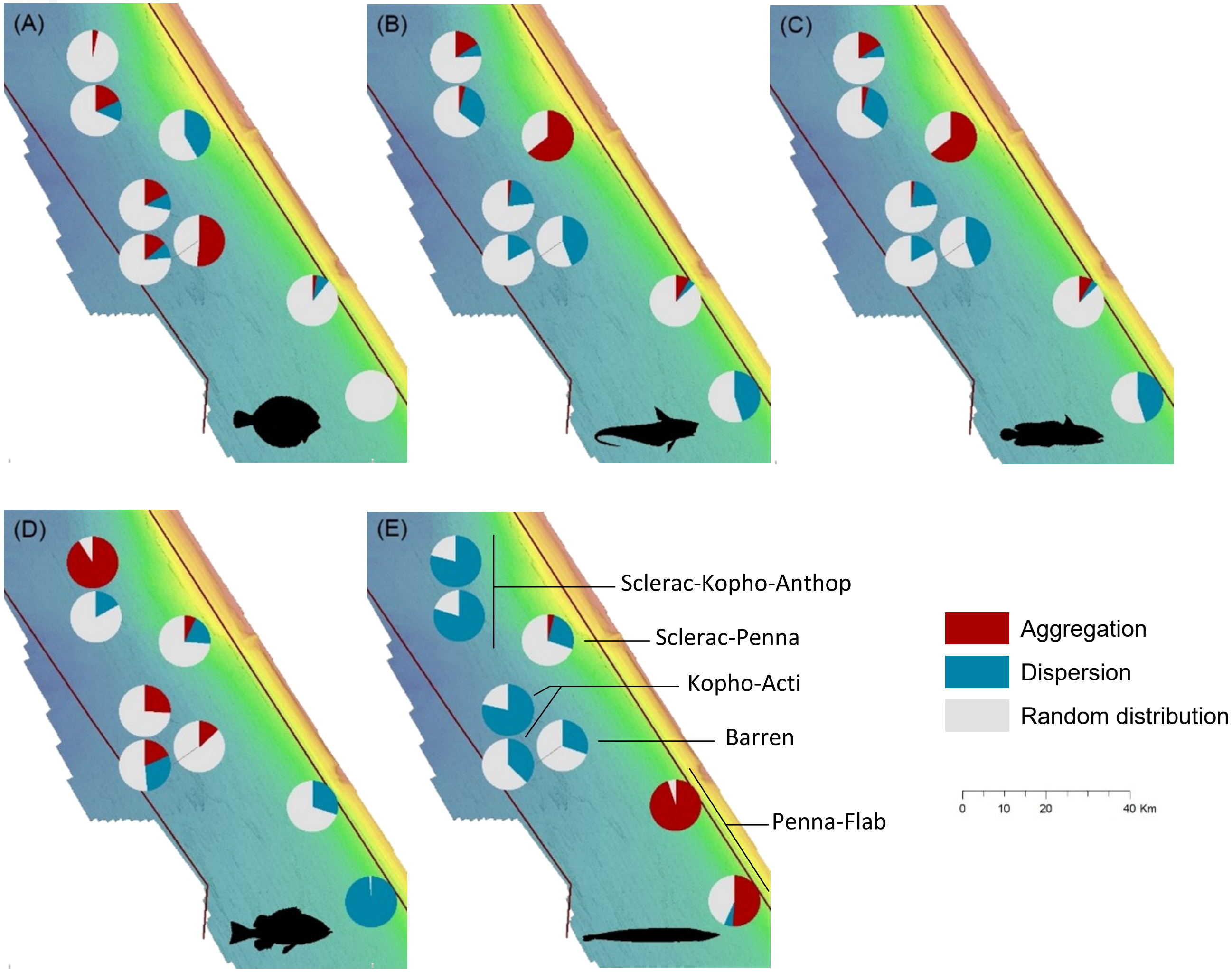

Fig. 2-8 | Distribution patterns across stations in the Laurentian Channel MPA of (A) Witch Flounder, (B) Marlin-Spike Grenadier, (C) Longfin Hake, (D) Redfish, (E) Teleostei sp1. Pie charts represent the percentage of 10-m segments that present an aggregation pattern (red), a dispersion pattern (blue) or a random distribution (grey) based on the Getis-Ord hot-spot analysis ran on fish densities. Clusters of segments with high fish densities formed hot-spot clusters, representative of an aggregation pattern, and clusters of segments with low fish densities formed cold-spot clusters, representative of a dispersion pattern. While most of the stations are dominated by one benthic habitat type, we differentiated the 'Barren' habitat from 'Kopho-Acti' at station LC13 (see Fig. 1-5 for station locations).

Redfish presented a medium percentage of aggregation within ‘Sclerac-Kopho-Anthop’ (44%) and low percentages of aggregation within the ‘Barren’ habitat, ‘Kopho-Acti’ and ‘Sclerac-Penna’ (7 to 24%). Redfish also presented a high percentage of dispersion within ‘Penna-Flab’ habitat (62%), low percentages of dispersion in all the other habitats (6 to 13%) and no aggregation pattern within ‘Penna-Flab’ and ‘Sclerac-Penna’ (**Fig. 2-8D**).

Teleostei sp1 presented a high percentage of aggregation within ‘Penna-Flab’ (61%) and low percentage within ‘Sclerac-Penna’ (4%). Teleostei sp1 also presented high percentages of dispersion within ‘Sclerac-Kopho-Anthop’ and ‘Kopho-Acti’ (63 and 79%), low percentages of dispersion in all the other habitats (19 to 31%) and no aggregation pattern in ‘Sclerac-Penna’, ‘Sclerac-Kopho-Anthop’ and ‘Kopho-Acti’ (**Fig. 2-8E**).

2-4 | Discussion

For this study on fish-habitat associations we developed several quantitative measures of benthic community attributes, focused specifically on epibenthic invertebrate taxa potentially contributing to habitat structure within soft-bottom ecosystems. A more detailed investigation on the distribution of benthic invertebrate community types within the Laurentian Channel MPA, based on the same ROV survey, was undertaken concurrently by de Mendonça & Metaxas (**2023, 2024**). Because our video processing strategy included different subsets of the ROV mission data, the invertebrate assemblage parameters described and used in this paper may differ from their study.

2-4.1 | Habitat heterogeneity

Based on multivariate analysis of invertebrates, identified concurrently with fish identifications along seven near-seabed video transects, we identified four habitats dominated by six CWCs and two sea anemones, and one non-structural habitat in the Laurentian Channel MPA, offering different levels of habitat complexity in a soft-bottom environment. Habitat heterogeneity was also provided by small-scale variations in the sediment, presumably of different origins such as hydrodynamics (*e.g.*, currents creating dunes), bioturbation (*e.g.*, burrows or depressions from faunal presence) or by the localized presence of scarce hard substrate. Overall, we found a greater level and extent of habitat heterogeneity than expected. Less than 3% of the study area covered was identified as non-structural (no physical or biological attributes). Moreover, in contrast to the common misconception that muddy/sandy bottoms are homogeneous and associated with low levels of epibenthic fauna (**Danovaro *et al*., 2014**), we found widespread and distinctive invertebrate-dominated habitats, with 95% of the area surveyed categorized as having epibenthic megafaunal invertebrate species presence.

2-4.2 | Fish assemblage

Here, we assessed groundfish distribution *in situ* with an underwater video system (UVS) in the Laurentian Channel for the first time, where fish surveys are traditionally conducted with scientific bottom trawls. The fish diversity observed by the ROV was similar to the fish diversity surveyed by bottom trawl in the channel from 1996 to 2009 (**Kulka & Templeman, 2013**), with 15 of the 22 species identified by trawl common to the ROV survey. Additionally, the relative contribution of fish surveyed by the ROV was very similar to bottom-trawl assessments, with four of the five most dominant taxa observed on videos being among the five most dominant fish species caught by trawl (*i.e.*, Redfish, Longfin Hake, Witch Flounder and Marlin-Spike Grenadier). Two fish taxa contributed to dissimilarity between these two survey datasets. Teleostei sp1 was identified as the fifth most dominant taxon on the ROV videos, while we observed only one Black Dogfish (*Centroscyllium fabricii*) during the same survey. Conversely, Black Dogfish was identified as the second most dominant species in the 1996-2009 trawl survey, while neither Sandlance nor Barracudina were identified as one of the 22 abundant taxa of the assemblage.

Differences in fish assemblages caught by different gear can be explained by various factors. Geographic survey location can bias observations as some fish species have very localized areas of distribution within the channel (*e.g.*, Black Dogfish and Northern Wolffish (*Anarhichas denticulatus*) mostly found in the northern half of the MPA). Seasonal and annual variability can contribute to differences in fish assemblages; while bottom-trawl surveys are generally conducted in April/May in the area, our ROV videos were recorded in September. Finally, gear selectivity can bias results as some fish species are more likely than others to escape bottom trawl or UVS. For instance, Sandlance and Barracudina are elongated fast swimmers, mostly found in the water column or burying and hiding in the soft sediment, whose abundances are often underestimated by scientific bottom trawls (**Harry, 1953**).

Using univariate analyses we examined if and which biotic and abiotic parameters contributing to habitat heterogeneity were predictors of fish distribution, focusing our study on the five most dominant fish taxa observed. We found evidence of the influence of habitat abiotic and biotic features on fish in a soft-bottom environment, but the fish-habitat associations were not as strong as associations in hard-bottom deep-sea CWC ecosystems.

2-4.3 | Influence of depth on fish density

In spite of the small depth range in the study area, depth was identified as a co-dominant factor of distribution for all fish taxa. These results are in alignment with the known preferred depth distributions of the four identified taxa (**Powles & Kohler, 1970 | Langton & Bowman, 1980 | Savvatimsky, 1989 | Cargnelli, 1999 | Pikanowski *et al.*, 1999 | Baker *et al.*, 2012a***).* In the case of Teleostei sp1, consistency with known specific depth distributions is contingent on confirmation of whether this morphotype consists of Sandlance, Barracudina, or a combination of the two (**Post, 1990 | Robards *et al.*, 2000**).

In bottom-trawl surveys conducted from 2015 to 2019 in the Laurentian Channel, higher Sandlance densities have been reported on the eastern bank than at any other location (6 out of 138 surveyed areas, **Appendix 24A**). Sandlance aggregations in waters deeper than 200 m are not generally observed (**Robards *et al.*, 2000**). On the other hand, Barracudinas were found in more locations within the channel (33 out of 138 surveyed areas, **Appendix 24B**), at various depths and in similar local densities to those recorded by the ROV for Teleostei sp1, *Arctozenus* sp. or *Paralepis* spp. Barracudinas are most often found between 200 and 1000 m, along upper slopes, canyons, and canyon heads

(**Mundy, 2005**). These results suggest that both taxa co-exist in the channel, displaying different but overlapping areas of distribution according to their preferred depth range.

Influence of depth on fish distribution is common, although most studies found depth influence at a larger spatial and bathymetric scale, with distinct fish assemblages found at different depth zones and water masses (*e.g.*, continental shelf, slope and mid-slope) (**Koslow *et al*., 2000 | Lorance & Trenkel, 2006 | Buhl-Mortensen *et al*., 2010 | Kenchington *et al*., 2010 | Baker *et al*., 2012a | Henderson *et al*., 2020***)*. Large scale gradients still play an important role at a finer resolution, although the relationships that link fish distribution to depth are not fully understood (**Hewitt *et al*., 1998 | Baker *et al*., 2012b**). Current theories concerned with fish community shifts with depth suggest that depth captures the combined influence of biotic (*e.g.*, food availability, productivity) and abiotic factors (*e.g.*, temperature, current regime differences, changes in topography and sediments) (**Koslow *et al*., 2000 | Baker *et al*., 2012a**).

2-4.4 | Influence of substrate on fish density

Lacharité *et al*. (**2020**) characterized eight large-scale benthoscapes in the Laurentian Channel MPA based on four environmental parameters: depth, slope, and density of iceberg scours and pockmarks. Their classification was ground-truthed with small-scale sediment samples and underwater imagery. We found a similar spatial contribution of surficial sediments as described in their study, with most of our stations being covered in fine muddy/sand sediment and a slightly higher percentage of hard-bottom features found at station LC04 (presence of gravel in benthoscape A2 (**Lacharité *et al*., 2020**)). The two stations located in this pockmark-dominated benthoscape (LC04 and LC14) were the only two stations highly dominated by soft-bottom micro-habitat features (depressions, burrows and dunes) (**Fig. 2-2A**).

We found a taxon-specific influence of soft-bottom micro-habitat features as well as hard-bottom substrate on fish density. These results suggest that substrate features were not high predictors of fish distribution. The influence of soft-bottom micro-habitat features on fish distribution has been reported in other studies, where fish-habitat associations were linked to additional factors.

Auster *et al.* (**1995**) reported that 75% of all the fish species they studied, including Longfin Hake and Witch Flounder, showed non-random associations with biogenic depressions and burrows at three depths on the continental shelf and upper slope off southern New England. Differences in use of soft-bottom micro-habitat features were linked to diurnal feeding-related migrations and ontogenetic life stages. Although they defined the relationship as facultative, as fish were also found associated with other substrates and micro-habitats, they attributed this behavior as a way to reduce predation and enhance prey capture. The size of physical structures could play an important role for more sensitive early life stages. For instance, Diaz *et al*. (**2003**) found a strong positive correlation between juvenile fishes and size of micro-habitat features in a soft-bottom shallow environment, with more fish being associated with features taller than 30 cm.

Surprisingly, while both Longfin Hake and Redfish were encountered within similar depressions during our video survey, our analysis revealed that Redfish density was negatively related with soft-bottom micro-features; conversely, Redfish density was found positively associated with hard substrate. Evidence of small depression use by two Redfish species was suggested in the Northwest Atlantic (**Templeman, 1959**) and proved within three depth zones within Monterey Bay, California for five related rockfish species (**Hallenbeck *et al*., 2012**). Notably, Hallenbeck *et al*. (**2012**) found that more early life-stage rockfish and flatfish were associated with depressions, suggesting a potential use of those features as nurseries to shelter from currents and predators. While showing a great flexibility in substrate affinity within their preferred depth zones (**Templeman, 1959 | Haldorson & Love, 1991 | Henderson *et al*., 2020**), Redfish are typically associated with complex rocky structures, which are thought to be used to avoid or reduce predation (**Richards, 1986 | Shepard *et al.,* 1986 | Haldorson & Love, 1991 | Love *et al*., 2002 | Du Preez & Tunnicliffe, 2011**).

Within our study area, we identified one local aggregation spot (700 m^2) of Redfish in the only area where tall boulders and gravel were present; however, no specific pattern of distribution associated with small, isolated boulders in muddy sediments was observed. Similarly, Du Preez & Tunnicliffe (**2011**) found a strong positive correlation between rockfish abundance and the percent area of higher substrate relief; these results suggest that high cover of hard-bottom substrate could attract a larger Redfish population.

Moreover, the Getis-Ord analysis revealed a small aggregation patch of Redfish in the 'Barren' habitat (invertebrates absent), although no specific connection with any bottom type was found. Interestingly, this 'hot spot' was located in a small valley-like environment and thus the observation may be linked to the broader-scale topography. The influence of habitat physical heterogeneity at several spatial scales on *Sebastes* spp. was demonstrated by Anderson *et al*. (**2009**) on Cordell Bank off the coast of California. Their study showed that rockfish distribution was strongly correlated with fine scale heterogeneity (1-10s of m) within the broad-scale landscape. Their results indicated that considering the spatial configuration of the small-scale habitat characteristics within the broader-scale landscape was important to predict fish assemblages and assess habitat association.

While we found a weak influence of substrate on fish density, strong associations between fish taxa and specific bottom types demonstrated in other studies suggest that other habitat factors might better explain fish-habitat relationships (*e.g*., larger-scale parameters such as bottom current or topography, size or density of abiotic habitat features, and habitat cover).

2-4.5 | Influence of biotic parameters on fish density

In order to understand the importance of epibenthic invertebrates for fish, we conducted a multi-statistical univariate approach on fish specific densities. The analysis revealed that soft-bottom benthic habitat types and invertebrate density have a taxon-specific influence on fish distribution, but are not strong predictors of fish densities. Higher fish densities were predicted in benthic habitat types compared to barren areas, but not always with the densest invertebrate assemblages, nor with the most dominant invertebrate taxa of the assemblages.

Conversely, similar studies conducted in deep-sea rocky-bottom environments and cold-water coral reefs demonstrated preferred associations of groundfish with denser benthic structures. Henderson *et al*. (**2020**) found evidence of increased probability of rockfish presence with increased densities of the gorgonian *Plumarella longispina*, the reef-forming scleractinians *Lophelia pertusa* or sponges in the Southern California Bight, off the west coast of North America. Similarly, abundance of *Nezumia baiirdi* was positively correlated with abundance of the small gorgonian *Acanella* sp. In both soft and hard-bottom environments, in deep canyons off Newfoundland, Canada (**Baker *et al*., 2012b**).

We opted to assess the influence of benthic feature size by comparing the influence of specific dominant invertebrate taxa densities to explain fish distribution. CWC taxa, specifically sea pens and solitary cup corals, dominated all invertebrate assemblages surveyed, which made it difficult to assess the importance of CWC habitats in comparison to other invertebrate assemblages. We also compared the influence of specific invertebrate taxa to help us assess 1) the influence of CWC taxa *vs.* other potentially habitat-forming invertebrate taxa and 2) the influence of sea pen taxa *vs*. other CWCs. The influence of invertebrate size on fish was taxon-specific and not exclusive, as only a few fish showed positive associations with invertebrate of different sizes. Our results suggest that invertebrate size cannot be defined as a strong fish distribution predictor in this soft-bottom environment. Of all fish species, Redfish showed the strongest affinity for tall invertebrates, particularly *Anthoptilum* spp. These findings are in agreement with many reports of strong associations of *Sebastes* species with tall structure habitat-forming invertebrates in hard-bottom ecosystems (**Buhl-Mortensen *et al*., 2005 | Du Preez & Tunnicliffe, 2011 | Henderson *et al*., 2020**).

Within CWC habitats, in addition to coral density, habitat cover and coral height were also often cited as the main driver of Redfish distribution (**Starr *et al*., 1995 | Diaz *et al*., 2003 | Buhl-Mortensen *et al*., 2005 | Du Preez & Tunnicliffe, 2011**). Juvenile fishes were found to be quantitively more associated with both habitat size and the number of biogenic structures in a soft-bottom shallow environment off the northeastern coast of the USA (**Diaz *et al*., 2003**). Large and tall gorgonians *Primnoa* sp. and *Paragorgia* sp. create highly complex reef habitats in the Northeast Atlantic, offering a multitude of small niches thought to be used by *Sebastes* fish as shelter against currents and predators (**Buhl-Mortensen *et al*., 2005**). Similarly, in the macrotidal setting of Learmonth Bank, British Columbia, the majority of Redfish observed in ROV surveys was found near sponges >50 cm-tall or associated with the large gorgonian *Primnoa pacifica* >30 cm-tall (**Du Preez & Tunnicliffe, 2011**). It was hypothesized that these tall structures might provide shelter from current or help with Redfish feeding behavior (**Tissot *et al*., 2006 | Auster, 2007 | Quattrini *et al*., 2012**). Henderson *et al*. (**2020**) showed that in deep environments off the west coast of North America, year-one Redfish were found closer to tall corals, suggesting the size of habitat-forming invertebrate could be important rearing areas for certain, more vulnerable life stages.

We did not find any specific influence of CWCs compared to other invertebrates, as all fish assessed were positively associated with at least one CWC and one actiniaria taxon. Similarly, we did not find any specific influence of sea pens compared to other CWCs, as several fish were positively associated with one sea pen and one scleractinia taxa. Yet, no specific association between fish and nephtheid soft coral was found. The importance of several taxa of soft corals for fish has been demonstrated in other studies conducted in soft and hard-bottom ecosystems (**Krieger & Wing, 2002 | Buhl-Mortensen *et al*., 2005 | Edinger *et al*., 2007**). Finally, we found a taxon-specific influence of sea pens on fish distribution, with *Anthoptilum* spp. and *Pennatula* spp. having a stronger influence on fish than *Kophobelemnon* sp. Those associations could be linked to *Anthoptilum* spp. being taller and *Pennatula* spp. denser than *Kophobelemnon* sp. These results suggest that soft-bottom CWCs have a taxon-specific influence on fish distribution, but the fish-CWC relationship is not exclusive and not as strong as expected, compared to associations in hard-bottom deep-sea CWC ecosystems.

The importance of CWCs for fish in both hard and soft-bottom environments has been debated and demonstrated in many studies (**Auster, 2005 | Edinger *et al*., 2007 | Du Preez & Tunnicliffe, 2011 | Baillon *et al.*, 2012a | Baker *et al*., 2012b | Henderson *et al*., 2020**). The assessment of fish-habitat association conducted by Linley *et al*. (**2017**) using a baited camera across four European study sites from the Norwegian Arctic to the Mediterranean Sea supported strong relationships of fish with CWC habitats. Despite latitudinal differences, higher fish abundances and diversity were recorded in coral habitats than in non-coral habitats. These results are not unique: fish diversity and abundances have been positively associated with hard-bottom small scleractinarian and dense corals, respectively (**Edinger *et al.*, 2007**). Strong fish-coral associations have been found between rockfish and gorgonian *Primnoa* sp*.* in the Gulf of Alaska (**Krieger & Wing, 2002**), or between juvenile Redfish and sea pens in the Laurentian Channel and Southwest Grand Banks region (**Baillon *et al*., 2012**). CWC assemblages dominated by *Anthoptilum* and *Pennatula* sea pens were identified as important nursery habitats for Redfish.

On the other hand, as previously mentioned, not all studies have reported positive associations between fish and CWCs. For instance, Baker *et al*. (**2012a**) found differences in fish assemblages between sea pen fields, highly complex habitats and scleractinian fields in three submarine canyons on the slope of the Grand Banks south of Newfoundland, but not with other coral and sponge habitats. No distinct fish assemblages were found associated with dense coral habitats when compared to other equivalent epifauna habitat or less complex hard-relief habitat (**Auster, 2005**).

For most of the fish taxa we analyzed, our results are in agreement with studies that have suggested a coincidental co-occurrence of fishes and habitats created by invertebrate taxa. Facultative relationships, rather than obligate, are expected for fish-invertebrate associations. CWCs likely provide important, and perhaps preferred, habitats for fishes, but not exclusive habitats.

2-4.6 | Notable patterns of fish distribution across benthic habitat types

The most recent study of fish-sea pen association in the Laurentian Channel found that Redfish (*S. mentella* and *S. fasciatus*) larvae collected by bottom trawl were consistently found within diverse sea pen habitats, notably dominated by *Anthoptilum* spp. (**Baillon *et al.*, 2012**). Redfish larvae were more abundant on corals collected in April than in May, but the biomass trend was the reverse, presumably as the larvae grew. *Anthoptilum* habitats were assumed to be used as spawning, nursing and shelter areas (**Baillon *et al.*, 2012**). On the other hand, no positive correlation between adult Redfish and sea pen abundance was reported. Our results support conclusions made by Baillon *et al*. (**2012**) about the facultative importance of *Anthoptilum* spp. to Redfish. Here, however, we have provided for the first time direct evidence of an association between Redfish and *Anthoptilum* spp. in September. This suggests that Redfish continue occupying sea pen habitats months after spawning, commonly using them for more activities than as nursing grounds.

Interestingly, Teleostei sp1 was the taxon showing the strongest association for one benthic habitat type. The three univariate-approach analyses demonstrated the affinity of Teleostei sp1 for the densest *Pennatula* habitats found mostly above 350 m, as well as for all three most abundant invertebrate taxa contributing to the benthic habitat type. It is difficult to determine in this study which of Sandlance or Barracudina would be more likely to be associated with *Pennatula* habitats due to their potential overlapping area of distribution in the channel. Sandlance are commonly found in shallow depths (up to 100-200 m off the southeast coast of Newfoundland), but shift to deeper waters in the summer (**Robards *et al.*, 2000**). Moreover, Sandlance bury themselves in the sediment when they are not feeding in the water column, and are therefore more dependant on fine-grained substrates (they display a high affinity for coarse sand) (**Bizzarro *et al.*, 2016**). Although our GAMs did not show any specific influence of bottom type for Teleostei sp1, the densest *Pennatula* habitat that Teleostei sp1 were strongly associated with, was located within the only bare mud area with no soft-sediment micro-habitat features (**Fig. 2-2A**).

Here, we did not consider grain size in our analysis, as fine grain size and difference between mud and sand percentages is difficult - if not impossible - to assess from underwater videos. A grain size assessment was conducted from *in-situ* push core sediment samples collected during the R2017 survey (**Miatta & Snelgrove, 2021**). Sediment composition did not vary between stations, with silt and clay being the two most dominant sediment types. These results suggest that influence of fine grain size is unlikely to explain fish distribution across the channel. Moreover, more data would need to be collected, as the *in-situ* sediment sampling was very sparse and did not match the spatial scale we used to assess fish distribution in relation to habitat characteristics.

Due to low abundances sampled by bottom trawl and difficulty to distinguish species from the same family, Barracudina are often overlooked in surveys, and little is known about their ecology (**Harry, 1953 | Davis, 2010**). However, stomach content analyses indicate that both Sandlance and Barracudina are forage taxa for many predators, including sharks, squids or other groundfish species (*e.g.*, Atlantic Cod, Pollock, Redfish, Flounder) (**Robards *et al.*, 2000 | Moteki *et al.*, 2001 | Preti *et al.*, 2008**). These studies suggest that both Sandlance and Barracudina might be key species and play a similar ecological role in the Laurentian Channel, supporting the need for future surveys to examine their potential relationship with *Pennatula* habitats.

It is difficult to establish if the co-occurrence of Teleostei sp1 and *Pennatula* is coincidental (*e.g.*, overlapping of their respective areas of distribution, shared preference for similar sediment types) or causative (Teleostei sp1 presence positively related to *Pennatula* fields), as we do not know the extent of Teleostei sp1 and *Pennatula* field distributions, nor if there are other benthic habitat types in the same depth range. Future dedicated studies could consider increasing the study area extent, while assessing fine-scale sediment influence, accounting for seasonality, and incorporating additional sampling approaches to better define the relative distributions of Sandlance and Barracudina.

Witch Flounder was the fish taxon the least influenced by the habitat attributes we analyzed. Our statistical analysis did not highlight the influence of bottom type or benthic habitat type, yet our models showed weak associations of Witch Flounder with invertebrate attributes, such as total density and specific invertebrate taxa. Based on the comparison of trawl samples within depth strata, Edinger *et al*. (**2007**) found a statistical relationship between Witch Flounder and sea pens, but suggested it could reflect a shared habitat preference for muddy environments in the Laurentian Channel. Here, our results also suggest this shared habitat preference, without a strong direct biological association between sea pens and Witch Flounder.

The Getis-Ord hot-spot analysis revealed small-scale aggregation patches for Witch Flounder, within the 'Barren' and 'Kopho-Acti' habitats. The two habitats are located at the same station, with the 'Barren' habitat representing a small patch (<1 ha) within the invertebrate assemblage. We assume that other environmental factors could explain this pattern. For instance, Diaz *et al*. (**2003**) suggested that proximity between habitats of different complexity was linked to the diurnal use of habitats by juvenile fishes. Indeed, fish were suggested to use complex habitats as refuges from predation during the day, and simpler habitats as foraging areas at night

While we found a weak influence of benthic habitat types and invertebrate taxa on fish density, strong associations between these factors and fish taxa demonstrated in other studies suggest that other variables might better explain fish-habitat relationships (*e.g.*, seasonality, time of day, fish size, fish prey-predator relationships, and habitat cover).

Overall, we did find evidence for the influence of biotic and abiotic habitat features on fish distribution in soft-bottom environments, and also, of specific invertebrate taxa. However, specific habitat features could not be defined as general predictors of fish distribution. As the range of habitat heterogeneity in soft-bottom environments is not as great as that found in hard-bottom ecosystems, it is not surprising that habitat-related responses of fish are weaker and more variable. It is likely that other factors not included in this study may have a greater influence on fish distribution and, in aggregate, may better explain fish-habitat associations. In addition, reasons for weak fish-habitat relationships could include the lack of benthic habitat type diversity (*e.g.*, *Pennatula* fields in the shallow depth range), the potential shared area of distribution (depth-related) of specific fish and invertebrate taxa, or that we may not have surveyed the preferred area of distribution of specific fish taxa (*e.g.*, Black Dogfish and Marlin-Spike Grenadier more abundant at higher latitudes in the channel).

2-4.7 | Monitoring and conservation implications

The use of ROV surveys in the Laurentian Channel MPA contributed to the acquisition of novel valuable data on small-scale fish-habitat relationships in a deep-sea soft-bottom environment. Traditionally, surveys of demersal fish species are conducted with mobile or fixed bottom-tending gear, especially bottom trawls. In Atlantic Canada, data on commercial and non-commercial fish and invertebrate species are collected during multispecies annual trawl surveys, yielding information on fish distribution and abundance, population dynamics, community structure and habitat associations (**Stoner *et al.*, 2008 | DFO, 2015a**). Although this tool provides valuable data, its use in MPAs is controversial due to their impacts on the habitat being conserved (*e.g.*, habitat destruction, resuspended sediment, and fauna removal) (**Auster, 2005**). Moreover, because trawl surveys generally cover a large spatial scale (*e.g.*, 1.5 km per tow in the Northwest Atlantic), small-scale processes to which fish respond (~m to 100-m scale) are often masked (**Edinger *et al.*, 2007 | Baker *et al.*, 2012a**), which can lead to knowledge gaps or misinterpretation.

Underwater video systems, such as ROVs, are effective non-destructive and non-extractive monitoring tools that can be deployed in both trawlable and non-trawlable areas, and assist in reducing those knowledge gaps (**Graham *et al.*, 2004 | Pacunski & Palsson, 2008 | Stoner *et al.*, 2008 | Sward *et al.*, 2019**). The use of video-based surveys can provide additional *in-situ* observations on fish habitat use, community composition and behaviour in structurally complex habitats and at a finer spatial scale (**Trenkel *et al.*, 2004 | Lorance & Trenkel, 2006 | Ross & Quattrini, 2007 | Clark *et al.*, 2016**). Moreover, UVSs have been shown to capture higher fish densities in deep-sea environments than bottom trawls (**Ayma *et al.*, 2016 | Chimienti *et al.*, 2018)**. Factors than can limit trawl efficiency at capturing accurate fish abundance estimates are related to gear selectivity as well as fish specific biology and ecology (**Engås, 1994**).

ROVs have been proven to be a very efficient monitoring tool that meet MPAs' conservation goals (**Field *et al*., 2006 | Stoner *et al*., 2008**). However as with any survey gear, there are limitations in using UVS to record mobile fauna, especially fish, that can potentially bias results. Fish are known to react to UVS which can induce *in-situ* observation bias. Their behavioral responses, including avoidance, attraction or no reaction have been well documented **(Trenkel *et al*., 2004 | Stoner *et al*., 2008 | Laidig *et al*., 2013** | **Sward *et al*., 2019**). The type and intensity of fish reactions to UVS can be influenced by many variables including fish species, trophic position, body size, mobility or position above the seafloor, as well as environmental conditions such as habitat, substrate, temperature or current speed. Different aspects of UVS such as the type of vehicle, light, motion, speed, noise or water displacement can also alter fish natural behavior (**Lorance & Trenkel, 2006 | Stoner *et al*., 2008 | Ryer *et al*., 2009 | Uiblein, 2011 | Sward *et al*., 2019**).

In addition, due to fish mobility, UVS-based surveys must also be designed to limit fish abundance overestimation. Sward *et al*. (**2019**) presented a selection of common ROV survey designs used in many studies to visually assess fish assemblages and recommended optimal transects to be designed in consideration of species-specific distributions and characteristics. For instance, aggregating species are more likely to react to UVS than species presenting a dispersed or more random distribution pattern, increasing the risk of abundance overestimation. Following a straight-line trajectory across depth, substrate or habitat gradients can reduce this bias, and appears to be the most suitable transect design to observe fish *in situ* and study fish-habitat relationships. Multiple parallel transects are common as well and allow for a greater replication. Moreover, although they did not specify any transect length, the longer the transect, the greater variety of habitats encountered and the higher chance to observe rare or cryptic species, as well as those presenting a patchier distribution.

Another common limitation related to video-based surveys we faced was the inability to identify some fish at a low taxonomic level (*i.e*., species, genus or family), based on morphological characteristics only. Taxonomic identification from video footage is challenged by many factors such as environmental conditions (*e.g*., turbidity), the imaging system resolution, aspect and distance at which individuals are encountered, their position in the water column and their reaction to UVS. It is therefore usual to identify taxa at a higher taxonomic level and refer them as morphotypes or morphospecies. For instance, Teleostei sp1 was relatively small compared to other groundfish (< 30 cm long, 2 cm wide), and commonly reacted to the ROV (*e.g.*, quickly swam away from ROV/field of view), which limited our ability to verify its taxonomy and resulted in grouping two morphologically similar taxa, belonging to different families together. Depending on the objectives of the study, such a simplification can further limit analyses and understanding of ecosystem relationships. In those instances, it is common to group taxa into functional groups (**Tilman, 2001**), combining taxa that share similar functional, morphological and/or life history traits, habitat requirements or place in the trophic chain (**Ladds *et al.*, 2018**).

Though grouping taxa into morphological and/or functional morphotypes seems to be a suitable approach in the case of Teleostei sp1, this approach proved to be limited for other taxa. Indeed, we grouped two species of skates together known to occur in the channel (Thorny Skate and Smooth Skate) as we could not differentiate them from the imagery mainly due to their behavioral reactions toward ROPOS (*i.e.*, tendency to swim away from ROV/field of view and/or to create sediment plumes to hide and camouflage). Smooth Skate is one of the six protected species included in the MPA conservation objectives, and thus the pairing of this species with another limited our efforts to inform on its distribution and habitat associations in the channel using underwater imagery data only. Combining imagery sampling with minimal complementary physical sampling (*e.g.*, dredges and trawls), as well as increased collaboration with expert taxonomists, may present efficient solutions to mitigate this bias.

Getis-Ord hot-spot statistical analysis was a useful tool to quickly and easily visualize small-scale patterns of fish distribution in relation to habitats based on *in-situ* underwater video observations. We were able to develop small-scale fish and habitat distribution maps in the Laurentian Channel MPA and generated predictive data that could be used to feed species distribution models (SDM). SDMs provide a robust method to identify species drivers of distribution and locate taxa suitable habitat and where important ecological processes occur. The identification and location of fish-habitat relationships is valuable data that could inform MPA managers and support conservation measures (**Rosenberg *et al.*, 2000 | Henderson *et al.*, 2020**).

Conservation and research objectives of the MPA include 1) the protection of six species of interest including sea pens, Black Dogfish, Smooth Skate, Northern Wolffish and Porbeagle Shark (*Lamna nasus*), and 2) the identification of sensitive marine benthic areas and habitats (**Lewis *et al.*, 2016**). However, the Laurentian Channel MPA is not well studied, and several knowledge gaps have been identified in the understanding of the ecosystem's function, structure and processes.

Here we provided valuable information that can help address some of the MPA goals and contribute to the assessment of the MPA management effectiveness. Northern Wolffish was not observed by ROPOS in 2017, but the ROV encountered one Porbeagle shark, one Black Dogfish and 170 undifferentiated skates. They were numerically too few to conduct specific statistical analyses, but we were able to add information on the distribution of those fish taxa at local and regional scales.

While sea pens are a particular conservation target for the MPA, there is little known beyond correlative observations (*e.g.*, higher diversity of fish in trawl sets associated with high bycatch of sea pens) in terms of understanding the ecological and functional role of sea pen assemblages as habitat for fish (**Auster, 2007**). The five fish taxa on which we focused this study were the most abundant taxa of the assemblage but are not key species targeted by the MPA protection measures. Despite having not found strong associations for all five fish taxa with CWC habitats, nor with sea pen habitats, our results did reveal weak, insofar unexplained relationships.

Several Sensitive Benthic Areas (SBA), equivalent to VME habitats outside Canadian waters, have been identified for sea pens in the Laurentian Channel and most of them are now protected within the MPA (**FAO, 2009 | Kenchington *et al.*, 2011, 2016**). In order to identify SBAs, benthic habitats must be first designated as Ecologically and Biologically

Significant Areas (EBSA) (*i.e.*, habitat features or structures provide essential biological and ecological function), following similar criteria necessary to the identification of VMEs (**FAO, 2009**). The second step is the determination of habitat sensitivity to risks of serious or irreversible harm induced by fishing activity (**DFO, 2004**). In light of sea pen habitats status, our study supports the necessity to continue monitoring the MPA using *in-situ* UVS, especially in SBAs where the use of trawls is not suited. Moreover, we suggest that the MPA objectives should be extended to include the protection of coral habitats rather than protecting sea pen species only, which would bring benefits for groundfish.

2-5 | Conclusion

This study revealed that small-scale heterogeneity of specific biotic and abiotic habitat features in a soft-bottom environment has a taxon-specific influence on fish distribution, but not as strong as heterogeneity in hard-bottom ecosystems. Nonetheless, our results suggested that CWC taxa, including sea pens, in soft-sediment environments have a stronger influence on groundfish abundance and distribution than other invertebrate taxa and than abiotic features. Overall, the attributes we tested were not strong predictors of fish distribution, suggesting more factors would need to be considered to understand the links between fish and habitats. Finally, the ROV has proven to be an efficient, non-destructive tool to assess *in-situ* fish small-scale distribution in association with habitat features.

Chapter 3

Local size structure and distribution of groundfish in relation to sea pens and other benthic habitats in a deep-sea soft-bottom environment[2]

Abstract

Many fish species undergo ontogenetic habitat shifts as they grow to fulfill new biological, ecological and environmental requirements. While relationships between fishes and large hard-substrate cold-water corals (CWC) (*e.g.*, *Desmophyllum pertusum* reefs) have frequently been studied, there are relatively fewer studies examining the relationships of fish with habitat provided by smaller corals (*e.g.*, sea pens) in soft-bottom environments. Despite this knowledge gap around soft-bottom corals, growing evidence of their importance has nonetheless justified their inclusion as conservation targets in numerous Marine Protected Areas (MPA), including the Canadian Laurentian Channel MPA.

Here, we performed ROV and near-seabed drift-camera system surveys within the Laurentian Channel MPA in 2017 and 2018 to assess the influence of fish body size and habitat type on fish small-scale distribution in a low-relief deep-sea soft-sediment environment. We compared the local size structure of the four most abundant deep-sea groundfish taxa of the channel (Redfish (*Sebastes* spp.), Witch Flounder (*Glyptocephalus cynoglossus*), Marlin-Spike Grenadier (*Nezumia bairdii*) and Longfin Hake (*Phycis chesteri*)) across one barren and five structural benthic habitats defined by the presence of nine dominant epibenthic invertebrates (actiniarians and CWCs). We used generalized additive models to identify biotic (benthic habitats) and abiotic (depth, bottom types) covariates of size for each taxon.

We observed 15,381 fish within the 43.6-ha study area, of which 7,511 fish were measured. Juveniles represented 99% of all fish measured, with a notable increase in average fish size in 2018. While we did not find any associations between benthic habitats

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and fish life stages, the analysis revealed a significant increase in fish size within sea pen habitats for all four taxa. Conversely, we found a taxon-specific influence of bottom type on fish size for all taxa. In addition, Redfish and Longfin Hake size was positively correlated with depth.

For deep-sea groundfish taxa of the MPA, our results suggest that 1) sea pens provide nursery habitat for early-life stages, 2) fish undergo ontogenetic shifts in micro-habitat use and specialization, and 3) fish-habitat associations appear to be facultative rather than obligate. Through the use of *in-situ* video data, this study provided evidence that small and large fish do not use the same micro-habitats, and that sea pens contribute significantly to fish habitat despite providing less habitat heterogeneity than reef-forming scleractinians or large gorgonians. These results contribute to empirical understanding of fish-habitat relationships at different fish life stages and may inform fisheries management, as well as monitoring efforts in the MPA and other protected deep-sea environments.

3-1 | Introduction

Body size has been recognized as one of the most important biological traits for organisms, including for fish, as it has a great influence on many aspects of their physiology and ecology (*e.g.*, fitness, community dynamics) (**Elton, 1927 | Wootton, 1979 | Peters, 1983 | Reiss, 1988 | Cohen *et al.*, 1993 | Kingsolver & Pfennig, 2004, 2007**). As fish individuals age and develop, they require different resources for growth, reproduction and survival. Therefore, fish undergo multiple ontogenetic shifts associated with increase in body size over their lifespan (**Saborido–Rey & Kjesbu, 2005**). These shifts tend to occur in fish as larvae metamorphose into small juveniles and before they reach their final adult morphology and sexual maturity (**Pittman & McAlpine, 2003 | Bergstad, 2009**).

Size specific shifts are often associated with changes in fishes' morphology, species interactions, diet, position in the trophic chain, swimming abilities, vulnerability to predation, and habitat selection (**Warner & Schultz, 1992 | Persson *et al.*, 1996**). Ontogenetic habitat shifts are vital for fish to fulfil their life-history functions as different habitats provide access to a variety of resources, and will determine fish recruitment, optimize their growth rates and reduce mortality risks (**Olson, 1996 | Grober-Dunsmore *et al.,* 2009 | Sheaves, 2009**).

Moreover, ontogenetic habitat shifts have also been linked to shifts in habitat specialization. Indeed, individuals of different sizes do not display the same vulnerability to stressors during their lifespan, and it is therefore suspected that early-life stages are more habitat-dependent than adults (**Werner & Gilliam, 1984 | Olson, 1996**). Small fish are often restricted to structurally complex micro-habitats that provide shelter, small prey availability, and protection from predation (**Auster *et al.*, 2005 | Costello *et al.*, 2005 | Etnoyer & Warrenchuck, 2007 | Moore *et al.*, 2008 | Roberts *et al.*, 2009**). Conversely, certain large fish can be less specialized, as they have greater mobility and capacity to cover large distances, and can therefore take advantage of a wider range of habitats than small fish (**Bergstad, 2009**).

An important factor that influences fish distribution at specific life stages is habitat heterogeneity and complexity. At the local scale, habitat heterogeneity provided by both physical (*e.g.*, variation in sediment type and topography) and biological features (*e.g.*, habitat-forming invertebrates) can serve as refuge, feeding, resting and nursery areas for many groundfish species (**Auster *et al.*, 1995 | Costello *et al.*, 2005 | Stone, 2006 | Roberts *et al.*, 2009 | Hallenbeck *et al.*, 2012 | Stone, 2014**). Fish-habitat relationships have been broadly studied in hard-bottom ecosystems, and specifically in cold-water coral (CWC) habitats (**Edinger *et al.*, 2007 | Biber *et al.*, 2014 | Ross *et al.*, 2015 | Arnaud-Haond *et al.*, 2017 | D'Onghia, 2019 | Devine *et al.*, 2020**). Conversely, there is comparatively limited knowledge about the importance of physical and biological features in soft-bottom ecosystems that are assumed to provide less habitat heterogeneity (**Tissot *et al.*, 2006 | D'Onghia *et al.*, 2011, 2012 | Baillon *et al.*, 2012 | Danovaro *et al.*, 2014**). In any case, the majority of existing studies were limited to comparing fish diversity, abundance and/or biomass between habitats providing different levels of heterogeneity. Interestingly, very few studies aimed to compare fish occurrence in relation to developmental stage, small-scale habitat selection and CWCs (**Diaz *et al.*, 2003 | Baillon *et al.*, 2012 | Henderson *et al.*, 2020**).

CWCs increase habitat heterogeneity on both hard and soft substrates by forming complex three-dimensional structures. Habitat-forming CWCs are considered deep-sea ecosystem engineers as they locally increase structural and biological complexity in homogeneous deep-sea environments, create biogenic habitats for many benthic species, and support diverse and productive ecosystems (**Roberts *et al.*, 2006 | Auster, 2007 | Buhl-Mortensen *et al.*, 2010**). Deep-sea coral habitats are ecologically important as they provide local feeding, resting, shelter and nursery areas for benthic communities, especially in hard-bottom ecosystems (**Reed & Hoskin, 1987 | Husebø *et al*.**, **2002 | Auster, 2005 | Buhl-Mortensen & Mortensen, 2005 | Costello *et al*., 2005 | Roberts *et al.*, 2006 | Stone, 2006 | Auster, 2007 | Etnoyer & Warrenchuk, 2007 | Ross & Quattrini, 2007 | Moore *et al*., 2008 | Roberts *et al*., 2009 | Buhl-Mortensen *et al*., 2010 | Baillon *et al*., 2012 | Baker *et al*., 2012a | Stone, 2014 | De Clippele *et al*., 2015**). Most CWCs and other epifaunal suspension feeders settle on rocky substrates in high-current environments, and are generally regarded as ecosystem engineers in these environments (*e.g*., *Desmophyllum pertusum* and *Madrepora* spp. reefs, large gorgonian corals) (**Costello *et al*., 2005 | Stone, 2006 | Roberts *et al.*, 2009 | Stone, 2014**). On the other hand, other CWCs (*e.g*., sea pens, some sea fans and some solitary scleractinians) anchor themselves in soft sediments or rest on soft-bottom substrates in low-current environments. Sea pens are a traditionally overlooked group of CWCs that are typically quite small and can have a relatively sparse distribution compared to dense CWC reefs. While there is evidence that sea pen fields provide important ecological habitat functions to many species, including fish and invertebrates (**Tissot *et al*., 2006 | Buhl-Mortensen *et al*., 2010 | Garcia-Matucheski & Muniain, 2011 | Baillon *et al*., 2012**), their relationship with different size (and age) classes of demersal fish species remains unclear.

Associations between both juvenile and adult demersal fish and a variety of benthic invertebrates have been previously documented (**Valentine *et al*., 1980 | Auster *et al*., 1997, 2003**). One of the earliest studies of the associations between fish and sea pens in the Northwest Atlantic reported a strong association between Redfish larvae and diverse sea pen habitats, which were assumed to be used as spawning areas, and also as shelters by early-life stage fishes (**Baillon *et al*., 2012**). Our study, carried out in the same area revealed that CWC taxa, including sea pens, had a stronger influence than both abiotic features and other invertebrate taxa on the abundance and distribution of the most dominant groundfish of the assemblage, including Redfish (**Chapter 2**). Yet, the ecological role of sea pen habitats for fish in the area is not fully understood. Identifying the ecological, biological and environmental factors that influence fish-habitat relationships at different life stages is essential to understanding ecosystem processes and fulfilling conservation and commercial purposes (**Crooks & Sanjayan, 2006 | Grober-Dunsmore *et al.,* 2009 | Boström *et al.,* 2011**).

In this context, we analysed video data collected *in situ* by a remotely operated vehicle (ROV) and a near-seabed drift-camera system during two benthic habitat surveys, to examine fish size structure in relation to biogenic habitats in the Laurentian Channel MPA. Our objectives were 1) to describe the local size structure of four deep-sea groundfish taxa in the MPA, 2) to assess the influence of fish body size and benthic habitats on fish distribution, and 3) to identify abiotic drivers of size for each taxon, in order to 4) assess fish habitat use variability, as well as the importance of sea pen habitats for specific fish life stages.

3-2 | Methodology

3-2.1 | Data preparation

The four fish taxa we decided to focus this study on were Redfish (*Sebastes* spp.), Witch Flounder (*Glyptocephalus cynoglossus*), Marlin-Spike Grenadier (*Nezumia bairdii*) and Longfin Hake (*Phycis chesteri*) (**Fig. 3-1**). These demersal fish were chosen as they were identified as the most abundant of the 23 taxa that make up the assemblage in the study area (**Chapter 2**). For both surveys we extracted images from the downward-looking camera every time fish individuals were in the field of view.

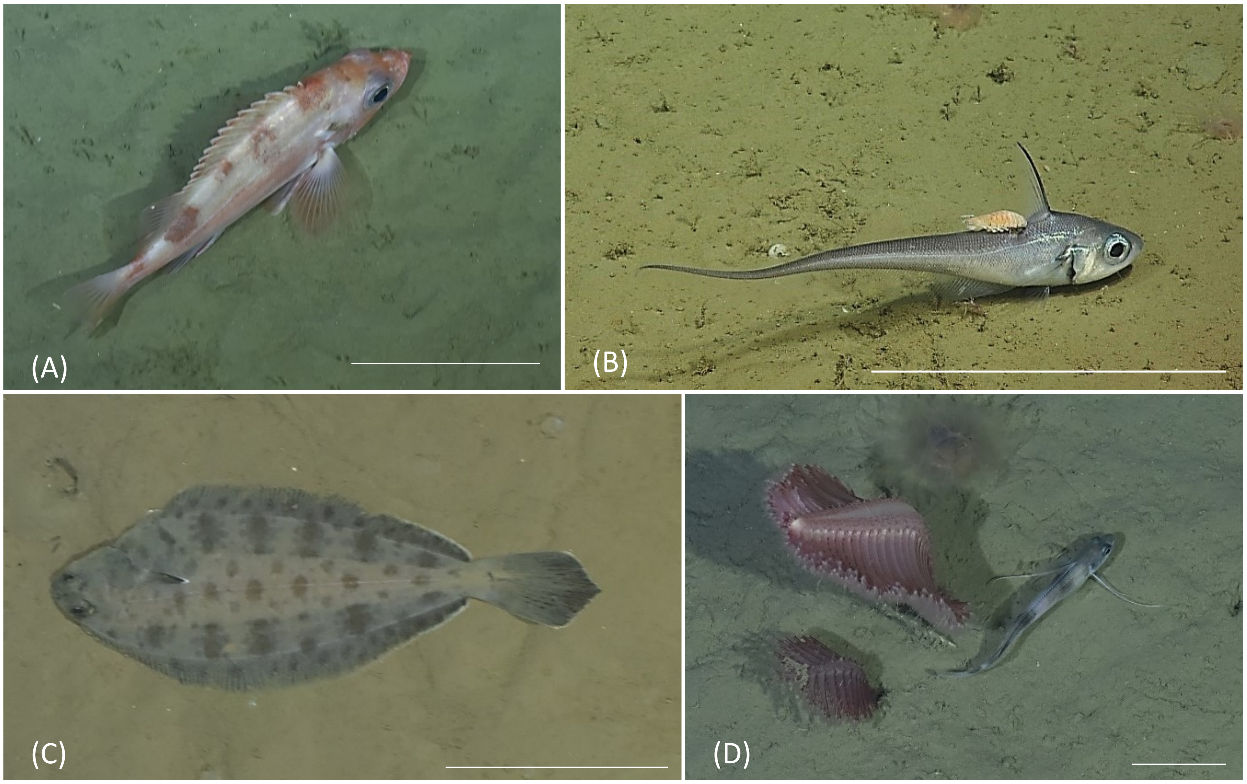


Fig. 3-1 | Frame captures from underwater video recordings of the four groundfish taxa analyzed. (A) Redfish (*Sebastes* spp.), (B) Marlin-Spike Grenadier (*Nezumia bairdii*) with parasitic copepod behind the dorsal fin, (C) Witch Flounder (*Glyptocephalus cynoglossus*), (D) Longfin Hake (*Phycis chesteri*) near *Pennatula* sea pens and one *Flabellum* coral. All pictures were taken from a downward-looking camera except for picture B, which was taken from a forward-looking camera. Scale bar: 10 cm.

To characterize benthic habitat type, the presence of the most dominant epibenthic invertebrate taxa was recorded (**Fig. 3-2**). Nine invertebrate taxa comprising actiniarias, cerianthids, solitary cup corals and sea pens were identified as contributing to invertebrate assemblages (**Chapter 2**). To characterize bottom type, four unique substrates (mud, shell debris, gravel and boulders) and three local soft-sediment micro-habitat features (burrows, depressions and dunes) were recorded.

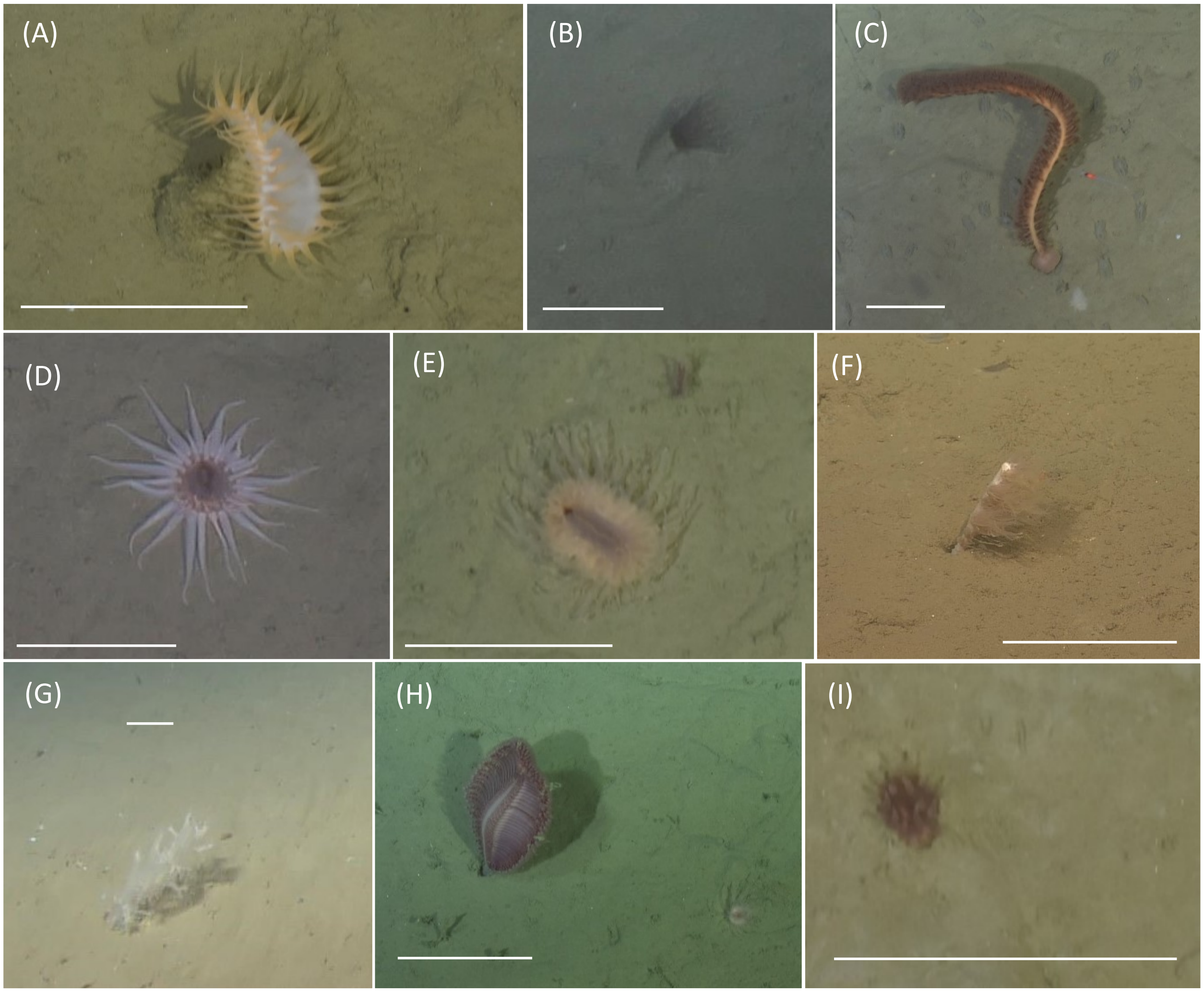


Fig. 3-2 | Frame captures from underwater video recordings of the most dominant invertebrate taxa contributing to invertebrate assemblages. (A) *Actinauge cristata*, (B) Actiniaria sp6. (C) *Anthoptilum* spp., (D) Cerianthid sp1., (E) *Flabellum (Ulocyathus) alabastrum*, (F) *Kophobelemnon* spp., (G) Nephtheidae sp., (H, left) *Pennatula aculeata*, (H, right) *F. alabastrum*, (I) *Flabellum (Ulocyathus) angulare*. All pictures were taken from a downward-looking camera except pictures F and G, which were taken from a forward-looking camera. Scale bar: 10 cm.

Based on the approach taken by Baker *et al.* (**2012**) and in Chapter 2, we divided the video data into 10-m segments, which were used as minimum spatial sample units to match with the small-scale distribution of habitat attributes.

Each segment was assigned a bottom type according to the presence or absence of substrates and soft sediment micro-habitat features: 1) ‘Flat’: mud only, absence of micro-habitat features and hard-bottom substrate (**Fig. 3-3A**), 2) ‘Soft negative’ relief: presence of micro-habitat features such as depressions and burrows, absence of hard-bottom substrate (**Fig. 3-3B**), 3) 'Soft positive' relief: presence of micro-habitat features such as dunes, absence of hard-bottom substrate (**Fig. 3-3C**), 4) 'Soft mixed' relief: presence of both positive and negative relief micro-habitat features, absence of hard-bottom substrate (**Fig. 3-3B & 3-3C**) and 5) Hard-bottom substrate: presence of hard substrate, presence of micro-habitat features possible (**Fig. 3-3D**).

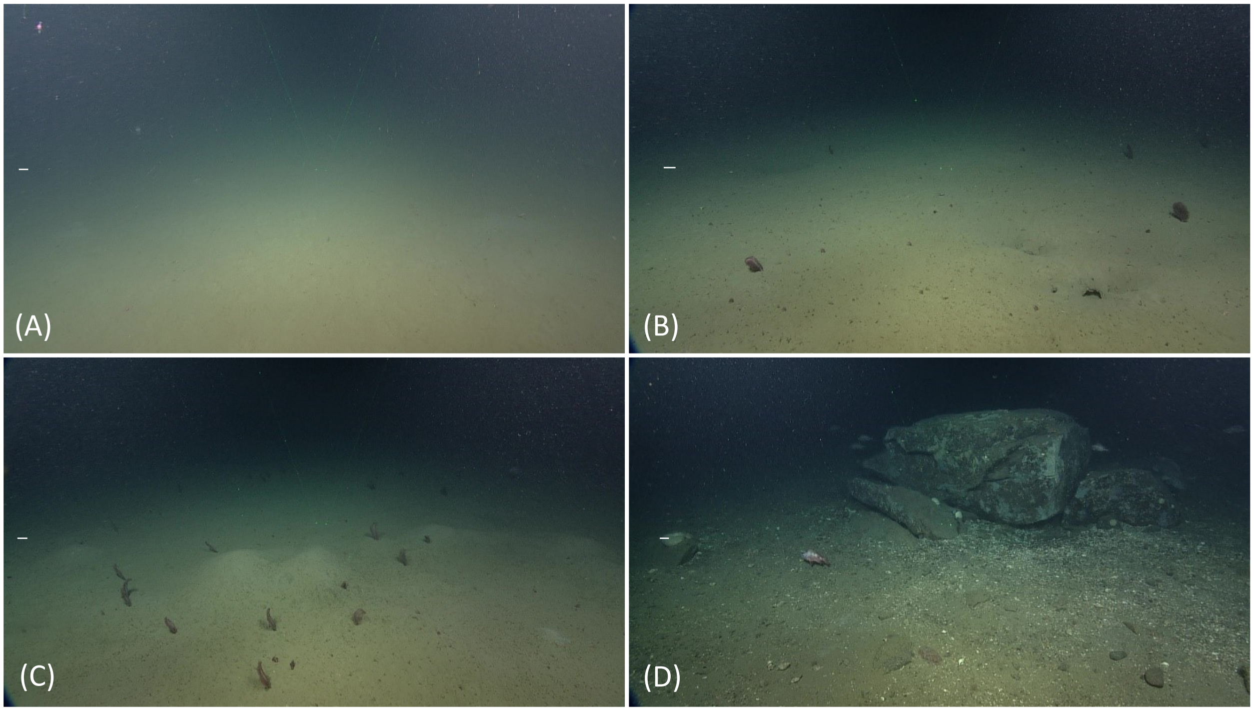


Fig. 3-3 | Frame captures from underwater video recordings of the main substrates and soft-sediment micro-habitat features observed in the Laurentian Channel MPA used to define bottom types. (A) 'Flat': no-relief muddy sediment, (B) 'Soft negative': depressions and burrows in soft sediment, (C) 'Soft positive': small soft-sediment dunes, (D) 'Hard': hard substrate comprised of boulders, gravels and shell debris. 'Soft mixed' was a fifth bottom type characterized by the presence of soft negative and soft positive relief features. Scale bar: 10 cm.

We quantified the presence of each epibenthic invertebrate taxon per segment. Each segment was further assigned a benthic habitat type based on the presence or absence of invertebrate taxa (see section 2.5.1).

For both surveys we extracted images from the downward-looking camera for each fish individual in the field of view. We took total length (TL) measurements (cm) of each individual in ImageJ (**Schneider *et al.*, 2012**) using the lasers as a scale. Fish were classified as 'Small juvenile', 'Large juvenile' or 'Adult' based on estimations of their life cycle stages. These estimations were guided by sizes at maturity assessed in a number of studies, facilitating the differentiation of life cycle stages for this study (**Table 3-1**). We differentiated the 'Small' from 'Large' juveniles life stages to account for variability in size at maturity between studies, geographic locations, males and females, or species (*e.g.*, three species of *Sebastes* spp. pooled in our study). We then used this typology to calculate fish abundance per life stage.

Table 3-1 | Estimated life stage and corresponding size classes (cm) for each fish taxon.

Fish taxon	Life stage	Size class (cm)	Reference
Longfin Hake	Small juvenile	1-20	Beacham, 1983a | Cohen et *al.,* 1990 | Coad & Reist, 2004
	Large juvenile	20-35	
	Adult	35+	
Marlin-Spike Grenadier	Small juvenile	1-25	Savvatimsky, 1989 | Cohen et *al.*, 1990
	Large juvenile	25-30	
	Adult	30+	
Redfish	Small juvenile	1-20	Vaskov, 2005 | Wilhelms, 2013 | Brassard et *al.*, 2017
	Large juvenile	20-40	
	Adult	40+	
Witch Flounder	Small juvenile	1-25	Beacham, 1983b | Bowering, 1976, Bowering & Brodie, 1984, 1991
	Large juvenile	25-40	
	Adult	40+	

3-2.2 | Statistical analysis

3-2.2.1 | Benthic habitat types characterized by invertebrate assemblages

All data analyses were performed using R (**R Core Team, 2019**). We determined benthic habitat types by conducting multivariate analyses on the Hellinger-transformed quantified presence of invertebrates per 10-m segment (**Legendre & Gallagher, 2001**). We used the Hellinger transformation as it is adapted to multivariate analyses dealing with datasets with many zeros. First, we used the Gap statistic analysis, using the function 'clusGap' from the 'cluster' package, to estimate the optimal number of clusters necessary to describe benthic habitat types in the study area (**Tibshirani *et al.*, 2001 | Maechler *et al.*, 2021**). In order to identify and extract the clusters in the dataset, we measured the dissimilarity between the Hellinger-transformed values using the Euclidean distance ('dist' function from the 'cluster' package) and used the dissimilarity matrix to perform a Hierarchical Clustering Analysis using the Ward's method ('hclust' function from the 'cluster' package), accounting for the optimal number of clusters identified by the Gap statistic method. Then, we used the 'cutree' function ('cluster' package) to add each segment to the cluster it belongs to. We use the term 'benthic habitat type' herein to describe the clusters defined by the statistical analysis. This usage does not imply these are fully representative invertebrate community types, as we did not consider all epibenthic invertebrate taxa observed on the video, nor their abundances to run our analysis. Benthic invertebrate community composition in these Laurentian Channel sites is reported in de Mendonça & Metaxas (**2023, 2024**).

3-2.2.2 | Quantification of physical and biological habitat attributes

To quantify habitat heterogeneity in the study area, we grouped the five bottom types into three physical categories: 'Flat' (mud), 'Soft' (soft negative, positive and mixed reliefs) and 'Hard'. We also identified two biological categories: absence or presence of epibenthic invertebrates ('No Invertebrates' and 'Invertebrates'). We calculated the relative contribution (percentage of 10-m segments) of the six following physical-biological combinations: 'Flat-No invertebrates', 'Flat-Invertebrates', 'Soft-No invertebrates', 'Soft-Invertebrates', 'Hard-No invertebrates' and 'Hard-Invertebrates'.

3-2.2.3 | Influence of benthic habitat type, year and time of day on fish size

We ran analyses of covariances (ANCOVA) on fish sizes to test for significant differences between benthic habitat types (defined by the cluster analysis), years and times of day. Here we tested the influence of time of day on fish size to assess if fish size composition changes during the day as a result of fish dial feeding migration (**Beamish, 1966**). We categorized time of day as 'day' and 'night', defined according to local times of sunrise and sunset, during the two data collection periods. We verified data independence, homoscedasticity and normality to ensure compatibility with the assumptions of ANCOVA analyses by plotting the model diagnostics. Then, we performed Tukey tests as a *post-*

hoc analysis to run pairwise mean comparisons between benthic habitat types, years and times of day when significant differences were found.

3-2.2.4 | Influence of ecological covariates of fish specific size

In order to identify small-scale ecological predictors of fish size, we performed generalized additive models (GAMs) for each fish taxon, using the 'mgcv' package (**Wood, 2011**). GAMs are an adaptation of generalized linear models in which the beta coefficient from standard linear regressions is replaced by several non-linear smoothing functions (or splines) to model linear and non-linear relationships between predictors and the response variables. Potential biotic and abiotic covariates included in the models were year, time of day, depth, bottom temperature, benthic habitat type and bottom type. This analysis was run to strengthen our interpretation of the results generated by the ANCOVA, and to address the effect size of smooth values (*e.g.*, depth, bottom temperature). Prior to running the models, we checked for collinearity among predictors using Variance Inflation Factor analysis (VIF) and kept variables with a VIF lower than 3 (**Zuur *et al.*, 2010**). Based on this analysis, it was concluded that both depth and bottom temperature could not be included in the same model because they were highly correlated.

To determine if we should account for spatial autocorrelation in our models, we included the 'corSpatial' function ('nlme' package), following a gaussian distribution, to all models (**Pinheiro *et al.*, 2022**). We performed *a posteriori* residual diagnostic tests on the model outputs using the package 'DHARMa' to ensure assumptions (normality, homoscedasticity and independence) were met (**Hartig, 2022**). We tested if there was a relationship between residuals and specific predictors. We also tested for outliers, overdispersion and spatial autocorrelation (using functions 'simulateResiduals', 'testDispersion' and 'testSpatialAutocorrelation'). We created smooth and parametric effect plots using the 'visreg' function from the 'visreg package to visualize fish response to the different variables tested (**Breheny & Burchett, 2017**). The best fitting models (those that explained the most variance and had the lowest Akaike information criterion (AIC)) for predicting fish size were the same for each fish taxon:

Eq. 3: *Fish size* ~ s(Depth) + Benthic habitat type + Bottom type + Time of day + Year + s(Station, bs = “re”)

Eq. 4: *Fish size* ~ s(Temperature) + Benthic habitat type + Bottom type + Time of day + Year + s(Station, bs = “re”)

Where,

Fish size = measured TL (cm) of Witch Flounder, Marlin-Spike Grenadier, Longfin Hake or Redfish, measured from images extracted from the videos

Depth = mean depth (m) of the 10-m segment

Temperature = bottom temperature (℃) recorded when the image was captured

Benthic habitat type = factor representing the benthic habitat type 10-m segments were attributed to according to the invertebrate taxa composition

Bottom type = factor that identifies the dominant substrate type in each segment

Year = confounding factor representing the year (2017, 2018), the month (September, July) and the UVS (ROPOS, CAMPOD)

Time of day = categorical factor classified as either ‘day’ or ‘night’.

We integrated an interaction between the benthic habitat type and time of day factors if an influence was revealed by the ANCOVA performed on fish size for each taxon. Stations were added as a random factor (bs = “re”). *s* represents the smoothing functions of the given covariates. A Gamma family distribution with a log link was used in the model as it works well for positive-only data.

3-2.2.5 | Distribution maps of fish local size structure

We used ArcGIS V10.7 (**Esri Inc., 2020**) to produce distribution maps of fish local size structures for each fish taxon and each survey. For each taxon we used pie charts to represent the proportion of taxon-specific life stages (‘Small juvenile’, ‘Large juvenile’ and ‘Adult’) per station surveyed and per survey.

3-3 | Results

3-3.1 | Data summary

A total of 95 h of video footage was acquired using the two UVSs at depth ranging from 179 to 455 m (**Table 1-1**). The surveys covered 86.7 km in total linear extent and an area of approximately 43.6 ha within the study area. Recorded bottom temperatures ranged from 3.6 to 8.9 °C. A larger area was covered in 2017 than in 2018; during the day than at night; and within the 300-350 m and 400-455 m depth ranges (**Appendix 3-1**).

3-3.2 | Quantification of physical and biological habitat attributes

The bottom types most observed in the survey were ‘Flat’ (59%, **Fig. 3-3A**) and ‘Soft negative’ (36%, **Fig. 3-3B**). ‘Soft mixed’ (2%, **Fig. 3-3B & 3-3C**), ‘Soft positive’ (<1%, **Fig. 3-3C**) and hard-bottom substrate (3%, **Fig. 3-3D**) were the least encountered bottom types (**Table 3-2**). A distribution map of bottom types across stations is presented in Appendix 3-2A.

Table 3-2 | Frequency of occurrence (number of 10-m segments) of different combinations of physical bottom types and epibenthic invertebrate faunal representation.

Bottom type	Benthic habitat		Total
	No invertebrates	Invertebrates	
Flat	447	3992	4439
Soft	372	2496	2868
Negative	340	2357	2697
Positive	0	8	8
Mixed	32	131	163
Hard	108	96	204
Total	927	6584	7511

Invertebrates were present in 88% of the area surveyed. They contributed to habitat heterogeneity in flat areas (‘Flat-Invertebrates’) in 53% of the segments, and in soft-bottom areas with micro-reliefs (‘Soft-Invertebrates’) in 33% of the segments (**Table 3-2**). Only 6% of the area covered was considered as homogeneous, defined as ‘Flat-No Invertebrates’. Segments dominated with hard-bottom substrates with and without invertebrates (‘Hard-No Invertebrates’ and ‘Hard-Invertebrates’) contributed to 1% each.

A distribution map of physical and biological attributes across stations is presented in Appendix 3-2B.

3-3.3 | Benthic habitat types characterized by invertebrate assemblage composition

The Gap statistic analysis identified six clusters, based on invertebrate presence, to best describe the different fauna assemblages: 1) ‘Barren’: absence of epibenthic invertebrate taxa, 2) ‘Acti-Ceriant’: dominance of *Actinauge cristata* and Cerianthid sp1 (present in 62% of 10-m segments), presence of *Pennatula aculeata* and *Flabellum (Ulocyathus) alabastrum* (12 and 14%, respectively), 3) ‘Kopho-Acti-Ceriant’: dominance of *Kophobelemnon* sp. (49%), *Actinauge cristata* (25%) and Cerianthid sp1 (12%), 4) ‘Sclerac-Anthop-Kopho’: dominance of *Flabellum (Ulocyathus) angulare* (28%), *Anthoptilum* spp. (24%) and *Kophobelemnon* sp. (22%), 5) ‘Flab-Penna’: dominance of *Flabellum (Ulocyathus) alabastrum* (63%) and *Pennatula aculeata* (37%) and 6) ‘Penna’: dominance of *Pennatula* spp. (96%) (**Appendix 3-3**).

We used the classification provided in Chapter 1 to group invertebrates in size categories (**Appendix 2-1**). Overall, invertebrates of medium size (5-25 cm tall) and small size (<5 cm tall) were the most dominant (57 and 37%, respectively) (**Appendix 3-3**). Small invertebrates, dominated by solitary cup corals, were mostly present in ‘Flab-Penna’. Medium-size invertebrates, dominated by sea pens, were mostly present in ‘Acti-Ceriant’, ‘Kopho-Acti-Ceriant’ and ‘Penna’. Tall invertebrates (25-100 cm tall), dominated by *Anthoptilum* sea pens, were mostly present in ‘Sclerac-Kopho-Anthop’ and represented 24 % of the assemblage. We did not find any relation between benthic habitat types and bottom types, as 87 to 99 % of benthic habitat types were dominated by ‘Flat’ and ‘Soft negative’ bottom types. ‘Barren’ habitat was the habitat with the highest coverage of ‘Hard’ bottom type (10%) (**Appendix 3-3**). Distribution maps of benthic habitat types and invertebrate size classes across and within stations are presented in Appendices 3-2C & 3-2D.

3-3.4 | Fish occurrence and life stage distribution

A total of 15,381 fish were observed and 7,511 (49 %) were measured (**Table 3-3**). Over 96 % of fish were observed on or near the seabed (<50 cm above seafloor). Most fish were observed in 2017, and within the 300-350 m and 400-455 m depth ranges. Most fish were measured in 2017 and between 350-400 m deep. A relatively similar number of fish was observed and measured between day and night (**Appendix 3-4**). All benthic habitat types and bottom types were assessed during both surveys and both times of day, and all four fish taxa were observed in all benthic habitat types. No fish was measured associated with ‘Kopho-Acti-Ceriant’ during the day or in the 2018 survey. For all fish taxa aside from Redfish, fewer than 11 fish per taxon were measured associated with ‘Barren’ and ‘Acti-Ceriant’ at night. For all four taxa, fewer than 10 measured fish per taxon were associated with ‘Soft positive’ relief, and so we decided to remove data associated with this bottom type for this study (**Appendix 3-4**).

Table 3-3 | Size range (TL in cm) and number of fish measured per life stage, total number measured and observed, and percentage measured for four fish taxa.

		Longfin Hake				
Life stage	Small juvenile	Large juvenile	Adult	**Total measured**	**Total observed**	%
Size range (cm)	4-20	20-35	35-38			
Count	726	462	11	1199	3083	39
		Marlin-Spike Grenadier				
Life stage	Small juvenile	Large juvenile	Adult	**Total measured**	**Total observed**	%
Size range (cm)	3-25	25-30	30-37			
Count	772	63	21	856	1827	47
		Redfish				
Life stage	Small juvenile	Large juvenile	Adult	**Total measured**	**Total observed**	%
Size range (cm)	8-20	20-40	40-47			
Count	1643	2623	37	4303	8114	36
		Witch Flounder				
Life stage	Small juvenile	Large juvenile	Adult	**Total measured**	**Total observed**	%
Size range (cm)	3-25	25-39	>39			
Count	696	457	0	1153	2357	49
Total	3837	3605	69	7511	15381	40

Overall, fish measured between 3 and 47 cm in TL. 'Small juveniles' represented 51% of all fish measured, 'Large juveniles' represented 48% and 'Adults' 1%. A total of 1,199 Longfin Hake were measured out of 3,083 observed (39%). Longfin Hake measured between 4 and 38 cm in TL. 'Small juveniles' (4-20 cm) and 'Large juveniles' (20-35 cm) represented 99% of all Longfin Hake measured (**Table 3-3**). No Longfin Hake were measured in 'Acti-Ceriant' at night. A total of 856 Marlin-Spike Grenadier were measured out of 1,827 observed (47%). Marlin-Spike Grenadier measured between 3 and 37 cm in TL. 'Small juveniles' (3-25 cm) and 'Large juveniles' (25-30 cm) represented 98% of all Marlin-Spike Grenadier measured (**Table 3-3**). No Marlin-Spike Grenadier were observed above 200 m during the day. A total of 4,303 Redfish fish were measured out of 8,114 observed (36%). Redfish measured between 8 and 47 cm in TL. 'Small juveniles' (8-20 cm) and 'Large juveniles' (20-40 cm) represented 99% of all Redfish measured (**Table 3-3**). A total of 1,153 Witch Flounder fish were measured out of 2,357 observed (49%). Witch Flounder measured between 3 and 39 cm in TL. No 'Adults' fish was measured (**Table 3-3**). No Witch Flounder were observed above 200 m during the day. Distribution maps of fish size structures across and within stations for each taxon are presented in Appendix 3-5.

3-3.5 | Fish local size structures in relation to benthic habitat type, year and time of day

We observed a significant increase in size in 2018 relative to 2017 for all fish taxa (**Appendices 3-6 & 3-7**). Longfin Hake 'Small juveniles' dominated the assemblage in 2017 (78%) while 'Large juveniles' were the dominant life stage in 2018 (79%). Marlin-Spike Grenadier 'Small juveniles' dominated the assemblages both years (97 and 76% respectively), while we found a higher percentage of 'Large juveniles' and 'Adults' in 2018 (16.5 and 7.5% respectively). Redfish 'Small' and 'Large juveniles' were both dominating the assemblage in 2017 (43.5 and 56% respectively), while 'Large juveniles' were the dominant life stage in 2018 (92%). Witch Flounder 'Small juveniles' dominated the assemblage in 2017 (73.5%) while 'Large juveniles' dominated the assemblage in 2018 (66%).

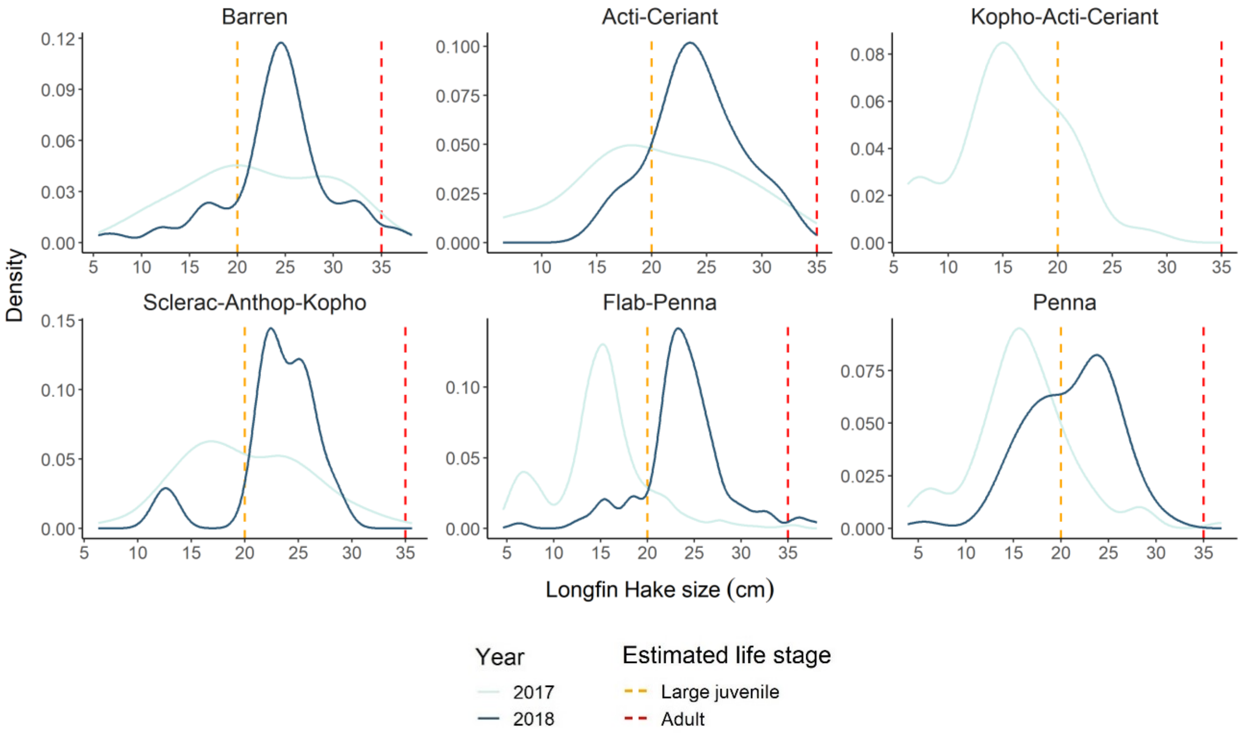


Fig. 3-4 | Frequency distribution of Longfin Hake size (TL in cm) within benthic habitat types, in 2017 (light blue) and 2018 (dark blue). The vertical dashed lines represent the estimated transition threshold to the 'Large juvenile' (orange) and 'Adult' (red) life stages of the taxon. No fish was measured in 'Kopho-Acti-Ceriant' in 2018.

Longfin Hake 'Small juveniles' were dominant in 'Kopho-Acti-Ceriant', 'Flab-Penna' and 'Penna' in 2017 (80-87%), and co-dominant with 'Large juveniles' in the other benthic habitat types. 'Large juveniles' were dominant in all benthic habitat types in 2018 (61-91%). On average, the smallest fish measured for Longfin Hake were associated with 'Kopho-Acti-Ceriant', 'Flab-Penna' and 'Penna' in 2017 and with 'Penna' only in 2018. On average, the largest fish measured were associated with 'Barren' and 'Acti-Ceriant' both years.

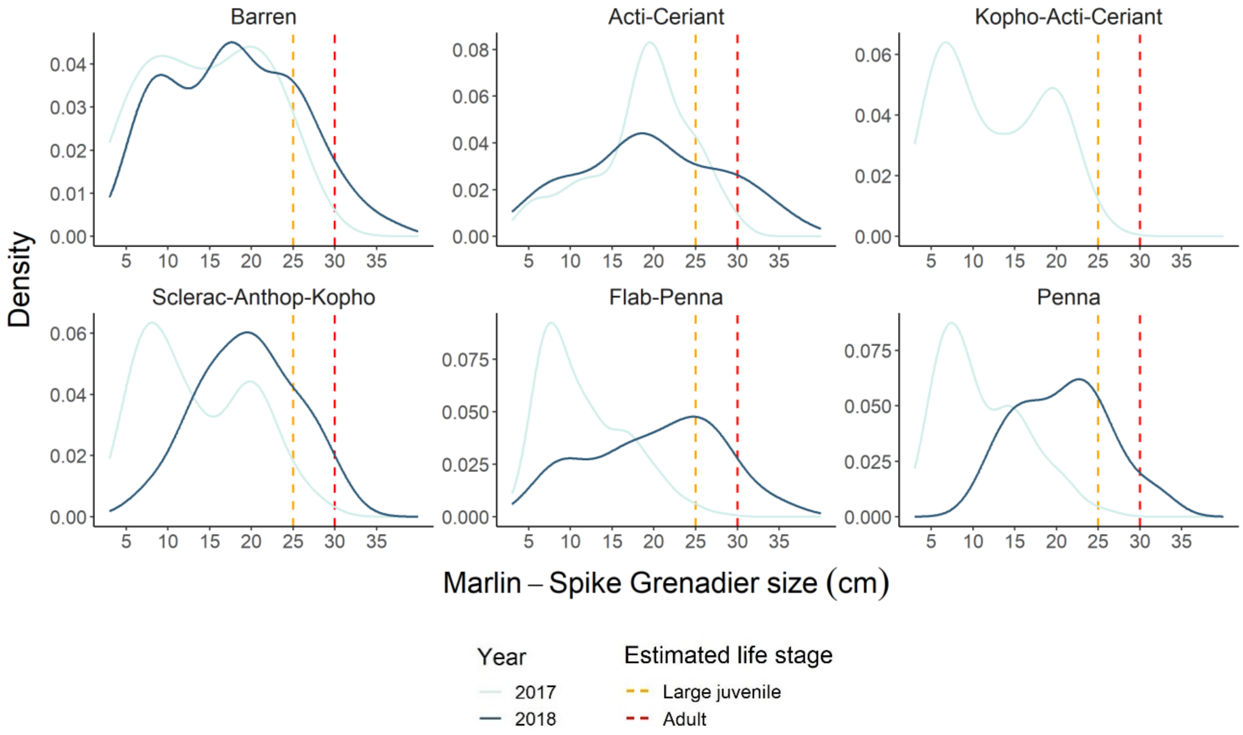


Fig. 3-5 | Frequency distribution of Marlin-Spike Grenadier size (TL in cm) within benthic habitat types, in 2017 (light blue) and 2018 (dark blue). The vertical dashed lines represent the estimated transition threshold to the 'Large juvenile' (orange) and 'Adult' (red) life stages of the taxon. No fish was measured in 'Kopho-Acti-Ceriant' in 2018.

Marlin-Spike Grenadier 'Small juveniles' were dominant in all benthic habitat types in 2017 (>83%) and in 2018 (65-83%). The smallest fish measured for Marlin-Spike Grenadier in 2017 were associated 'Flab-Penna' and 'Penna', and the largest with 'Barren' and 'Acti-Ceriant'. On average, the smallest fish measured in 2018 were associated with 'Barren' and 'Acti-Ceriant', and the largest with 'Flab-Penna' and 'Penna'.

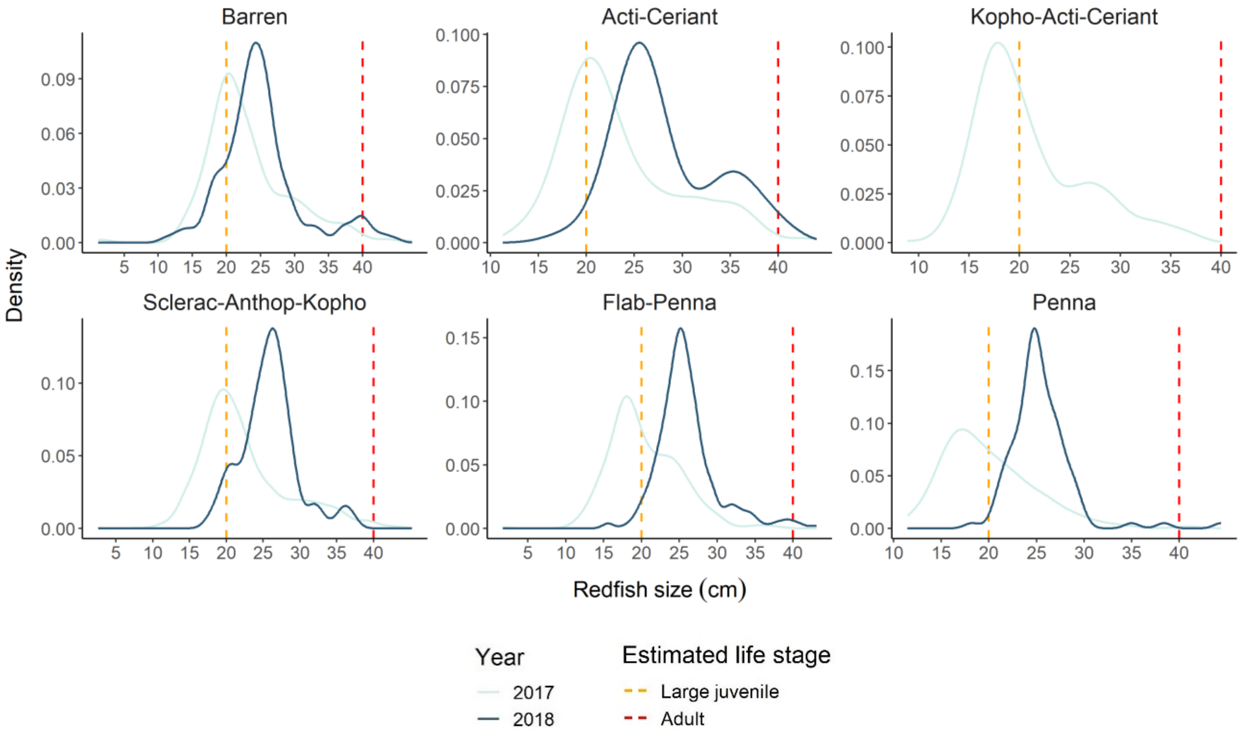


Fig. 3-6 | Frequency distribution of Redfish size (TL in cm) within benthic habitat types, in 2017 (light blue) and 2018 (dark blue). The vertical dashed lines represent the estimated transition threshold to the 'Large juvenile' (orange) and 'Adult' (red) life stages of the taxon. No fish was measured in 'Kopho-Acti-Ceriant' in 2018.

Redfish 'Small juveniles' were dominant in 'Kopho-Acti-Ceriant', 'Flab-Penna' and 'Penna' (54-56%) in 2017, and 'Large juveniles' in the other habitats (58-67%). 'Large juveniles' were dominant in all benthic habitat types in 2018 (>80%). On average, the smallest fish measured for Redfish in 2017 were associated with 'Flab-Penna' and 'Penna', and the largest with 'Barren' and 'Acti-Ceriant'. We did not find any differences in size of Redfish between benthic habitat types in 2018.

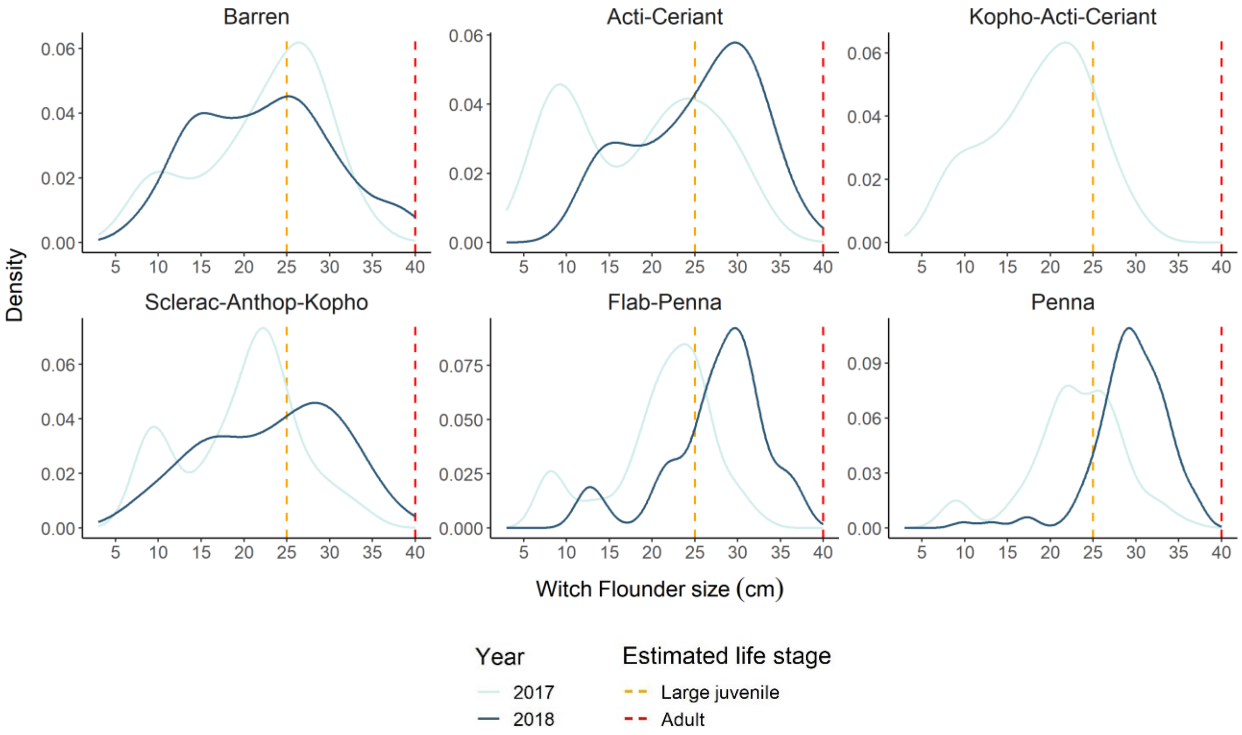


Fig. 3-7 | Frequency distribution of Witch Flounder size (TL in cm) within benthic habitat types, in 2017 (light blue) and 2018 (dark blue). The vertical dashed lines represent the estimated transition threshold to the 'Large juvenile' (orange) and 'Adult' (red) life stages of the taxon. No fish was measured in 'Kopho-Acti-Ceriant' in 2018.

Witch Flounder 'Small juveniles' were dominant in all benthic habitat types (55-87%) in 2017, and in 'Barren' and 'Sclerac-Anthop-Kopho' in 2018 (54-60%). 'Large juveniles' were dominant in 'Acti-Ceriant', 'Flab-Penna' and 'Penna' in 2018 (57-89%). The smallest fish measured for Witch Flounder in 2017 were associated with 'Acti-Ceriant', 'Kopho-Acti-Ceriant' and 'Sclerac-Anthop-Kopho', and the largest with 'Penna'. On average, the smallest fish measured in 2018 were associated with 'Barren' and 'Sclerac-Anthop-Kopho', and the largest with 'Penna' and 'Flab-Penna'.

Moreover, all fish presented a significant increase in TL in 2018 relative to 2017 within certain benthic habitat types (**Appendix 3-7**): Longfin Hake within 'Flab-Penna' and 'Penna' (**Fig. 3-4**), Marlin-Spike Grenadier within 'Sclerac-Anthop-Kopho', 'Flab-Penna' and 'Penna' (**Fig. 3-5**), Redfish within all benthic habitat types but 'Kopho-Acti-Ceriant' (not surveyed in 2018) (**Fig. 3-6**), and Witch Flounder within 'Acti-Ceriant', 'Flab-Penna' and 'Penna' (**Fig. 3-7**).

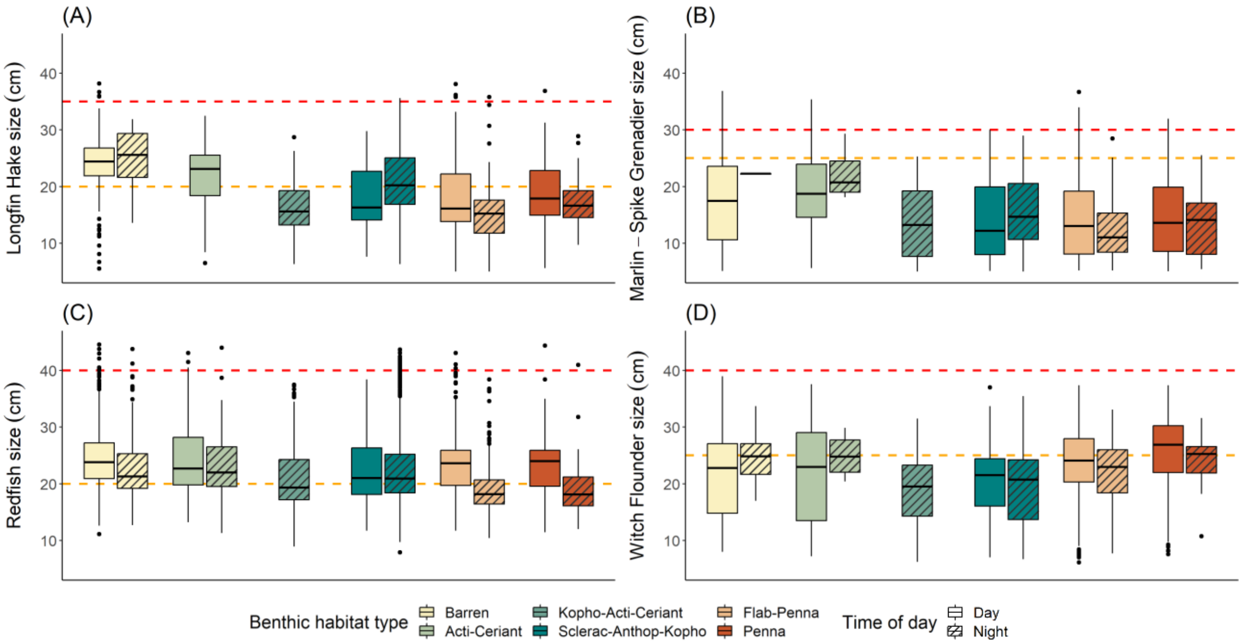


Fig. 3-8 | Size (TL in cm) of (A) Longfin Hake, (B) Marlin-Spike Grenadier, (C) Redfish, (D) Witch Flounder per benthic habitat type and time of day (solid-color boxes correspond to daytime and striped color boxes to nighttime). The lower and upper boundaries of the box plots correspond to the first and third quartiles (25th and 75th percentiles). The black line within the box plots indicates the median. The upper and lower whiskers indicate the 10th and 90th percentiles. The orange line represents the estimated 'Large juvenile' size and the red line represents the estimated 'Adult' size of each taxon.

We found an overall influence of time of day on fish body size for Redfish and Longfin Hake, with smaller juveniles more present at night than during the day for both taxa (**Fig. 3-8 & Appendix 3-7**). Differences in TL within specific benthic habitat types between day and night were also revealed for both taxa. Smaller juveniles were found associated with 'Flab-Penna' at night for Longfin Hake, and associated with 'Barren', 'Flab-Penna' and 'Penna' at night for Redfish than within the same habitats during the day.

3-3.6 | Influence of ecological covariates on fish size

The ANCOVA performed to test the influence of year and benthic habitat type revealed differences in fish size between benthic habitat type and year for all four taxa. Therefore, we tested the interaction between benthic habitat type and year as a factor in the model for all fish taxa. We also tested the interaction between benthic habitat type and time of day for Longfin Hake and Redfish. For all fish taxa, the model that included the interaction between benthic habitat type and year explained a higher variance and had a smaller AIC than the model without the interaction. Similarly, the same model was selected over the model that included the interaction with time of day for both Longfin Hake and Redfish. For all fish taxa, Model 3 (Eq. 3 using depth) explained a similar variance and had a similar AIC compared to Model 4 (Eq. 4 using temperature). Moreover, depth and temperature had a similar influence on fish size for all fish taxa analyzed. We therefore, decided to present results for Model 3 only for all fish taxa. The model summary tables and effect plots generated for each fish taxon are presented in Appendices 3-8 to 3-15.

Model 3 for Longfin Hake explained 30% of variance (**Appendix 3-8**). Overall, smaller sizes were predicted in 2017 and during the day (**Table 3-4**). Longfin Hake size was positively correlated with depth. Smaller sizes were associated with ‘Soft mixed’ relief, while larger sizes were associated with hard-bottom substrate. In the 2017 survey, smaller sizes were associated with ‘Kopho-Acti-Ceriant’, ‘Flab-Penna’ and ‘Penna’, while larger sizes were associated with ‘Barren’ and ‘Acti-Ceriant’. In the 2018 survey, smaller sizes were associated with ‘Barren’, ‘Acti-Ceriant’ and ‘Sclerac-Anthop-Kopho’, while larger sizes were associated with ‘Penna’ and ‘Flab-Penna’.

Model 3 for Marlin-Spike Grenadier explained 23% of variance (**Appendix 3-10**). Overall, smaller sizes were predicted in 2017 and during the day (**Table 3-4**). No relationship was found between Marlin-Spike Grenadier size and depth. Larger sizes were associated with hard-bottom substrate. In the 2017 survey, smaller sizes were associated with ‘Kopho-Acti-Ceriant’ and ‘Sclerac-Anthop-Kopho’, while larger sizes were associated with ‘Barren’ and ‘Acti-Ceriant’. In the 2018 survey, smaller sizes were associated with ‘Barren’ and ‘Acti-Ceriant’, while larger sizes were associated with ‘Flab-Penna’ and ‘Penna’.

Table 3-4 | Influence of year, time of day, depth, bottom type and benthic habitat type on fish size (TL) per taxon as predicted in Model 3 (Eq. 3) ($p < 0.05$). Here shallow and deep refer to our minimum and maximum depth surveyed (178-455 m). NS: not significant. Model summary tables and effect plots for each taxon are presented in Appendices 3-8 to 3-15.

Taxon	Predictor	Relationship with size						
Longfin Hake	Year	2017	<	2018				
	Time of day	Day	<	Night				
	Depth	Shallow	<	Deep				
	Bottom type	Soft mixed	<	Flat Soft negative	<	Hard		
	Benthic habitat type 2017	Kopho-Acti-Ceriant	<	Flab-Penna Penna	<	Sclerac-Anthop-Kopho	<	Barren Acti-Ceriant
	Benthic habitat type 2018	Barren Acti-Ceriant Sclerac-Anthop-Kopho	<	Penna	<	Flab-Penna		
Marlin- Spike Grenadier	Year	2017	<	2018				
	Time of day	Day	<	Night				
	Depth	NS						
	Bottom type	Flat Soft negative Soft mixed	<	Hard				
	Benthic habitat type 2017	Kopho-Acti-Ceriant Sclerac-Anthop-Kopho	<	Flab-Penna Penna	<	Barren Acti-Ceriant		
	Benthic habitat type 2018	Barren Acti-Ceriant	<	Sclerac-Anthop-Kopho	<	Penna Flab-Penna		
Redfish	Year	2017	<	2018				
	Time of day	Day	<	Night				
	Depth	Shallow	<	Deep				
	Bottom type	Hard	<	Soft negative Soft mixed	<	Flat		
	Benthic habitat type	Flab-Penna	<	Kopho-Acti-Ceriant	<	Sclerac-Anthop-Kopho	<	Acti-Ceriant

	2017	Penna						Barren
	Benthic habitat type 2018	Sclerac-Anthop-Kopho	<	Acti-Ceriant Barren	<	Penna Flab-Penna		
Witch Flounder	Year	2017	<	2018				
	Time of day	Day	<	Night				
	Depth	NS						
	Bottom type	Soft negative	<	Flat Soft mixed Hard				
	Benthic habitat type 2017	Flab-Penna Penna	<	Acti-Ceriant	<	Sclerac-Anthop-Kopho Kopho-Acti-Ceriant	<	Barren
	Benthic habitat type 2018	Barren Acti-Ceriant	<	Sclerac-Anthop-Kopho	<	Flab-Penna Penna		

Model 3 for Redfish explained 11.5% of variance (**Appendix 3-12**). Overall, smaller sizes were predicted in 2017 and at night (**Table 3-4**). Redfish size was positively correlated with depth. Smaller sizes were associated with 'Soft negative' and 'Hard' bottom types at night. In the 2017 survey, smaller sizes were associated with 'Flab-Penna' and 'Penna', while larger sizes were associated with 'Barren' and 'Acti-Ceriant'. In the 2018 survey, smaller sizes were associated with 'Sclerac-Anthop-Kopho', while larger sizes were associated with 'Flab-Penna' and 'Penna'.

Model 3 for Witch Flounder explained 20% of variance (**Appendix 3-14**). Overall, smaller sizes were predicted in 2017 and at night (**Table 3-4**). No relationship was found between Witch Flounder size and depth. Smaller sizes were associated with 'Soft negative' relief. In the 2017 survey, smaller sizes were associated with 'Flab-Penna' and 'Penna', while larger sizes were associated with 'Barren'. In the 2018 survey, smaller sizes were associated with 'Barren' and 'Acti-Ceriant', while larger sizes were associated with 'Flab-Penna' and 'Penna'.

3-4 | Discussion

The habitat requirements of marine fish change over various temporal and spatial scales due to environmental (*e.g.*, physicochemical factors), ecological (*e.g.*, prey-predator relationships, competition, mating opportunities) and biological changes (*e.g.*, ontogenetic shifts) (**Schlosser, 1982 | Secor, 2015 | Fields *et al.,* 2017**). Here, we used direct *in-situ* observational techniques to assess fish size-habitat relationships in the Laurentian Channel MPA during two summer months over two different years. This study is one of the largest-known *in-situ* surveys to assess fish size structure and the small-scale distribution of groundfish taxa across habitats providing low heterogeneity in a soft-bottom environment.

3-4.1 | Benthic physical and biological micro-habitat characterization and distribution

With the addition of the 2018 CAMPOD survey, we continued the characterization of habitat heterogeneity and the mapping of benthic micro-habitats in the Laurentian Channel started in Chapter 2, based on the 2017 ROPOS survey. The 2018 assessment of habitat heterogeneity provided by physical and biological features was similar to that described in 2017. Here, only 6% of the study area covered was identified as non-structural (no physical or biological attributes) and 87% of the area surveyed was categorized as having epibenthic megafaunal invertebrate species presence. We found a similar spatial contribution of surficial sediments as described in previous studies and in Chapter 2 (**Lewis *et al*., 2016 | Lacharité *et al*., 2020**), with most of our stations being covered in fine muddy/sand sediment and a slightly higher percentage of coarser sediment on the banks (*e.g*., sand, gravel, shell debris and boulders).

Based on multivariate analysis of invertebrate presence, we identified five habitats dominated by six CWCs and two sea anemones, and one non-structural habitat in the Laurentian Channel MPA, potentially offering different levels of habitat complexity in a soft-bottom environment. Our results slightly differed from the previous description of benthic habitat types in the Laurentian Channel (**Chapter 2**). Here, we characterized a new non-coral habitat dominated by two sea anemones, surveyed more barren areas, and reclassified assemblages dominated by *Pennatula* sea pens. It should be noted that while invertebrate assemblage identification was based on invertebrate taxon densities in Chapter 2, invertebrate densities were not collected from the 2018 video survey. Thus, we used invertebrate presence from both surveys as a proxy. Running the cluster analysis including invertebrate taxon densities, instead of their presence, should refine the preliminary characterization of benthic habitats in the Laurentian Channel MPA.

3-4.2 | Fish local size structure in the Laurentian Channel MPA

The four deep-sea demersal fish taxa selected for analysis were identified as the most abundant taxa of the fish assemblage assessed by UVSs in the area during both surveys, representing 86% of all fish observed (**Chapter 2 | Chapter 4**). As 99% of fish measured were identified as juveniles, our results suggest that the Laurentian Channel was mostly dominated by early-life stage deep-sea groundfish during the years and months surveyed.

Previous studies have suggested the dominance of small fish and the absence of large (mature) fish to be the result of past fishery activities, from which targeted fish populations have not recovered (**Laidig *et al.*, 2009**). All activities that could disturb, damage, destroy or remove living marine organisms or any part of their habitats have been prohibited within the MPA since its designation in 2019 (**DFO, 2019**). Unfortunately, data collection for this study occurred prior to the MPA implementation, so the effectiveness of the MPA cannot be assessed yet. Fishing activity within the MPA has been low (in recent years) (**DFO, 2019**), compared to areas around the channel (*i.e.*, banks, continental shelf slope and inshore) where fishing intensity was more concentrated (Eastern Canada Commercial Fishing). As a point of reference, we examined Redfish population size structure assessed by DFO bottom trawls between 2000 and 2019 in April/May inside and within 200 km of the MPA (**Appendix 3-16**). For the last twenty years, 'Small' and 'Large' juveniles have been mostly dominating the population, both in low and high fishing intensity areas. This supports the premise that the small fishes assessed in this study were immature fish and not small mature fish.

Moreover, the significant increase in average size for all four taxa from 2017 to 2018 suggests that fish may stay in the channel over multiple years to grow, and that the Laurentian Channel is used as a nursery for numerous groundfish species. It should be noted however, that our results are preliminary and no general conclusions can be drawn on the yearly presence and distribution of early-life stage fishes in the channel. In this study, we only measured a subsample of all the fish observed on videos, and data were collected during two months, over two years, by two different UVSs and within a limited depth range. Thus, differences in fish size between the two years can either be interpreted as interannual growth or attributed to seasonality or gear selectivity.

Individual growth is typically measured as the increase in length or weight with increase in age for a given species. The von Bertalanffy growth function (VBGF) is the most common growth curve used to model growth as an average size-at-age relationship for many species, including fish (**Quince *et al.*, 2008**). While other studies have fitted von Bertalanffy curves or assessed age-length relationships for Redfish, Witch Flounder and other Hakes and Grenadiers, here we can only rely on increase in size between two years to estimate fish growth rates. In our study, the average increase in size (TL) measured between 2017 and 2018 was 6-7 cm for three of the fish taxa and 3 cm for Redfish. All taxa reviewed in the literature displayed relatively linear age-length relationships for lengths up to 30 cm. Acknowledging variability in growth rate with geographic location, species, as well as between males and females, increases in sizes measured in the MPA fall within the growth rate ranges previously estimated in other studies for Redfish (**Mayo *et al.*, 1990 | Saborido-Rey *et al.*, 2004 | Cadigan & Campana 2017 | Campana, 2016**), Witch Flounder (**Bowering, 1976 | Burnett *et al.*, 1992 | Wigley & Burnett, 2003**), Offshore Hake (*Merluccius albidus*) and Silver Hake (*Merluccius bilinearis*) in the Northwest Atlantic (**Hunt, 1980 | Helser, 1996 | Traver *et al.*, 2012**), as well as Roundnose Grenadier (*Coryphaenoides rupestris*) in west Greenland waters (**Jørgensen, 1996**). This supports that the increases in size we observed for all four taxa are a sign of interannual growth.

If differences in fish body size between September and July were attributed to seasonality, it would mean that many small fish would migrate to the area between July and September. At the large scale, demersal fish may undertake seasonal migrations for breeding, spawning or wintering (**Bergstad, 2009**). Spawning season varies between the four fish taxa, and consequently, so does juvenile settlement in benthic habitats (**Wenner, 1983 | Kenchington, 1984 | Middleton & Musick, 1986 | Cohen *et al.*, 1990 | Cargnelli *et al.*, 1999 | Burnett *et al.*, 1992**). Based on fish age-size relationships for the four taxa, the smallest fishes we measured in our study area (1-20 cm in TL) were estimated to be 4-18 months-old (**Powles & Kohler, 1970 | Bowering, 1976 | Wenner, 1983 | Burnett *et al.*, 1992 | Hoff *et al.*, 2000 | Saborido-Rey *et al.*, 2004 | Brassard *et al.*, 2017**). Further, based on the life histories of the four taxa, we know that juveniles settle on the seafloor between fall and winter (**Bigelow & Shroeder, 1953 | Kelly & Barker, 1961 | Middleton & Musick,**

1986). These results suggest that juvenile migration and settlement in benthic habitats in the MPA occur before July (or after September), and thus that seasonality is unlikely to explain differences in size between September and July, which supports signs of fish interannual growth.

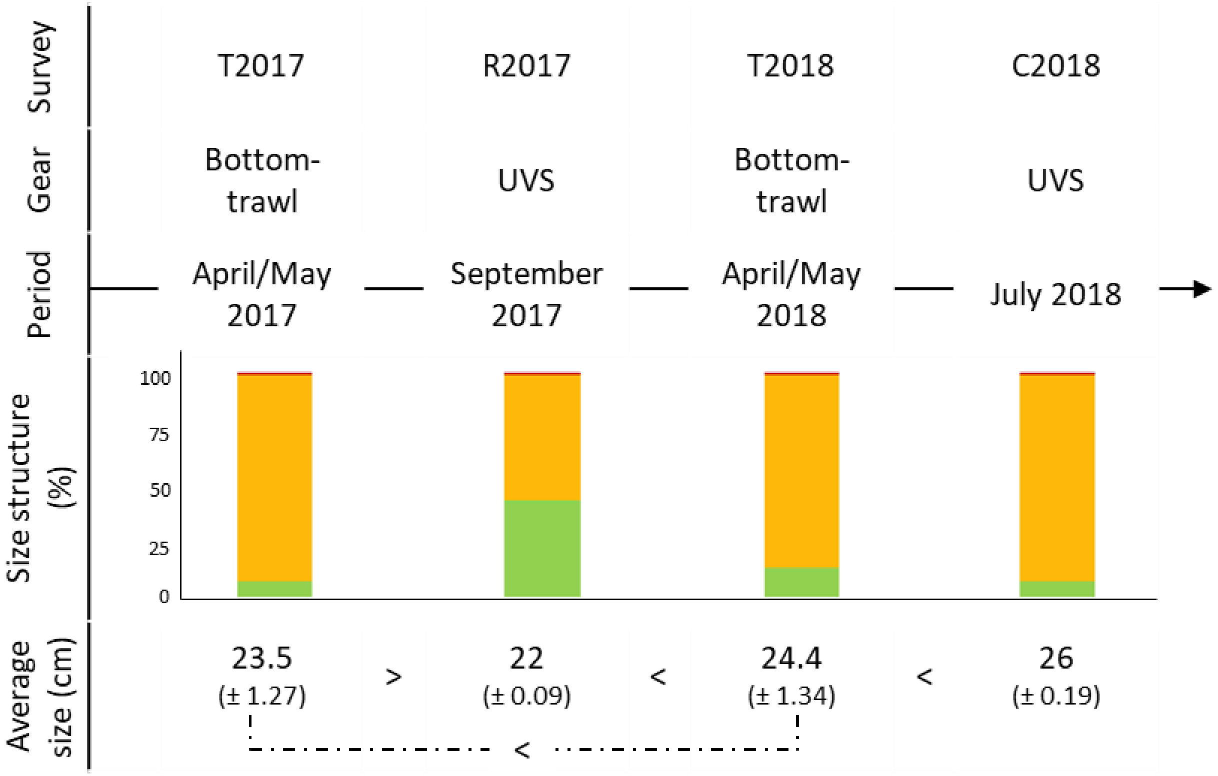


Fig. 3-9 | Redfish size structure (percentage represented by each life stage) and average size (± standard error) assessed by two underwater video systems (UVS) and scientific bottom trawl during four benthic surveys in 2017 and 2018. Green: 'Small juvenile'. Orange: 'Large juvenile'. Red: 'Adult'. Corresponding size classes for Redfish are presented in Table 3-1.

If differences in fish body size between September and July were attributed to gear selectivity, it would mean that ROPOS underestimates 'Large juveniles' and/or CAMPOD underestimates 'Small juveniles'. We compared Redfish size structure and average size per UVS survey to Redfish DFO bottom-trawl assessments. More than 12,000 Redfish were caught and measured during two scientific multi-species bottom-trawl surveys conducted in April/May in 2017 and 2018 in the MPA. While 'Adults' represented only 1% of Redfish in all surveys (videos and trawls), 'Large juveniles' were dominant during both trawl surveys (86 and 92% respectively) (**Appendix 3-17A & 3-17B**), whereas ‘Small juveniles’ were the dominant life stage of the assemblage assessed by UVS in 2017 (**Fig. 3-9**). An increase in Redfish average size assessed by bottom trawl between the two years was also observed (**Appendix 3-17C**), although the average size assessed in April/May 2017 (bottom trawl) was larger than that assessed in September 2017 (UVS), and the average size assessed in April/May 2018 (bottom trawl) was smaller than that assessed in July 2018 (UVS) (**Fig. 3-9**). Though only 36% of Redfish observed on video (n = 4303) were measured, similar size structures were assessed by bottom trawl and CAMPOD, while bottom trawl seemed to under-represent ‘Small juveniles’ compared to ROPOS, despite the small mesh size of the net’s codend (12.5 mm) (**McCallum & Walsh, 1996**).

This suggests that there may be a larger gear selectivity between bottom trawl and UVS (ROV) than between UVSs, and that differences in fish size do not seem to be explained by seasonality, which supports signs of fish interannual growth. Future dedicated *in-situ* studies in the MPA should consider using the same UVS from one survey to another, and should ideally conduct surveys during the same months to reduce bias and confirm the patterns we observed.

Using uni- and multivariate analyses we found evidence of a weak but measurable influence of abiotic and biotic habitat features on fish size in a soft-bottom environment. However, fish-habitat associations were not as strong as expected compared to associations in hard-bottom deep-sea CWC ecosystems. Our GAM models explained only 11-30% of variance for all four taxa, suggesting that 1) the attributes we tested were not strong predictors of fish distribution at different life stages, and more factors would need to be considered to understand the links between fish and habitats at different developmental stages, and/or 2) there are less differences in small-scale distribution between ‘Small’ and ‘Large juveniles’ than between ‘Small juveniles’ and ‘Adults’. This suggests that ‘Large juveniles’ represent a ‘transition’ life stage, mostly comprising individuals that are just starting to mature and some individuals more developed, thus displaying behavior of habitat use of both mature and immature fishes.

3-4.3 | Influence of time of day on fish body size

We found a weak taxon-specific influence of time of day on fish size. The models revealed significant differences in fish body size between day and night for all four taxa. Larger fish were predicted at night than during the day for all fish but Redfish, although the effect sizes were quite small.

At the small scale, demersal fish may undertake frequent daily foraging travels, moving horizontally, between resource patches or vertically in the water column, following nictemeral cycles (**Isaacs *et al.,* 1974**). Daily feeding migrations have been reported for all four taxa, with higher fish abundances near or on the seafloor during the day, assessed from scientific bottom-trawl surveys (**Sedberry, 1978 | Savvatimsky, 1989 | Cohen *et al*., 1990 | Marin *et al*., 1994 | Auster *et al*., 1995**). In comparison, only a few studies have linked feeding migrations to developmental stages. Auster *et al*. (**1995**) hypothesized that diurnal shifts were a way to reduce predation and enhance prey capture. Here, the assessment and comparison of fish density at different life stages between day and night was not feasible, as most of the time only one fish was measured per 10-m segment and per taxon.

The stronger signal revealed for Redfish could be attributed to a larger measured size range compared to the other three taxa, highlighting differences between the very small and the very large fishes. All Redfish life stages have been reported to feed at night in the water column, with a positive fish size-height in the water column relationship (**Marin *et al*., 1994**). This would indicate that while all life stages co-occur on the seafloor during the day, smaller individuals are found near the seafloor, and larger fish higher in the water column. This pattern was revealed within one barren habitat and two CWC habitats, suggesting these habitats serve as feeding grounds for Redfish.

The overall weak influence of time of day can also be attributed to the unbalanced sample between day and night, as the original survey was not designed to test this hypothesis. Our results suggest that for at least three of the four taxa there is no difference between

'Small' and 'Large' juveniles distribution in relation to time of day, but juveniles and adults may have different preferred times of habitat use. Future dedicated studies should consider integrating time of day in the sampling design, accounting for fish density at different life stages, as a failure to do so might bias the assessment of fish size structure.

3-4.4 | Influence of depth on fish body size

Despite the small depth range in the study area (179-455 m), the influence of depth on fish body size was revealed for two fish taxa. Body size was positively correlated with depth for Longfin Hake and Redfish, indicating that larger fish were distributed in deeper waters than smaller individuals. These results are in agreement with known preferred depth distributions of life stages for the two fish taxa (**Brown & Hennemuth, 1965 | Wenner, 1983**). Indeed, for both taxa, adults are found deeper than juveniles, as a way to reduce interspecific competition and predation between life stages for Longfin Hake (**Sedberry, 1975**), while mature Redfish migrate to settle in deeper habitats (**DFO, 2011b**). While past studies have reported different preferred depth ranges for juveniles and adults, here we provided evidence of a similar behaviour between 'Small' and 'Large juveniles' for these two taxa.

No significant influence of depth on fish size was found for Marlin-Spike Grenadier and Witch Flounder, though our GAM models indicated a positive correlation between depth and fish size for Marlin-Spike Grenadier, and a negative correlation for Witch Flounder. These results indicate that for both taxa, 'Small' and 'Large' juveniles co-exist at similar depths but could be distributed in a different depth range than adults. This would be in alignment with known preferred depth distribution of Marlin-Spike Grenadier and other macrourids in the Northwest Atlantic at different life stages (**Munroe *et al*., 1981 | Snelgrove & Haedrich, 1985**). The depth distribution of Witch Flounder at different life stages is still being debated. While some studies reported that adults are distributed shallower than juveniles, others suggested that both life stages have overlapping depth ranges (**Bowers, 1960 | Powles & Kohler, 1970 | Bowering, 1987 | Walsh, 1987 | Burnett *et al*., 1989**). Differences in depth distribution for Witch Flounder are associated with ontogenetic seasonal shifts, and seem to be triggered by temporal variability of local conditions (*e.g.*, water temperature and food supply availability) (**Bowering, 1976**). Witch Flounder is mostly distributed between 50-200 m deep and can be found up to 400 m deep. We did not measure any 'Adults' in the study area, but our results could indicate that larger Witch Flounder could be distributed in shallower waters off eastern Newfoundland, at depths we did not survey.

3-4.5 | Influence of substrate on fish body size

We found a taxon-specific but weak influence of soft-bottom micro-habitat features and hard-bottom substrate on fish body size for all four taxa. The relationship between fish body size and habitat structural complexity was not as linear as expected. Yet, patterns of distribution for all four fish taxa at different life stages emerged.

Witch Flounder, like many flatfish species, are highly associated with soft sediments where they feed on meiofauna and bury themselves for camouflage and protection (**Powles & Kohler, 1970 | Phelan *et al.*, 2001 | Stoner & Ottmar, 2003**). *Ex-situ* experiments conducted on Winter Flounder (*Pseudopleuronectes americanus*) showed that adults had a higher ability to dig through coarse sediment than juveniles, which were more restricted to fine-grain sediment (**Phelan *et al.*, 2001**). In addition, other studies have reported a strong association between Witch Flounder juveniles and soft-sediment depressions, presumed to be used to shelter from current and predation in addition to provide food supply (**Auster *et al.*, 1995 | Hallenbeck *et al.*, 2012**). Here, our results are in agreement with known associations of Witch Flounders and known behaviors of flatfishes generally, and suggest that 'Large juveniles' are less specialized to bottom types than 'Small juveniles' (**Scott, 1982**).

Redfish is the only taxon for which a linear correlation between body size and habitat complexity has been revealed. Our results are in agreement with previous findings reported by Auster *et al*. (**2003**). Indeed, in their study the authors demonstrated that small juveniles (0-10 cm) were associated with boulder reefs, large juveniles (10-20 cm) with boulder reefs and structural biogenic habitats, and redfish >20 cm with structural biogenic habitats only (**Auster *et al*., 2003**). Moreover, Redfish is known to display high flexibility in substrate affinity (**Hallenbeck *et al*., 2012**), with reports of associations with complex rocky structures (**Du Preez & Tunnicliffe, 2011**) or with soft-sediment depressions (**Templeman, 1959 | Scott, 1982**). While it has been suggested that both micro-habitats are used as shelter against current and predation, no connection with Redfish size or life stages were mentioned. Here we suggest that one explanation of Redfish flexibility in substrate affinity is variability between life stages.

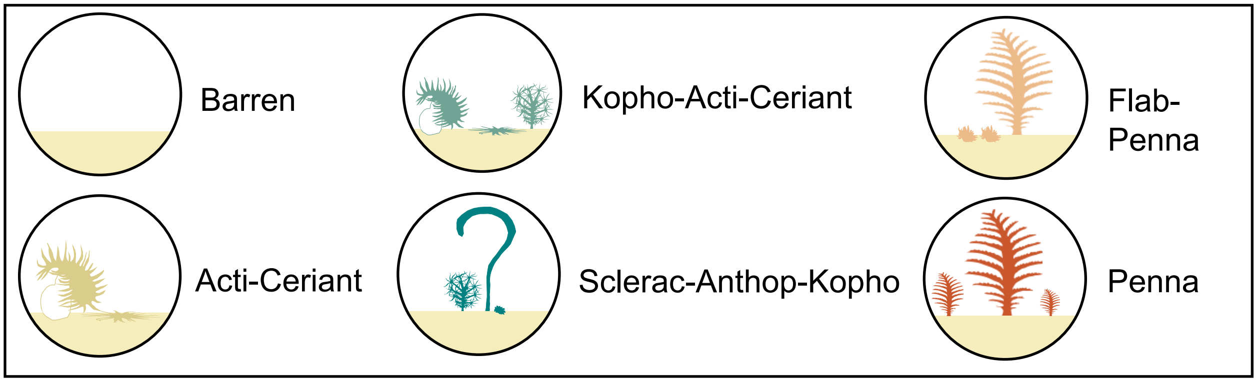
While previous studies have reported the association of Longfin Hake with both hard- and soft-bottom substrates, or with soft-sediment depressions, no connection with Longfin Hake size or life stages were mentioned (**Cohen *et al*., 1990 | Auster *et al*., 1995**). Here, our results are in agreement with known associations of Longfin Hake and suggest that as juveniles grow, they progressively become less restricted first to complex muddy sediments and later to muddy sediments in general.

Marlin-Spike Grenadier 'Small juveniles' were invariably associated with all soft-bottom habitats (with or without relief) while 'Large juveniles' appeared more dependent on hard-bottom substrates. The ecology of Marlin-Spike Grenadier, and macrourids in general, is quite overlooked, and no known associations of Grenadiers with bottom types have been reported. Here we provided for the first time differences in micro-habitat distribution in relation to physical features for this taxon.

While associations between groundfish species and specific bottom types have been reported in other studies (**Templeman, 1959 | Haldorson & Love, 1991 | Love *et al*., 2002 | Du Preez & Tunnicliffe, 2011**), the relationships between physical micro-habitat features and fish body size have been less commonly demonstrated, especially in deep-sea soft-bottom environments. Diaz *et al*. (**2003**) found a strong positive correlation between juvenile fishes and size of micro-habitat features in a soft-bottom shallow environment off the northeastern coast of the US, with more fish being associated with features taller than 30 cm. Our results indicate that all four fish taxa undergo ontogenetic shifts in use and specialization of micro-habitats provided by physical attributes in a low-relief soft-sediment environment. We also provided evidence that those shifts occur before the adult life stage. In addition, other associations demonstrated in other studies suggest that other habitat factors might further explain fish-bottom type relationships (*e.g.*, bottom current, size, density or extent of abiotic habitat features, prey/predator occurrence). Future dedicated studies in the MPA should consider integrating additional biotic and abiotic parameters when assessing fish small-scale distribution in relation to benthic physical attributes.

3-4.6 | Influence of benthic habitat on fish body size

We found a taxon-specific but weak influence of soft-bottom benthic habitat type on fish body size for all four taxa. Our analysis revealed significant increases in fish body size between the two years within three coral habitats exclusively for Longfin Hake and Marlin-Spike Grenadier, within the non-coral habitat and two coral-habitats for Witch Flounder, and within all habitats - including the non-structural habitat - for Redfish. Increase in fish body size within the *Pennatula* fields was the highest for three fish taxa, and similar to the coral habitat dominated by solitary cup corals and two other sea pen taxa for Marlin-Spike Grenadier (**Fig. 3-10**). Our results showed signs of interannual growth associated with habitats provided by epibenthic invertebrates for all four taxa, especially within sea pen habitats. However, fish-habitat relationships seem to be facultative rather than obligate as similar patterns were observed in other benthic habitats.



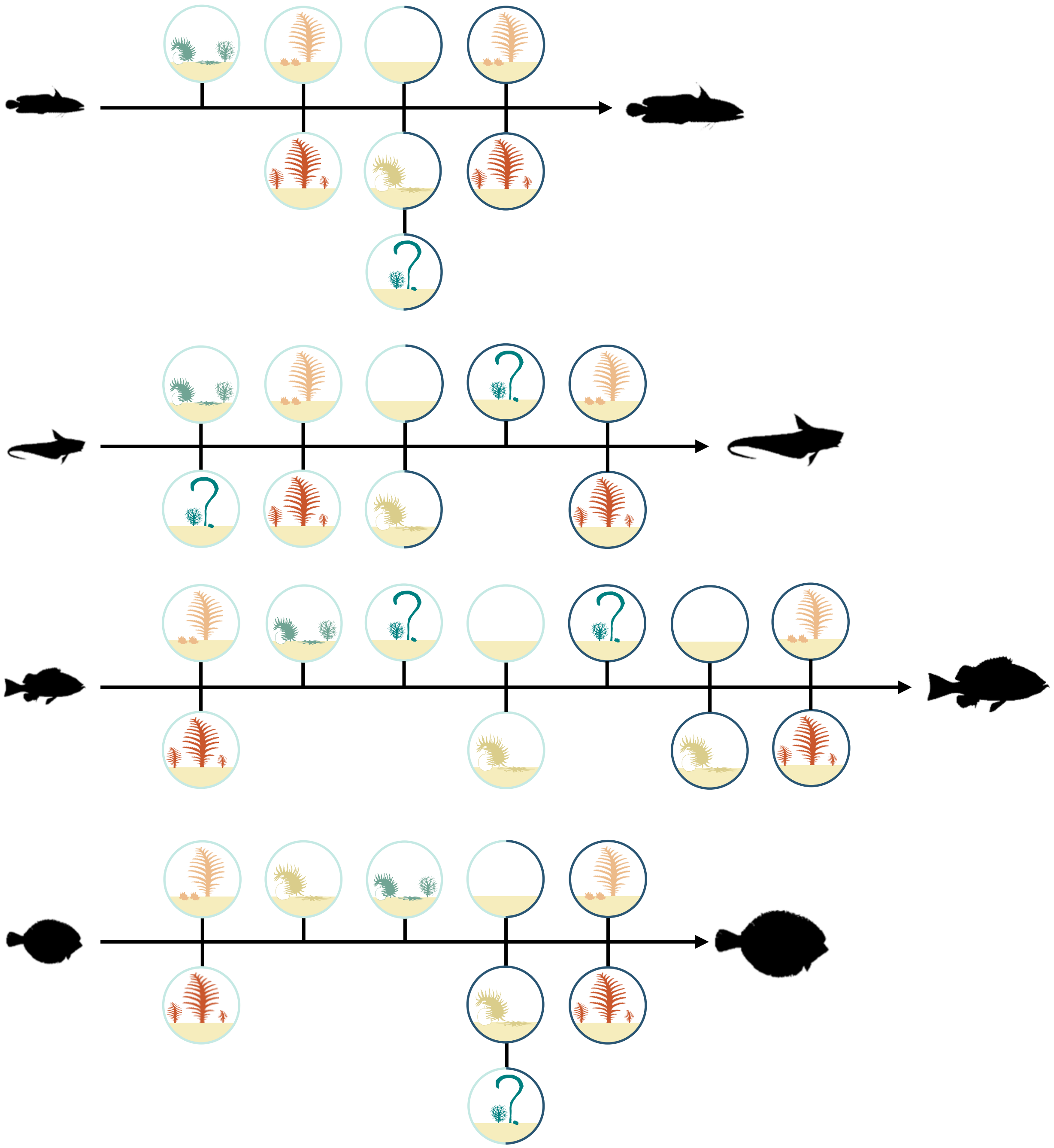


Fig 3-10 | Distribution of fish in relation to fish body size per benthic habitat type in 2017 (light blue) and 2018 (dark blue) estimated from the uni- and multivariate analyses for (top to bottom) Longfin Hake, Marlin-Spike Grenadier, Redfish and Witch Flounder. The arrows represent the increasing body size for each taxon between the two surveys. Benthic habitats circled in both shades of blue indicate no difference in fish body size between 2017 and 2018. Each plot is to be read independently and does not represent a comparison of fish size between taxa.

Many studies have reported coincidental co-occurrence of fishes and habitats created by invertebrate taxa, even in hard-bottom ecosystems (**Uiblein *et al.*, 2003 | Auster *et al.*, 2005, 2007 | Reed *et al.*, 2006 | Tissot *et al.*, 2006 | Edinger *et al.*, 2007 | Ross & Quatrini, 2007 | D'Onghia *et al.*, 2010, 2012 | Foley *et al.*, 2010 | Biber *et al.*, 2014 | Kutti *et al.*, 2014, 2015 | Milligan *et al.*, 2016**). Facultative relationships are expected for fish-invertebrate associations, particularly for adults as they are less habitat specific than juveniles. Despite common findings, here we provided evidence that fish juveniles are less habitat specific than expected in soft-bottom ecosystems. Soft-bottom CWCs likely provide important, and perhaps preferred, habitats for fishes, but not exclusive habitats.

In this study, we only considered the influence of benthic habitats characterized by invertebrate assemblages, and were able to compare CWC habitats to non-structural and non-coral habitats. However, it was difficult to assess and compare the influence of sea pen and/to other CWC habitats (*e.g.*, *Kophobelemnon* habitat not surveyed in 2018), as well as the taxon-specific influence of corals on fish body size. Increases in fish body size within *Pennatula* fields with or without the co-occurrence of *Flabellum* solitary scleractinians were similar, suggesting that elevated *Pennatula* sea pens could have a higher influence than ground-level solitary cup corals on fish size. Moreover, *Pennatula* densities assessed during the 2017 survey were the highest of all habitat-forming invertebrates in both habitats (**Chapter 2**), suggesting that coral density could also have an influence on fish growth. Influences of the density and height of biogenic features on fish juveniles have been demonstrated in both shallow and deep, as well as both soft- and hard-bottom environments in the Northwest Atlantic and Northeast Pacific (**Diaz *et al.*, 2003 | Rooper *et al.*, 2019 | Henderson *et al.*, 2020**). For instance, Rooper *et al.* (**2019**) found a correlation between fish size, feature size and distance to habitat features in both hard- and soft-bottom coral and sponge habitats.

All four fish taxa were described as sedentary taxa in other studies (**Bigelow & Shroeder, 1953 | Sedberry, 1975 | Wenner, 1983 | Middleton & Musick, 1986 | Scott, 1988**), showing limited movements after settlement, mostly consisting in daily migrations between feeding and resting areas (**Holmlund & Hammer, 1999**). Considering that juveniles have a low mobility compared to adults, their movements are even more limited in time and space. Diaz *et al*. (**2003**) underlined the importance of proximity between habitats of different complexity for fish juveniles, as close distinct habitats can fulfill many requirements within a short distance. Most of the benthic habitats surveyed in this study presented a patchy distribution within and/or between stations (**Appendix 3-2C**). It is assumed that benthic habitats where no increase in fish body size was assessed are used as resting grounds or corridors. Conversely, we predict that benthic habitats where fish body size increased between the two surveys are used as feeding grounds. In their study, Diaz *et al.* (**2003**) suggested that complex habitats were used as refuges from predation, while simpler habitats served as foraging areas. Here, we predicted an opposite use of habitats for three of the four taxa where barren areas are used as resting grounds and invertebrate assemblages used as feeding grounds. On the other hand, Redfish showed signs of interannual growth within all habitats, representative of a generalist behavior and multi-use of habitats.

Additionally, considering their migration patterns and poor swimming abilities, it is unlikely that juveniles (between ‘Small’ and ‘Large juveniles’) undergo ontogenetic habitat shifts (**Bigelow & Shroeder, 1953 | Sedberry, 1975 | Middleton & Musick, 1986 | Scott, 1988**). Had we not looked at fish distribution patterns across habitats per year, we probably would not have observed any influence of habitats on fish size, and would have interpreted results as ‘Small’ and ‘Large’ juveniles distributed in different benthic micro-habitats. While it is too early to conclude if fish undergo ontogenetic shifts in benthic habitats, here our results suggest otherwise, as both ‘Small’ and ‘Large’ juveniles co-occurred in the same habitats. More data should be collected to increase understanding of fish distribution patterns in the MPA.

3-4.7 | Ecological role of sea pens for juvenile fish

Preliminary results suggest that *Pennatula* sea pens have a greater influence on fish size than other invertebrates. Yet, the functional or ecological nature of fish-sea pen association is still unknown. CWCs are attributed the role of safe breeding, spawning and nursing areas for many invertebrate and fish species (**Reed & Hoskin, 1987 | De Clippele *et al.*, 2015**). In most studies, those assumptions were based on the anecdotal *in-situ* video observations of eggs or egg cases, gravid females, fish larvae or small fish within CWC habitats, both in hard-bottom habitats and in sea pen habitats, on both sides of the Atlantic (**Fosså *et al.*, 2000, 2002 | Costello *et al.*, 2005 | D'Onghia *et al.*, 2010 | Baillon *et al.*, 2012 | Henry *et al.*, 2013 | Buhl-Mortensen *et al.*, 2017b | Corbera *et al.*, 2019 | Rueda *et al.*, 2019**). In addition, while the majority of existing studies assessed fish abundance within coral and non-coral habitats, or fish assemblage/taxon size structure of the overall sample, only a few compared fish body size associated with CWC habitats (**Husebø *et al.*, 2002 | Laidig *et al.*, 2009 | Corbera *et al.*, 2019**). Husebø *et al*. (**2002**) and Laidig *et al.* (**2009**) reported larger fish (presumably mature) associated with *Desmophyllum pertusum*, *Paragorgia* spp. and *Primnoa* spp. coral habitats than in surrounding non-coral habitats in the Northeast Atlantic. They suggested that fish would find refuge in coral habitats from bottom-contact fishing activities, where they benefit from enhanced food supply to grow and survive (**D'Onghia *et al.*, 2019**).

De Clippele *et al*. (**2015**) compared the macrofauna associated with multiple hard-bottom and soft-bottom CWCs in the Norwegian Sea. Despite being smaller than their hard-bottom relatives, it was revealed that sea pens, such as *Pennatula* spp. and *Kophobelemnon* spp., create micro-habitats for smaller macrofauna than that associated with *Desmophyllum pertusum* reefs, *Paragorgia* or *Primnoa* gorgonians. While ostracods and amphipods were located on or in sea pen polyps, shrimps were found sitting on the sea pens. These findings on both sides of the North Atlantic suggest that sea pens create biogenic habitats for many small macrofauna taxa (**De Clippele *et al.*, 2015**). In a recent study conducted in the Laurentian Channel, Miatta & Snelgrove (**2022**) provided evidence that sea pens, especially *Pennatula* spp., locally and regionally increased the diversity and density of associated meiofauna, particularly in the upper 5-cm sediment layer, compared to surrounding barren environments. Their results suggest that sea pen fields create biogenic habitats that provide a 'constant' food supply for many macro- and megafauna taxa. Additionally, Tissot *et al*. (**2006**) demonstrated that sea pens can alter water current flow, thus affecting nutrient and planktonic supply near the seafloor.

According to the findings of these three studies, sea pens can enhance food supply above, on and in the sediment. Longfin Hake, Marlin-Spike Grenadier, Redfish and Witch Flounder all display an ontogenetic shift in diet. While adults can adopt a pelagic feeding strategy, juveniles are almost mostly zooplanktivorous benthic feeders, limited to feeding on small prey (*e.g.*, small copepods, amphipods, polychaetes, shrimps) (**Bigelow & Shroeder, 1953 | Sedberry, 1975 | Wenner, 1983 | Bowman & Michaels, 1984 | Mauchline & Gordon, 1984 | Konstantinov *et al.*, 1985 | Savvatimsky, 1989 | Cohen *et al.*, 1990 | Marin *et al.*, 1994**). Thus, it is likely that sea pen fields are used as feeding grounds providing quality food for fish (*e.g.*, adapted small size of prey), and that *Pennatula* corals, being the densest invertebrate taxon, provide a higher quantity of food supply, enhancing higher fish growths.

Alternatively, fish distribution patterns across stations, for the four taxa, were assessed in the Laurentian Channel during the ROPOS 2017 survey (Chapter 2). Strong dispersion patterns (low local fish densities) were associated with one or both *Pennatula* fields for all fish taxa. Conversely, fish presented higher local densities in the benthic habitats where we observed smaller increases in fish size between the two years compared to those observed in the *Pennatula* habitats. Fish distribution patterns (Chapter 2) combined with our results suggest that differences in fish body size increase between benthic habitats could be attributed to differences in fish local densities. High local densities likely enhance more intra-specific resource competition in the non-*Pennatula* habitats, potentially leading to food scarcity.

Our results are in agreement with studies that provided evidence of high fish growth rate associated with CWC habitats (**Husebø *et al.*, 2002 | Laidig *et al.*, 2009 | D'Onghia *et al.*, 2019**). At this stage, it is still too early to conclude if large increases in fish size associated with *Pennatula* fields are linked to high food supply availability, quality and quantity or to low fish intra-specific competition.

Many studies reported the simultaneous presence of all fish life stages (larvae, juveniles and adults) associated with CWCs, underlining the multipurpose role of corals (**Laidig *et***

***al*., 2009 | D'Onghia *et al*., 2010, 2019 | Corbera *et al*., 2019**). Baillon *et al.* (**2012**) provided evidence of sea pens being used as spawning grounds for Redfish (presence of larvae) in the Laurentian Channel. Here, we are contributing to new knowledge with the evidence of the presence and association of four groundfish taxa, including Redfish, in their early-life stages with those same sea pen fields. Our results suggest that sea pen habitats are used as nurseries and, based on other studies, as feeding grounds by four groundfish taxa juveniles.

Gaps in our analysis should be addressed in future studies, with focus on collecting more data in *Kophobelemnon*-dominated habitats, assessing invertebrate taxon density at the small-scale (*e.g.*, 10-m segments), and testing the influence of individual invertebrate taxa on fish size. Our study stresses the importance of integrating the temporal dimension, at small and large scales, when studying the spatial distribution and habitat-association of fish at different life stages, as well as fish density**.** While we observed a weak influence of benthic habitat types on fish size, it is likely that other factors not included in this study may have a greater influence on fish distribution and may better explain fish-habitat associations (*e.g*., size, density or extent of biotic habitat features, medium to large-scale distribution of micro-habitats, prey/predator relationships). Future dedicated studies in the MPA should consider integrating additional biotic and abiotic parameters when assessing fish small-scale distribution in relation to benthic biological attributes.

Overall, we found evidence of the influence of biotic and abiotic habitat features on fish small-scale distribution at different life stages in soft-bottom environments. Despite low signals from our analysis, many insights have been drawn from this study on fish habitat use and specialization in relation to ontogenetic shifts, and on the variability thereof. Here, we provided evidence of ontogenetic shifts between 'Small' and 'Large' juveniles, which has not been considered until now. However, differences in distribution between 'Small' and 'Large' juveniles were not as discernible as differences between juveniles and adults. This is not surprising as 'Large juvenile' cohorts might comprise both immature and mature fishes. Our study suggests that the Laurentian Channel MPA provides feeding and resting grounds for abundant groundfish juveniles where they can grow in a safe environment before presumably migrating and settling in their adult habitat.

3-4.8 | Implications for fish monitoring and MPA management

Traditionally, surveys of demersal fish species are conducted with mobile or fixed bottom-tending gear, especially bottom trawls. In Atlantic Canada, data on commercial and non-commercial fish and invertebrate species are collected during multispecies annual trawl surveys (**DFO, 2015a**). Although this tool provides valuable data, its use in MPAs is controversial due to their impacts on the habitat being conserved (*e.g.*, habitat destruction, resuspended sediment, and fauna removal) (**Auster, 2005**). Moreover, because trawl surveys generally cover a large spatial scale (*e.g.*, 1.5 km per tow in the Northwest Atlantic), small-scale processes to which fish respond (~1-100 m scale) are often masked (**Edinger *et al.*, 2007 | Baker *et al.*, 2012a**), which can lead to knowledge gaps or misinterpretation.

UVSs are effective non-destructive and non-extractive monitoring tools that can be deployed in both trawlable and non-trawlable areas, and assist in reducing knowledge gaps (**Graham *et al.*, 2004 | Pacunski & Palsson, 2008 | Stoner *et al.*, 2008 | Sward *et al.*, 2019**). The use of video-based surveys can provide additional *in-situ* observations on habitats, fish habitat use, community composition, and behaviour in structurally complex habitats and at a finer spatial scale (**Trenkel *et al.*, 2004 | Lorance & Trenkel, 2006 | Ross & Quattrini, 2007 | Clark *et al.*, 2016**).

Fish are known to react to UVSs which can induce *in-situ* observation bias, especially juveniles (**Stoner *et al.*, 2008 | Rooper *et al.*, 2019**). In this study, 96% of fish showed null or minor reactions (*i.e.*, light body movement that do not trigger fish to leave their position or the field of view) when UVSs were approaching (**Chapter 4**). Here UVSs proved to be an effective tool for capturing representative fish local size structures, despite fish mobility and the low subsample of fish measured, and thus could be a non-intrusive substitute to traditional scientific bottom trawling.

We acknowledge that our estimations of immature/mature fish ratio might be biased, and that only biological samples can validate our assessment. Analyses that consider fish size as continuous variable rather than discrete life stages could help to reduce bias and allow for additional insights from the resulting patterns (**Austin, 2007**). Nonetheless, complementing *in-situ* visual data with trawl surveys would enable the creation of a local baseline on fish size at maturity for each taxon (**Diaz *et al.*, 2003 | Pacunski *et al.*, 2016**). We therefore recommend the combination of UVS and bottom trawl be deployed in trawlable habitats, during a dedicated survey, both to collect data on fish life stage composition in the Laurentian Channel MPA and to calibrate the assessments.

This study was part of a broader suite of investigations that evaluated different aspects of benthic habitats within the Laurentian Channel MPA (**de Mendonça & Metaxas, 2021, 2023, 2024 | Miatta & Snelgrove, 2021, 2022 | Chapter 2**) using UVSs as a primary scientific investigation tool. The primary focus of the multi-species UVS surveys was to assess the spatial structure of corals in the MPA (**de Mendonça & Metaxas, 2023, 2024**), with the fish survey approach integrated into the existing coral survey design. Despite not being specifically optimized for fish assessments, we were nonetheless able to assess fish-habitat associations and to identify fish species and size relationships with respect to benthic habitat attributes. This new knowledge contributes to the understanding of the ecological role of sea pen habitats in the MPA for associated fauna. Although the four fish taxa we focused this study on are not key species targeted by the MPA protection measures, they are nonetheless significant members of the regional groundfish assemblage.

Sea pen fields have been recognized as VMEs and Essential Fish Habitats (EFH) on both sides of the North Atlantic (**Ardizzone, 2006 | Greathead *et al.*, 2007 | Fuller *et al.*, 2008 | FAO, 2009 | Murillo *et al.*, 2010 | Rogers & Gianni, 2010 | Kenchington *et al.*, 2013 | Burgos *et al.*, 2020**). Baillon *et al.* (**2012**) were the first to draw attention to the ecological importance of soft-bottom CWCs for early-life stage fish and their vulnerability to human activities in the area, arguing that coral habitats in the Laurentian Channel should be classified as VMEs and EFHs. Since then, several Sensitive Benthic Areas (SBA), equivalent to VME habitats outside Canadian waters, have been identified for sea pens in the Laurentian Channel and most are now protected within the MPA (**FAO, 2009 | Kenchington *et al.*, 2011, 2016**). Under the definition of EFHs in the United States, these are considered as ‘waters and substrates necessary to fish for spawning, breeding, feeding or growth to maturity’ (**USDOC, 1996**). This definition implies that such habitats are vital for fish to survive and for sustaining fish populations. Based on our observations on groundfish-habitat associations within the Laurentian Channel MPA, functional relationships between groundfish and coral habitats appear to be facultative (*i.e.*, fish survival benefits from sea pen habitats) rather than obligate (*i.e.*, fish survival depends on sea pen habitats). While the associations may not be obligate, sea pen fields in the MPA do provide nursery areas for abundant immature groundfish, and so play a significant ecological role in sustaining fish populations, and the remainder of the food chain that depend on them. More data should be collected in the MPA on both fish and corals (*i.e.*, CWC habitat spatial extent, fish trophic interactions, fish growth rates, fish competition) to better assess the status of sea pen habitats as biogenic habitats.

In addition to sea pens, conservation and research objectives of the MPA aim to protect five marine vertebrate species, including Black Dogfish (*Centroscyllium fabricii*) and Smooth Skate (*Malacoraja senta*) (**Lewis *et al.*, 2016**). Large densities of immature Black Dogfish and Smooth Skate have been reported in the channel, which indicates that the Laurentian Channel supports ecologically important nursing grounds for sensitive marine species (**Kulka, 2006 | Lewis *et al.*, 2016**). Here we provided new evidence that other early-life stage fishes not targeted by the MPA conservation measures occur in the channel and benefit from the protection of sea pens.

Our results support that micro- and meso-scale habitats (*e.g.*, cm, m to km) are ecologically important for fish juveniles, as they provide smaller niches adapted to fish size (small physical and biological features) (**Diaz *et al.*, 2003**). Fish-habitat associations are the strongest for juvenile fishes as they are the most vulnerable at this stage. There is a need to keep monitoring juvenile-habitat relationships as they likely affect fish survival and recruitment, which maintain ecosystem processes and sustain ecosystem services

(**Holmlund & Hammer, 1999**). Here, the use of UVSs in the Laurentian Channel MPA contributed to the acquisition of valuable new information on fish size structure and yielded information on small-scale distribution of fish in association with benthic habitat attributes. Future dedicated studies should take fish mobility and time of day into consideration when designing the sampling strategy (*i.e.*, transect design), reduce seasonal and gear selectivity, as much as feasible, and continue monitoring both coral and non-coral habitats.

3-5 | Conclusion

This study assessed groundfish local size structure in a deep-sea low-relief soft-bottom environment using two UVSs. Very little is known about the habitat requirements of the fish taxa assessed in this study. Here, we contributed to additional knowledge on the small-scale distribution of deep-sea demersal fish juveniles. We provided evidence of the use of sea pen habitats as nurseries for early-life stage fish, even though sea pens contribute less to habitat heterogeneity than hard-bottom corals. Our study suggests that fish may stay in the Laurentian Channel MPA over multiple years before presumably migrating and settling in their adult habitat. Where most studies compare the large-scale distribution of juvenile and adult fish, our results revealed differences in small-scale fish distribution between ‘Small’ and ‘Large’ juveniles. Finally, our results support the use of UVSs as an effective, non-destructive approach to conduct *in-situ* benthic surveys, and as a valuable tool for MPA management and monitoring.

Chapter 4

Fish *in-situ* behavior and variability of reactions to two underwater video systems in a soft-bottom deep-sea ecosystem

Abstract

Underwater video systems (UVSs) are increasing in use as an alternative to conventional scientific bottom trawls for multi-species benthic surveys. While providing valuable data on fish distribution and habitat requirements not acquired by bottom trawls (*e.g.*, *in-situ* observations of fish habitat use, fish behavior and small-scale fish-habitat associations), there are limitations in using UVSs to record mobile fauna, such as the potential bias induced by fish reactions to UVSs.

Here, we analysed the behavioral reactions of nine groundfish taxa to two UVS types in a deep-sea soft-bottom environment. Our objectives were to describe fish *in-situ* behavior and response behavior to UVSs, as well as to assess the variability of fish reactions in relation to several survey-related, environmental and fish-related factors.

Using multivariate analysis, fish taxa were grouped in three clusters based on their *in-situ* behavior: active pelagic, active bentho-pelagic and passive benthic fish. Variability of fish *in-situ* behavior attributes (*i.e.*, altitude, activity and locomotion) with depth, time of day, habitat type or fish life stage was low and taxon-specific. Of all fish observed, 95% of fish did not react or displayed minor reactions to UVSs. Multinomial logistic regression models revealed low variability in fish reactions to technical or environmental factors. On the other hand, we observed more taxon-specific variability in fish reactions with fish altitude, locomotion and activity, as well as with fish distance to UVSs. We did not observe any difference in fish reactions at different life stages.

For deep-sea groundfish taxa in a soft-bottom environment, our results suggest that 1) 'Neutral' reaction is the most common response to UVSs for most fish taxa, 2) most variability in fish reactions was influenced by fish *in-situ* behavior (*i.e.*, locomotion, altitude in water column) and 3) reactions observed did not induce any bias in estimating observed abundances. Two fish taxa (one undetermined Teleostei taxon and one Skate taxon)

displayed strong reactions which limited our ability to identify them at the species level, which can be detrimental in a conservation context. Complementary identification from biological samples and collaboration with expert taxonomists is advised to reduce this gap. Major attraction and following reactions to UVSs from two pelagic taxa stress the importance of relying on video footage instead of still images when conducting fish surveys to avoid overestimation of highly mobile fish abundances. Based on the overall limited fish reactions that we documented, UVSs could be used to document groundfish populations in a deep-sea soft-bottom environment.

4-1 | Introduction

Surveys of deep-sea demersal fish species are traditionally conducted with mobile or fixed bottom-tending gear, often bottom trawls. In Atlantic Canada, data on commercial and non-commercial fish and invertebrate species are collected during multispecies annual trawl surveys, yielding information on fish diversity, relative abundance and distribution, population dynamics and community structure (**Stoner *et al.*, 2008 | DFO, 2015a**). Scientific bottom-trawl surveys have the advantage of covering large areas and enabling the collection of biological samples, allowing for post-survey data collection including studies of genetics, gut contents and fish aging. Although bottom trawls provide valuable data, their use is controversial due to their impacts on populations and benthic habitats (*e.g.*, disturbance of populations, habitat destruction, resuspended sediment, and fauna removal) (**Auster, 2005**). Moreover, because trawl surveys generally cover a large spatial scale, small-scale features and processes to which fish respond (~m to 100-m scale) are often masked, which can lead to knowledge gaps or misinterpretation of data important for conservation and management (**Edinger *et al.*, 2007 | Baker *et al.*, 2012a | D'Onghia *et al.*, 2012**).

With advances in ocean technology over recent decades, imaging and acoustic underwater systems are increasingly used as an alternative to scientific bottom trawls to conduct deep-sea benthic surveys (**Sward *et al.*, 2019**). These systems are effective non-destructive and non-extractive monitoring tools that can be deployed in both trawlable and non-trawlable areas (*i.e.*, rocky-bottom substrates and protected areas), and assist in reducing knowledge gaps associated with scientific bottom-trawl surveys (**Lorance *et al.*, 2000 | Stoner *et al.*, 2008 | Sward *et al.*, 2019**). For instance, in addition to collecting comparable data on biodiversity, fauna abundance and distribution, population dynamics, biomass estimation or community structure, video-based surveys can provide valuable *in-situ* data that were previously impossible to collect in the deep sea, in structurally complex habitats and at a finer spatial scale (**Ross & Quattrini, 2007 | Laidig *et al.*, 2013 | Clark *et al.*, 2016 | Boldt *et al.*, 2018**). These include fauna density, small-scale habitat association of fish and habitat attributes, interactions of fish in their natural environment and fish population size structure (**Adams *et al.*, 1995 | Lorance *et al.*, 2000, 2002, 2006 | Uiblein *et al.*, 2002, 2003 | Trenkel *et al.*, 2004 | Stoner *et al.*, 2008 | Ryer *et al.*, 2009 | D'Onghia *et al.*, 2011**). Moreover, contrary to trawl surveys, video-based surveys can be used to conduct *in-situ* experiments and provide *in-situ* observations of species as well as information on several behavioral traits (**Laidig *et al.*, 2013 | Ayma *et al.*, 2016 | Collins *et al.*, 2017**).

A wide range of underwater video systems (UVS) are used to observe fish in their natural environment, including drop-cameras (**Rooper *et al.*, 2010, 2015**), remotely operated vehicles (ROV) (**Adams *et al.*, 1995 | Lorance & Trenkel, 2006 | Stone, 2006**), underwater towed vehicles (**Clarke *et al.*, 2009 | Lembke *et al.*, 2013**), human operated vehicles (HOV) (**Krieger, 1993 | Laidig & Yolavich, 2016**), baited cameras (**Widder *et al.*, 2005 | Devine *et al.*, 2019**) and autonomous underwater vehicles (AUV) (**Clarke *et al.*, 2009 | Meyer *et al.*, 2019**). Yet, these systems are relatively new and the technology is still improving, and so the behavior of deep-sea fish - and deep-sea organisms in general - is still poorly understood (**Lorance & Trenkel, 2006**). There is a need to conduct direct *in-situ* observations of fish to understand their natural, undisturbed behavior. However, as with any survey gear type, there are limitations in using UVSs to record mobile fauna, especially fish whose natural behavior can be affected in the presence of UVSs. Fish are known to react to UVSs which can potentially induce *in-situ* bias in observations and results. Documented behavioral responses include avoidance and attraction, which can respectively lead to the under or overestimation of fish abundances, as well as to missed or erroneous identifications of habitat associations (**Trenkel *et al*., 2004 | Stoner *et al*., 2008 | Ryer *et al*., 2009 | Laidig *et al*., 2013 | Sward *et al*., 2019**).

Fish may respond to various environmental stimuli such as visual, acoustic, mechanical, chemical and electromagnetic signals. Fish natural behaviour may also be altered due to a number of influences from UVSs or from the survey vessel at the surface, including vehicle type, motion, speed, motor noise, water displacement, chemical release or, most significantly, artificial light used for illumination purposes (**Uiblein *et al*., 2003 | Trenkel *et al*., 2004 | Lorance & Trenkel, 2006 | Stoner *et al*., 2008 | Ryer *et al*., 2009 | Uiblein & Lorance, 2007 | de Robertis & Handegard, 2013 | Sward *et al*., 2019**). The type and intensity of fish reactions to UVSs can be influenced by many variables including fish specific biology and ecology, as well as environmental conditions such as habitat, substrate, temperature or current speed (**Engås, 1994 | Trenkel *et al*., 2004**).

Yet, the influence of video systems on fish behaviour is rarely measured during dedicated fish surveys (**Stoner *et al*., 2008**) and when it is, measurements are limited to qualitative reports and/or *in-situ* behavior of fish (**Pacunski *et al*., 2008 | Rountree & Juanes, 2010 | Smith *et al*., 2010 | Consoli *et al*., 2016 | Thomson *et al*., 2018 | Dunlop *et al*., 2020 | Wetz *et al*., 2020 | Vigo *et al*., 2023**). There is a need to quantitatively study fish reactions to UVSs during surveys, as well as the nature and magnitude of these reactions. Most dedicated studies only use a simple scale to describe fish response behavior (*e.g.*, attraction, no reaction or avoidance) (**Moser *et al*., 1998 | Johnson *et al*., 2003 | Mitson & Knudsen, 2003 | Porteiro *et al*., 2013 | Laidig & Yolavich, 2016 | Devine *et al*., 2020 | Benoit-Bird *et al*., 2023**), but more detailed analysis of which factors drive these reactions is important to help reduce bias. Doing so will inform more accurate fish assessments and improve our understanding of UVS limitations, while providing insight into fish habitat utilization. An evaluation and standardization of video-based system surveys is essential to designing effective and replicable survey processes needed to support long-term conservation monitoring and fisheries management initiatives (**Stoner *et al*., 2008 | Laidig *et al*., 2013 | Aguzzi *et al*., 2015 | Ayma *et al*., 2016**).

Through quantitative analysis, *in-situ* or *ex-situ* experiments, factors proven or assumed to have an influence on the nature and magnitude of fish reactions were classified as being related to the physical environment, survey attributes or fish biology and ecology (**Uiblein *et al*., 1998 | Trenkel *et al*., 2004 | Widder *et al*., 2005 | Lorance & Trenkel, 2006 | Raymond & Widder, 2007 | Ryer *et al*., 2009 | Uiblein, 2011 | Laidig *et al*., 2013 | Stierhoff *et al*., 2013 | Aguzzi *et al*., 2015 | Rooper *et al*., 2015 | Ayma *et al*., 2016 | Somerton *et al*., 2017 | Campbell *et al*., 2021 | Geoffroy *et al*., 2021 | Williams *et al*., 2023**). Different UVSs can trigger different fish reactions, depending on UVS size and shape, or the presence of extra features such as a sampling arm or a tether (**Somerton *et al*., 2017**). Additionally, different survey operations will have specific requirements around UVS speed, altitude above seafloor, and other operational variables that may generate diverse fish reactions (**Lorance & Trenkel, 2006 | Stoner *et al*., 2008 | Uiblein, 2011 | Laidig *et al*., 2013 | Laidig & Yolavich, 2016 | Williams *et al*., 2023**). For instance, during sampling and investigative operations (*e.g.*, fauna specimen collection, sediment cores, close-up examination of an organism), an ROV remains relatively stationary for a long period of time with limited movements. While during video transect operations, a video system is in constant motion, usually within a consistent range of speed and altitude.

Many environmental factors known to have an influence on fish catchability by bottom trawls were shown to influence fish behavior and consequently their assessment during video surveys (**Stoner *et al*., 2008**). These factors include depth and bottom temperature, geographic location, macro-habitats and habitat complexity, bottom type, time of day and ambient light, and water currents (**Trenkel *et al*., 2004 | Lorance & Trenkel, 2006 | Stoner *et al*., 2008 | Uiblein, 2011 | Laidig *et al*., 2013 | Campbell *et al*., 2021**).

Further, species-specific differences in fish reactions were showed in several studies (**Lorance & Trenkel, 2006 | Stoner *et al*., 2008 | Laidig *et al*., 2013**). Additionally, Lorance & Trenkel (**2006**) suggested that differences in natural fish behavior could explain variability in their reactions to UVSs. For instance, differences in fish altitude were linked to differences in fish response behavior, with benthic inactive fish showing no reaction while fish swimming in the water column were more likely to display a major reaction in the presence of the UVSs. Other fish biological and ecological attributes known or suspected to influence their response behavior were fish size, fish feeding behavior, the presence of other species, and the distance to UVSs (**Trenkel *et al*., 2004 | Lorance & Trenkel, 2006 | Stoner *et al*., 2008 | Uiblein, 2011 | Frid *et al*., 2019 | Williams *et al*., 2023**).

Despite the difficulty to assess the exact influence of drivers on fish behavior due to confounding effects, there is a need to collect data over a wide range of variables in a given area in order to calibrate surveys prior to the development of long-term monitoring strategies (**Campbell *et al*., 2021**). In this context, we analyzed video data collected *in situ* during two benthic habitat surveys conducted by a remotely operated vehicle (ROV) and a near-seabed drift-camera system, to assess fish behavioral reactions to the presence of UVSs in the Laurentian Channel Marine Protected Area (MPA).

Our objectives were 1) to characterize fish *in-situ* behaviors according to their altitude, activity and locomotion, 2) to assess fish *in-situ* behavior variability at a taxon-specific level in relation to ecological factors (*e.g*., depth, fish size), 3) to describe fish response behavior to two UVSs and 4) to assess fish reaction diversity, magnitude and variability at a taxon-specific level in relation to environmental, technical and fish-related factors. Here, we define *in-situ* behavior as initial behavior displayed by fish at the time of first observation (**Devine *et al*., 2020**) or assumed to be a natural undisturbed behavior (**Trenkel *et al*., 2006**).

4-2 | Methodology

4-2.1 | Video processing

Following Lorance & Trenkel (**2006**), for each fish encountered we recorded their *in-situ* behavior (*i.e*., fish behavior presumably natural and undisturbed at the time of first observation (**Lauren & Trenkel, 2006**)) characterized by their altitude, their activity and their locomotion. Fish altitude was categorized relative to the seafloor and in the water column relative to the UVSs. Fish activity was defined in five categories ranging from no activity to highly active. Fish locomotion was defined in four categories ranging from no movement to strong swimming. The description of each *in-situ* behavior category is presented in Table 4-1.

Table 4-1 | Fish *in-situ* behavior (*i.e.*, behavior presumably natural and undisturbed) categories per attribute as observed on the UVS videos.

Attribute	Category	Abbreviation	Descriptor
Altitude	Buried	-	Fish is buried in a soft-sediment burrow
	On seafloor	-	Fish is in contact with the seafloor
	Above seafloor	Above SF	Fish is just above seafloor, but not considered in the water column (<5 cm)
	UVS level	-	Fish is in water column, at UVS level
	Above UVS	-	Fish is in water column, above UVS level
Activity	No activity	-	Fish is buried or in contact with the seafloor, not moving
	Resting	-	Fish is in contact with the seafloor, lying on its side, not moving (see **Fig. 4-1**)
	Low body movement	Low BM	Slow fin movement, but no body movement
	Medium body movement	Medium BM	Slow body movement (based on qualitative assessment)
	High body movement	High BM	Fast body movement (based on qualitative assessment)
Locomotion	No locomotion	No mvt.	Fish in contact with the seafloor, not moving
	Hovering	-	Fish is above seafloor or in the water column but not swimming
	Drifting	-	Fish is above seafloor or in the water column and displaying weak swimming (< 1 body length/s)
	Swimming	-	Fish is above seafloor or in the water column and displaying strong swimming (> 1 body length/s)

Fig. 4-1 | Frame capture from underwater video recordings illustrating three Redfish (*Sebastes* spp.) 'resting' on the seafloor (circled fishes). Their position is noticeable as they are leaning on one of their sides compared to the other three fish in the picture that are 'sitting' on the seafloor. Picture taken from a forward-looking camera. Scale bar: 10 cm.

For each fish encountered we recorded their response behavior to the UVSs (**Lorance & Trenkel, 2006**). In order to capture the relative magnitude of fish responses, their reactions were categorized into two 'Avoidance' reaction types ('Escaping' and 'Hiding'), three

'Neutral' reaction types ('No', 'Minor' and 'Major' reaction), three 'Attraction' reaction types ('Minor' and 'Major attraction', and 'Following'), and one 'Multitype' reaction. The description of each type of response behavior is presented in Table 4-2.

Table 4-2 | Fish response behavior categories per reaction type as observed on the UVS videos. FoV: Field of view

Reaction type	Response behavior	Descriptor
Avoidance	Escaping	Fish swims away from UVS and leaves the FoV
	Hiding	Fish hides in a burrow in soft sediment or in plume of sediment it resuspended
Neutral	No reaction	Fish does not move from its location
	Minor reaction	Fish shows light body movement but does not leave its position or the FoV
	Major reaction	Fish shows disoriented body movement but does not leave the FoV
Attraction	Attraction	Fish is attracted to the UVS/comes closer to the UVS
	Minor following	Fish follows the UVS once before sitting and/or leaving the FoV
	Major following	Fish is attracted to and follows the UVS multiple times
	Multi	Fish displays both avoidance and attraction types of reaction

In addition, for each fish encountered we recorded their distance relative to the UVS at the time of the response behavior, categorized as either 'Close', 'On the side' or 'Far'. Fish that appeared in the field of view (FoV) from behind the UVS were not recorded. We also recorded the timing of the reaction as either 'Before', 'During' or 'After' the passage of the UVS. A description of each category is presented in Table 4-3

Following the classification employed by Sameoto *et al*. (**2008**), we recorded the following survey operations each second of video footage: UVS 'On bottom', 'Investigating', 'Sampling', 'In maintenance', 'Drifting', 'Transect', 'Transit' and UVS 'Off bottom'. The description of each survey operation is presented in Table 4-3.

4-2.2 | Data preparation

Following the approach used in Chapter 3, we extracted images from the downward-looking camera for each fish individual in the FoV for both surveys. We took total length (TL) measurements (cm) of each individual in ImageJ (**Schneider *et al.*, 2012**) using the lasers as a scale. Fish were classified as small juveniles, large juveniles or adults, based on estimations of their life cycle stages. These estimations were guided by sizes at maturity assessed in a number of studies (**Table 3-1**). We differentiated the small from large juvenile life stages to account for variability in size at maturity between studies, geographic locations, males and females, or species.

Based on the approach taken by Baker *et al.* (**2012**) and in Chapter 2, we divided the video data into 10-m segments, which were used as sample units to match with the small-scale distribution of habitat attributes. For each snapshot extracted from the ROPOS forward-looking camera, the width of the FoV was measured in the software ImageJ, using the lasers as a scale to estimate the width covered (total of 5200 snapshots, 1 to 5 per segment, with an average width of 5.3 m). We calculated 4.7 m as the average FoV of ROPOS during the 'transect-mode' and used it as a proxy to estimate the FoV of CAMPOD. The surface area of each segment was estimated as the segment length multiplied by the average FoV. Total fish densities (ind./m^2) were calculated in each segment by dividing abundances by segment area. Fish densities were transformed into five discrete categories ranging from 'Very low' to 'Very high'. A description of fish density categories is presented in Table 4-3.

Each segment was assigned a bottom type according to the presence or absence of substrates and soft-sediment micro-habitat features, defined in Chapter 2 (**Fig. 4-5**). Each segment was assigned a benthic habitat type according to the presence of habitat-forming invertebrates, defined by the cluster analysis in Chapter 3. A description of each bottom type and benthic habitat type is presented in Table 4-3.

Additional environmental variables considered in this study included depth and time of day. Continuous depth data were transformed into six discrete categories representing 50-m intervals between 179 to 455 m. We categorized time of day as *day* and *night*, defined according to local times of sunrise and sunset, during the two data collection periods.

Table 4-3 | Description of the fish-related, environmental and technical categorical factors used to assess fish behavioral response variability to UVS. FoV: Field of view. Benthic habitat types and bottom types first described in Chapter 3.

Factor	Category	Abbreviation	Descriptor
Fish-related			
Total density	Very low	-	Fish density = 0.007 – 0.05 ind./m^2
	Low	-	Fish density = 0.05 – 0.1 ind./m^2
	Medium	-	Fish density = 0.1 – 0.2 ind./m^2
	High	-	Fish density = 0.2 – 0.5 ind./m^2
	Very high	-	Fish density ≥ 0.5 ind./m^2
Life stage	Small juvenile	Small juv.	Immature fish that have not reached sexual maturity
	Large juvenile	Large juv.	Transition life stage mostly comprised of mature and immature fish
	Adult	-	Mature fish that have reached sexual maturity
Distance to UVS	Close	-	Fish is located in front of UVS, within the illuminated FoV
	Side	-	Fish is located on the side of the illuminated FoV
	Far	-	Fish is located outside of the illuminated FoV
Reaction timing	Before	-	Fish reacts to UVS before UVS gets close to it
	During	-	Fish reacts to UVS when UVS is close to it
	After	-	Fish reacts to UVS after UVS passed it
	Before & During	Bef./Dur.	Fish reacts to UVS before and when UVS is close to it
	During & After	Dur./Aft.	Fish reacts to UVS when UVS is close to it and after it passed it
	Before & After	Bef./Aft.	Fish reacts to UVS before UVS gets close to it and after it passed it
Environmental			
Time of day	Day	-	From sunrise to sunset
	Night	-	From sunset to sunrise
Benthic habitat type	Barren	-	No epibenthic invertebrate observed
	Acti-Ceriant	Acti	Invertebrate assemblage dominated by small-size *Actinoscyphia* tube actiniarias and ground-level Cerianthids
	Kopho-Acti-Ceriant	Kopho	Invertebrate assemblage dominated by small-size *Actinoscyphia* tube actiniarias, ground -level Cerianthids and medium-size *Kophobelemnon* sea pens
	Sclerac-Anthop-Kopho	Sclerac	Invertebrate assemblage dominated by seafloor-level solitary cup corals, tall-size *Anthoptilum* and medium-size *Kophobelemnon* sea pens
	Flab-Penna	Flab	Invertebrate assemblage dominated by ground -level solitary *Flabellum* cup corals and medium-size *Pennatula* sea pens
	Penna	Penna	Invertebrate assemblage dominated by medium-size *Pennatula* sea pens

Bottom type	Flat	-	Mud only, absence of soft-bottom relief or hard-bottom substrate
	Soft negative relief	Soft neg.	Presence of depressions and burrows in soft sediment, absence of hard-bottom substrate
	Soft positive relief	Soft pos.	Presence of small dunes in soft sediment, absence of hard-bottom substrate
	Soft mixed relief	-	Presence of both positive and negative reliefs, absence of hard-bottom substrate
	Hard	-	Presence of hard substrate, presence of positive and negative reliefs possible
Technical			
UVS speed	No motion	-	UVS speed = 0 m/s
	Low	-	UVS speed = 0.1-0.5 m/s
	Medium	-	UVS speed = 0.5-1.5 m/s
	High	-	UVS speed ≥ 1.5 m/s
UVS altitude	On bottom	-	UVS altitude = 0-0.8 m
	Low	-	UVS altitude = 0.9-2 m
	Medium	-	UVS altitude = 2-3 m
	High	-	UVS altitude ≥ 3 m
Survey operation	On bottom	On bot.	UVS is stationary and on bottom, and not conducting any specific operation (<5 minutes[2])
	Investigating	Invest.	UVS has stopped operation (*e.g.*, sampling or transect) to examine *in-situ* specimens (2-15 minutes[2]) Usually stationary and on bottom
	Sampling	Sampl.	UVS[1] is collecting biological or sediment samples (5-15 minutes[2]) Usually stationary and on bottom
	In maintenance	Maint.	UVS has stopped operation (*e.g.*, sampling or transect) and is being remotely checked by vehicle operators (1-5 minutes[2]) Usually stationary and on bottom, can be in water column
	Transect	-	UVS is conducting a video survey following predefined trajectory
	Transit	-	UVS[1] is moving to/between transect/sampling location
	Drifting	Drift.	UVS is pulled off due to bottom currents and is not following pre-defined trajectory or conducting any specific operation (*e.g.*, sampling or transect) Can be on bottom or in water column (<5 minutes[2])
	Off bottom	Off bot.	UVS is in water column and not conducting any specific operation (*e.g.*, sampling or transect) Usually, seafloor is not visible

[1] Only applicable to ROPOS

[2] Times represent one isolated operation, several operations of the same type (*e.g.*, sampling, investigating, maintenance) may have occurred during the same dive

Additional technical factors considered in this study included UVS speed and UVS altitude. Continuous UVS speed and altitude data were transformed into four discrete categories ranging from no motion and on bottom to high speed and altitude. A description of each UVS speed and altitude category is presented in Table 4-3.

4-2.3 | Statistical analysis

4-2.3.1 | Fish *in-situ* behavior

All data analyses were performed using R (**R Core Team, 2019**). Following Lorance & Trenkel (**2006**), we conducted a multiple correspondence analysis (MCA) to investigate the relationship between all fish taxa and their *in-situ* behavior attributes (*i.e.*, fish altitude, activity and locomotion). We performed the MCA using the R package ‘FactoMineR’ (**Lê *et al*., 2008**). We visually explored the variability of fish *in-situ* behavior attributes in relation to depth, time of day, benthic habitat type and fish life stage for a selected number of fish taxa.

4-2.3.2 | Fish response behavior variability

We visually explored the range of fish response behavior to UVSs and their variability between fish taxa. We performed multinomial logistic regression species-specific models for a selected number of fish taxa to test the influence of several categorical factors (*i.e.*, fish *in-situ* behavior, fish-related attributes, survey attributes, environmental factors) on fish response behavior. We used the ‘multinom’ function from the ‘nnet’ package (**Venables & Ripley, 2002**). Multinomial logistic regressions are adapted to model categorical response variables and to predict probabilities of occurrence. We used the three fish reaction types (*i.e.*, avoidance, neutral and attraction) instead of the nine fish response behaviors (*e.g.*, hiding, minor reaction or following) to reduce the complexity of the analysis (**Williams *et al*., 2023**). For all models, neutral reaction type was selected as the reference level. The model calculated the probability that a given reaction would be dominant for each explanatory variable, using ‘Neutral’ as the reference level. We verified data linearity, independence and non-collinearity, as well as the absence of outliers to ensure compatibility with the assumptions of multinomial logistic regression analysis by plotting the model diagnostics. We also tested if there was a relationship between residuals and specific predictors. We extracted the predicted probabilities of each reaction type associated with the variables tested and plotted them.

Eq. 5: *Fish reactions* ~ Technical factors + Environmental variables + Fish *in-situ* behavior attributes + Fish-related factors

Where,
Fish reactions = ‘Avoidance’, ‘No reaction’ and ‘Attraction’
Technical factors = categories of the following factors: UVS type, UVS speed, UVS altitude, Survey operation
Environmental variables = categories of the following factors: Depth, Time of day, Benthic habitat type, Bottom type
Fish *in-situ* behavior attributes = categories of the following factors: Fish activity, Fish altitude, Fish locomotion
Fish-related factors = categories of the following factors: Fish total density, Fish life stage, Fish distance to UVSs, Fish reaction timing

4-3 | Results

4-3.1 | Data summary

A total of 95 h of video footage was acquired using the two UVSs at depth ranging from 179 to 455 m (**Table 1-1**). The surveys covered 86.7 km in total linear extent and an area of approximately 43.6 ha within the study area. The distribution of sampling effort by year, time of day and depth range is presented in Chapter 3 (**Appendix 3-1**).

4-3.2 | Fish occurrence

A total of 18,583 fishes were observed, comprising 26 morphotypes (**Table 4-4**). Most were identified to 17 species (8,925 specimens) and 5 genera (9,562 specimens). Only 84 individuals could not be identified at or below family level.

Table 4-4 | Number of fish individuals observed and their relative contribution (% of total abundance) sorted in descending percentage of total abundance.

Family	Scientific name	Common name/Taxon	Total number observed	Percentage of total abundance
Sebastidae	*Sebastes* spp.	Redfish	8114	44
Phycidae	*Phycis chesteri*	Longfin Hake	3083	17
Pleuronectidae	*Glyptocephalus cynoglossus*	Witch Flounder	2357	13
Macrouridae	*Nezumia bairdii*	Marlin-Spike Grenadier	1827	10
Teleostei[1]	Teleostei spp.	Teleostei sp1	1195	7
Zoarcidae	*Lycenchelys vyerrillii*	Wolf Eelpout	623	3
Myxinidae	*Myxine glutinosa*	Atlantic Hagfish	290	2
Zoarcidae	*Enchelyopus cimbrius*	Fourbeard Rockling	290	2
Rajidae	Rajidae spp.	Skate sp1	228	1
Gadidae	*Merluccius bilinearis*	Silver Hake	200	1
Zoarcidae	*Argentina silus*	Greater Argentine	116	1
Actinopterygii[2]	Actino sp. indet.	Actino sp1	73	< 1
Etmopteridae	*Centroscyllium fabricii*	Black Dogfish	45	< 1
Phycidae	*Urophycis tenuis*	White Hake	35	< 1
Gadidae	*Pollachius virens*	Pollock	25	< 1
Liparidae	Liparidae sp. indet.	Snailfish sp1	22	< 1
Lophiidae	*Lophius americanus*	Monkfish	14	< 1
Gadidae	*Gadus morhua*	Atlantic Cod	13	< 1
Actinopterygii[2]	Unidentified fish	Actino spp	11	< 1
Zoarcidae	Zoarcidae sp. indet	Zoarcidae sp1	8	< 1
Macrouridae	Macrouridae sp. indet.	Grenadier sp2	4	< 1
Ogcocephalidae	*Dibranchus* sp. indet.	Batfish sp1	3	< 1
Pleuronectidae	*Hippoglossus hippoglossus*	Atlantic Halibut	3	< 1
Squalidae	*Squalus acanthias*	Spiny Dogfish	2	< 1
Cryptacanthodidae	*Cryptacanthodes maculata*	Wrymouth	1	< 1
Lamnidae	*Lamna nasus*	Porbeagle Shark	1	< 1

[1] Subclass
[2] Class

4-3.3 | Fish assemblage behavior

4-3.3.1 | Fish *in-situ* behavior

Of all fish observed 64% were inactive, 13% were resting and 11% displayed high body movements; 78% were on the seafloor, 15% were above the seafloor and 6% were in the water column; 77% were motionless, 11% were hovering and 11% were swimming. A total of eight taxa were observed buried in soft-sediment burrows, or in the sediment (n = 110, < 0.5%), notably 27% of all Hagfish observed (**Table 4-5**).

Table 4-5 | Number of fish observed (and relative percentage) per cluster, as identified by the MCA model, per altitude, activity and locomotion category. The description of each category is presented in Table 4-1. C1: Pelagic fish, C2: Benthopelagic fish, C3: Benthic fish.

Attribute	Category	Fish cluster			Total observed	Relative percentage
		C1	C2	C3		
Activity	No activity	342	69	11244	11668	64
	Resting	0	0	2407	2407	13
	Low BM	42	866	335	1246	7
	Medium BM	48	726	145	921	5
	High BM	987	165	871	2102	11
Altitude	Buried	2	1	102	110	1
	On seafloor	296	57	13891	14253	78
	Above SF	312	1761	711	2796	15
	UVS level	548	5	175	743	4
	Above UVS	261	2	123	442	2
Locomotion	No mvt.	344	75	13690	14122	77
	Hovering	117	1609	369	2099	11
	Drifting	7	41	3	53	1
	Swimming	951	101	940	2070	11

All fish taxa, but two, were grouped in three clusters based on their *in-situ* behavior attributes, according to our MCA results (**Fig. 4-2**). A first cluster (C1) comprised active pelagic fish (8% of all fish observed) mainly including Pollock (*Pollachius virens*), Atlantic Cod (*Gadus morhua*), Teleostei sp1, Snailfish sp1 (Liparidae sp. indet.), Greater Argentine (*Argentina silus)*, Black Dogfish (*Centroscyllium fabricii*) and Porbeagle Shark (*Lamna nasus*). Fish taxa in this group were mostly actively swimming in the water column, displaying high body movements (68.5% of fish in this cluster) (**Fig. 4-2A & Table 4-5**).

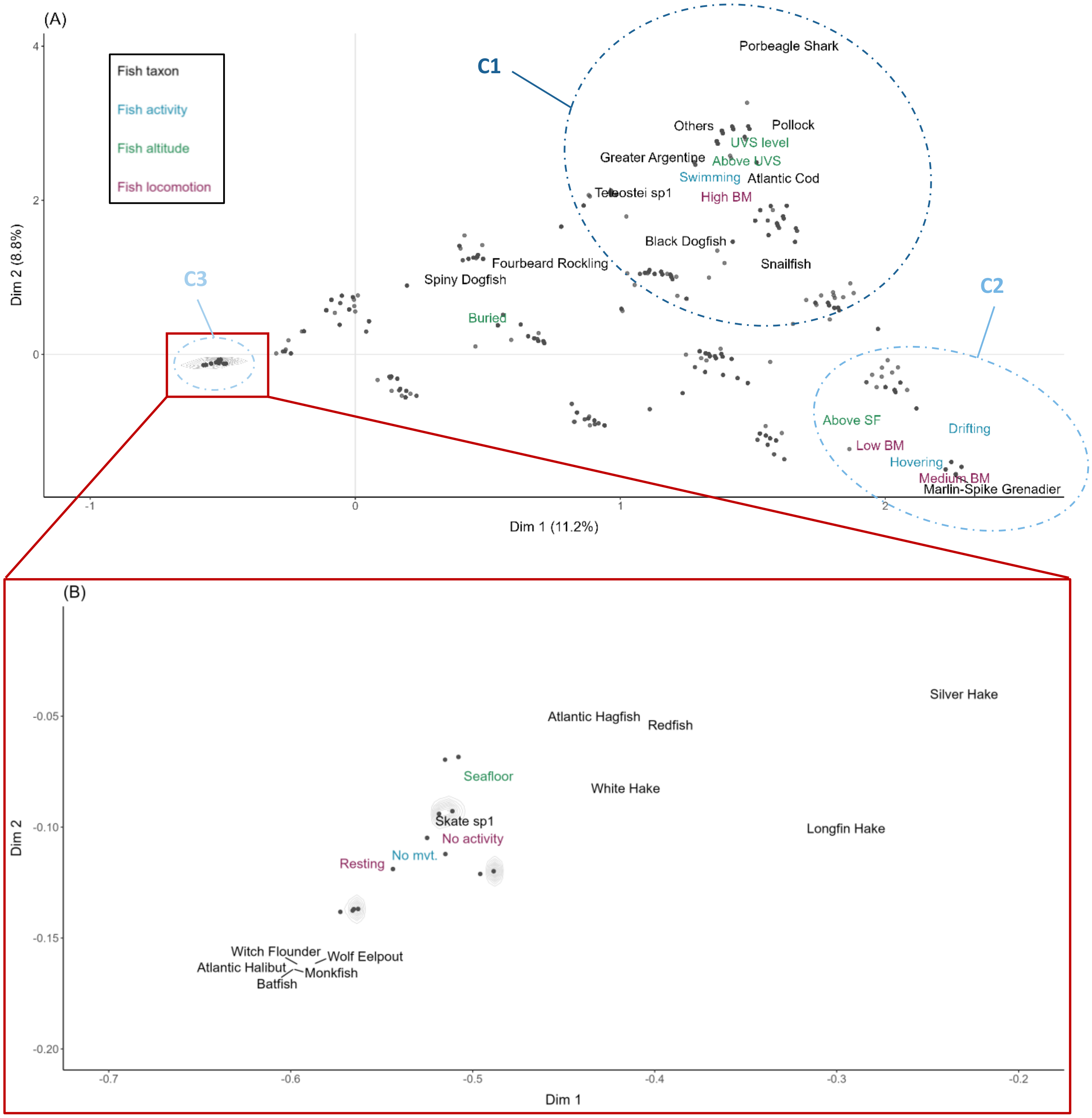


Fig. 4-2 | MCA plot showing the associations between fish taxa (black) according to their altitude (green), their activity (pink) and their locomotion (blue). Plot B is a close-up section of plot A. Points represent fish observations and curves (light grey) represent density curves where observations are concentrated. C1: Pelagic fish, C2: Benthopelagic fish, C3: Benthic fish. See Table 4-1 for details of fish *in-situ* behavior attributes.

The second cluster (C2) comprised low activity benthopelagic fish (10% of all fish observed) and comprised only Marlin-Spike Grenadier (*Nezumia bairdii*). This taxon was mostly found above the seafloor, displaying low to medium body movements and passive swimming (90% of all Marlin-Spike Grenadier observed) (**Fig. 4-2A & Table 4-5**). The last group (C3) comprised passive benthic fish (88% of all fish observed) including three species of Hakes (Longfin Hake (*Phycis chesteri*), Silver Hake (*Merluccius bilinearis*) and White Hake (*Urophycis tenuis*)), Redfish, Witch Flounder (*Glyptocephalus cynoglossus*), Skate sp1, Atlantic Halibut (*Hippoglossus hippoglossus*), Monkfish (*Lophius americanus*), Wolf Eelpout (*Lycenchelys vyerrillii*) and Batfish (*Dibranchus* sp. indet.). These fishes were mostly observed on the seafloor, displaying no movement or activity (92% of fish in this cluster) (**Fig. 4-2B & Table 4-5**). Spiny Dogfish (*Squalus acanthias*) and Fourbeard Rockling (*Enchelyopus cimbrius*) were two taxa that did not belong to any group, but whose behavior was a mix of active pelagic fish (C1) and inactive benthic fish (C3) (**Fig. 4-2A**).

4-3.3.2 | Fish response behavior to underwater video systems

Table 4-6 | Number of fish observed (and relative percentage of total fish) per cluster, as identified by the MCA model, per reaction type and response behavior to UVSs. The description of each category is presented in Table 4-2.

Reaction type	Fish cluster			Total observed	Relative percentage
Response behavior	C1	C2	C3		
Avoidance	**54**	**150**	**346**	**558**	**3**
Escape	53	149	239	449	2
Hide	1	1	107	109	1
Neutral	**1288**	**1658**	**14378**	**17406**	**95**
No reaction	273	1138	10718	12197	66
Minor reaction	136	520	3651	4320	24
Major reaction	879	0	9	889	5
Attraction	**61**	**18**	**265**	**351**	**2**
Attraction	48	16	210	281	2
Minor following	1	2	55	58	< 1
Major following	12	0	0	12	< 1
Multi	**16**	**0**	**13**	**29**	**< 1**

'Neutral reaction' was the most observed reaction to UVSs among fish (95%) (**Table 4-6**). Of all fishes observed, 66% did not react to the presence of UVSs, 24% displayed 'Minor reaction', and 5% 'Major reaction'. 'No reaction' and 'Minor reaction' were the dominant response behaviors for 20 of the 26 fish taxa (**Fig. 4-3**). The majority of 'Major reaction' responses observed (98%) were attributed to one taxon (Teleostei sp1). ‘Avoidance’ only accounted for 3% of the fish reactions and was the dominant reaction for two taxa (Skate sp1 and Spiny Dogfish). ‘Attraction’ only accounted for 2% of the fish reactions and was the dominant reaction for four taxa (Pollock, Atlantic Cod, Porbeagle Shark and Spiny Dogfish). A total of eight taxa displayed a multi-response behavior (<1% of all fish in abundance), notably Pollock and Atlantic Cod (**Fig. 4-3**).

‘Neutral reaction’ was the most observed reaction in all fish clusters (93% on average) (**Table 4-6**). ‘No reaction’ and ‘Minor reaction’ were the dominant response behaviors in clusters C2 and C3 (66.5% and 26% on average). Of all fish in cluster C1, 62% displayed ‘Major reaction’, 19% ‘No reaction’ and 10% ‘Minor reaction’.

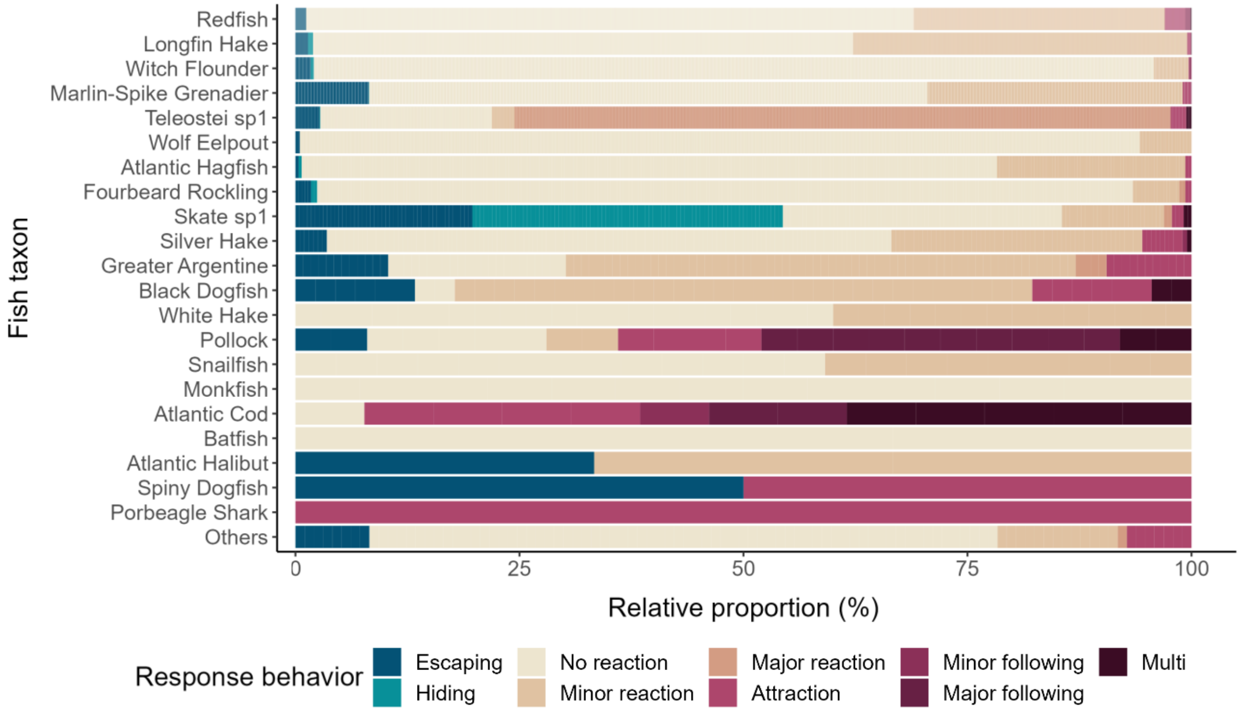


Fig. 4-3 | Patterns of fish response behavior to the presence of underwater video systems (UVS) per fish taxon observed. *Others* represent five taxa identified at a high taxonomic level and/or numerically low (n_{others} = 97). See Table 4-2 for details of fish reactions, and Table 4-4 for total number of fish observed per taxon.

In order to investigate the variability of fish *in-situ* and response behavior, we selected 9 of the 26 taxa to focus our analysis as they showed high abundances (Redfish, Longfin Hake, Witch Flounder, Marlin-Spike Grenadier, Teleostei sp1), displayed strong reactions to the UVSs (Skate sp1, Pollock), or are conservation targets in Atlantic Canada (Black Dogfish, Atlantic Cod) (**Fig. 4-4**).

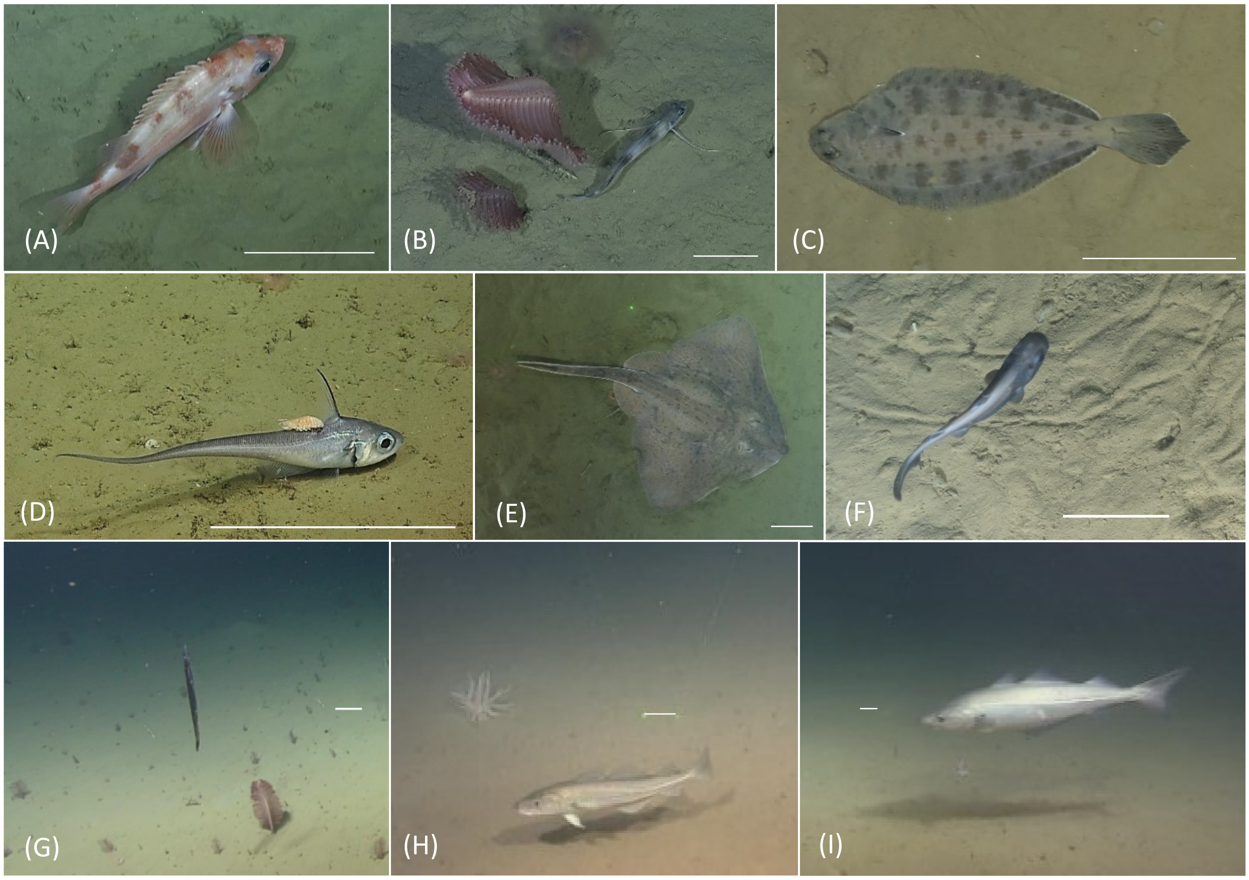


Fig. 4-4 | Frame captures from underwater video recordings of the nine groundfish taxa selected for detailed analysis. (A) Redfish (*Sebastes* spp.), (B) Longfin Hake (*Phycis chesteri*), near *Pennatula* sea pens, (C) Witch Flounder (*Glyptocephalus cynoglossus*), (D) Marlin-Spike Grenadier (*Nezumia bairdii*) with parasitic copepod behind the dorsal fin, (E) Skate sp1 (Thorny Skate (*Amblyraja radiata*) or Smooth Skate (*Malacoraja senta*)), (F) Black Dogfish (*Centroscyllium fabricii*), (G) Teleostei sp1 (Sandlance (*Ammodytes* spp.) and/or Barracudina (*Arctozenus* sp. and/or *Paralepis* spp.)), (H) Atlantic Cod (*Gadus morhua*), (I) Pollock (*Pollachius virens*). Pictures A, C, E and F were taken from a downward-looking camera while pictures B, D, G-I were taken from a forward-looking camera. Scale bar: 10 cm.

4-3.4 | Variability of fish *in-situ* behavior

4-3.4.1 | Fish average *in-situ* behavior

The number of fish observed for each *in-situ* behavior attribute is presented in Appendix 4-1. Four of nine taxa (Redfish, Longfin Hake, Witch Flounder and Skate sp1) did not display any noticeable activity (88-100%), were observed on the seafloor (90-100%) and were motionless (88-100%). Redfish and Longfin Hake were seen buried in soft-sediment burrows (n = 7 and 14 respectively) and 'Resting' (*i.e.*, fish in contact with the seafloor, lying on their side), on the seafloor (30% of Redfish and 16 individuals for Longfin Hake).

Four taxa (Teleostei sp1, Black Dogfish, Pollock and Atlantic Cod) were actively swimming (65-92%), displaying 'High' body movements (68-92%). Teleostei sp1 and Black Dogfish were swimming and displaying 'High' body movements in 65% and 80% of observations. Additionally, the two taxa were motionless and displayed no activity in 26% and 20% of respective observations. Marlin-Spike Grenadier were hovering in 88% of observations, displaying either 'Low' or 'Medium' body movements (47% and 40% respectively).

Three taxa (Marlin-Spike Grenadier, Black Dogfish and Atlantic Cod) were observed above the seafloor (62-96%). Additionally, 18% of Black Dogfish were observed on the seafloor, and 31% of Atlantic Cod were observed in the water column. Of all Teleostei sp1, 78% were observed in the water column and 22% on the seafloor. Pollock were evenly distributed in all altitudes in the water column.

4-3.4.2 | Influence of ecological factors on fish *in-situ* behavior

The number of fish observed per environmental and fish-related factors are presented in Appendices 4-2 and 4-3 respectively. As the distribution of fish observed per factor was often unbalanced between categories, we focused on the categories where fish were the most observed to analyse patterns. We considered fish *in-situ* behavior described in section 4-3.4.1 as their reference behavior for this analysis.

- **Depth**

For all fish taxa we did not find any influence of depth on *in-situ* behavior (**Fig. 4-5**). Their *in-situ* behavior presented in section 4-3.4.1 was always the dominant behavior in each depth range (62-100%). It should be noted that there were slight changes in percentages associated with certain attributes (*i.e.*, fish altitude, activity and locomotion) for a few taxa. We observed a decrease in body movement magnitude with depth for Marlin-Spike Grenadier (medium to low body movements, 58-32% to 59-29%). We also found an increase in percentage of behavior categories attributed to the inactive benthic fish group for this taxon in the 350-400 depth range (<5 to 16% on average). We found an increase in passive swimming for Teleostei sp1 with depth (6 to 15%). Moreover, Teleostei sp1, Pollock and Atlantic Cod were invariably distributed in all altitudes defined in the water column in all depth ranges where they were observed.

- **Time of day**

For all fish taxa but Teleostei sp1, we did not find any influence of time of day on *in-situ* behavior (**Fig. 4-6**). We observed a shift in body movement magnitude with time of day for Marlin-Spike Grenadier, with low body movements dominant during the day and medium body movements dominant at night. Pollock and Atlantic Cod were invariably distributed in all altitudes defined in the water column during both times of day. The *in-situ* behavior of Teleostei sp1 during the day was similar to the behavior attributed to the active pelagic fish group. Conversely, the behavior of Teleostei sp1 at night was similar to the behavior attributed to the passive benthic fish group. Differences observed for Teleostei sp1 could be attributed to an unbalanced sampling effort between day and night for this taxon, with over 1000 fish observed during the day and 91 at night.

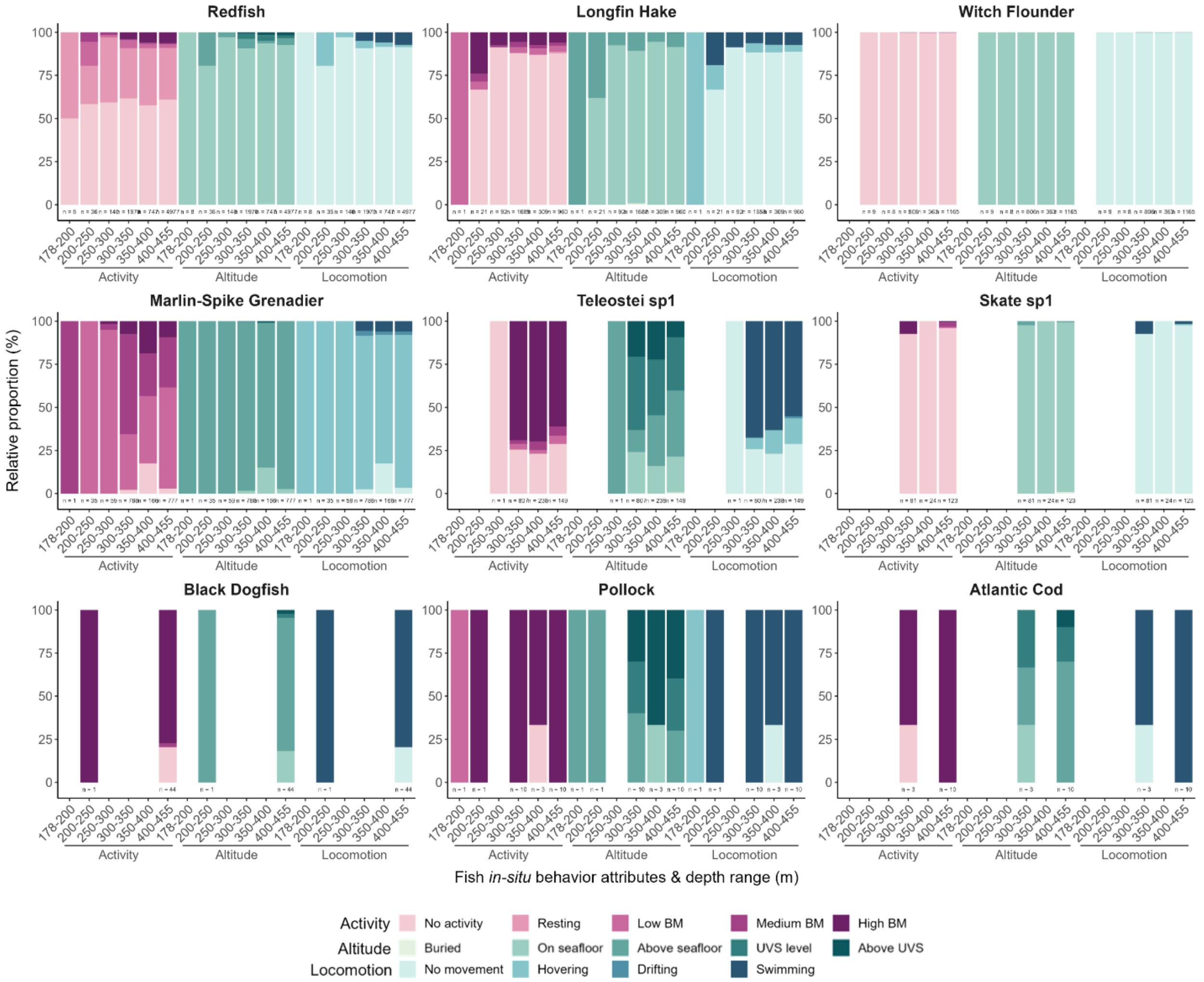


Fig. 4-5 | Variability of fish *in-situ* behavior per attribute and depth range (m).

- **Benthic habitat type**

For all fish taxa, we did not find any influence of benthic habitat type on *in-situ* behavior (**Fig. 4-7**). We observed an increase of resting behavior for Redfish associated with 'Kopho-Acti-Ceriant'. We found a shift in body movement magnitude with benthic habitat type for Marlin-Spike Grenadier, with low body movements dominant in 'Barren', 'Kopho-Acti-Ceriant' and 'Sclerac-Anthop-Kopho', and medium body movements dominant in 'Flab-Penna'. Moreover, we found an increase of high body movements within the 'Sclerac-Anthop-Kopho' and 'Penna' habitats. Teleostei sp1, Pollock and Atlantic Cod were invariably distributed in all altitudes defined in the water column in all benthic habitat types where they were observed.

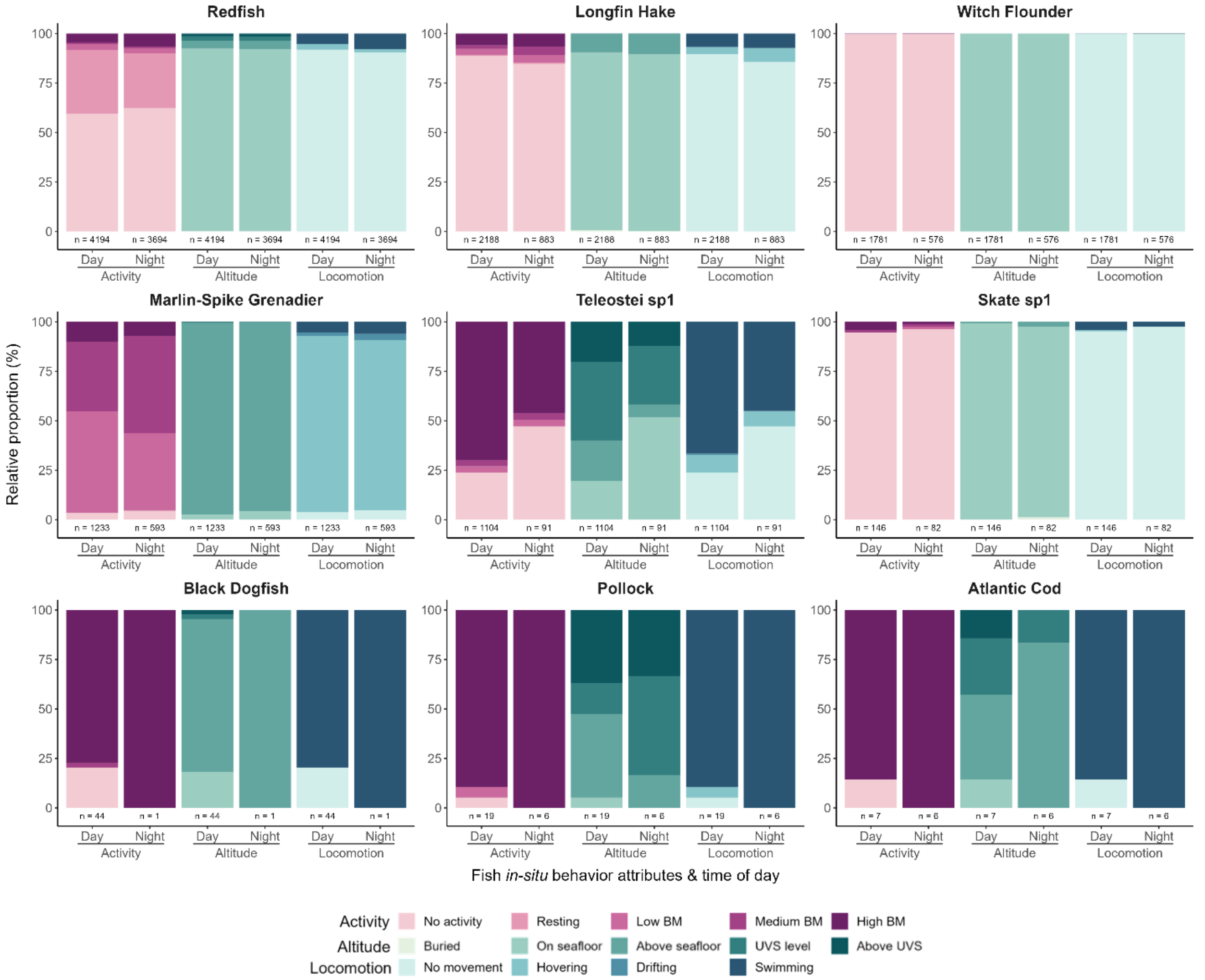


Fig. 4-6 | Variability of fish *in-situ* behavior per attribute and time of day.

- **Life stage**

As we could not measure all taxa, we selected Redfish, Longfin Hake, Witch Flounder and Marlin-Spike Grenadier for our analysis. A detailed assessment of fish TL measurements and life stage characterization is presented in Chapter 3. Overall, we did not find any influence of fish life stage on *in-situ* behavior for all fish taxa (**Fig. 4-8**). We observed a shift in body movement magnitude with life stage for Marlin-Spike Grenadier, with medium body movements dominant for small juveniles and low body movements dominant for large juveniles.

Fig. 4-7 | Variability of fish *in-situ* behavior per attribute and benthic habitat type.

4-3.5 | Variability of fish reactions to underwater video systems

4-3.5.1 | Fish average response behavior per taxon

‘Neutral’ was the dominant reaction (69-98%) in six of the nine taxa. Redfish, Longfin Hake and Marlin-Spike Grenadier did not react in 60-68% and displayed ‘Minor reaction’ in 28-37% of the observations. Of all Teleostei sp1, 73% displayed ‘Major reaction’ and 19% showed no reaction. Black Dogfish mostly displayed ‘Minor reactions’ (64%), 13% of them escaped the FoV, and 13% were attracted to the UVSs (**Appendix 4-4**).

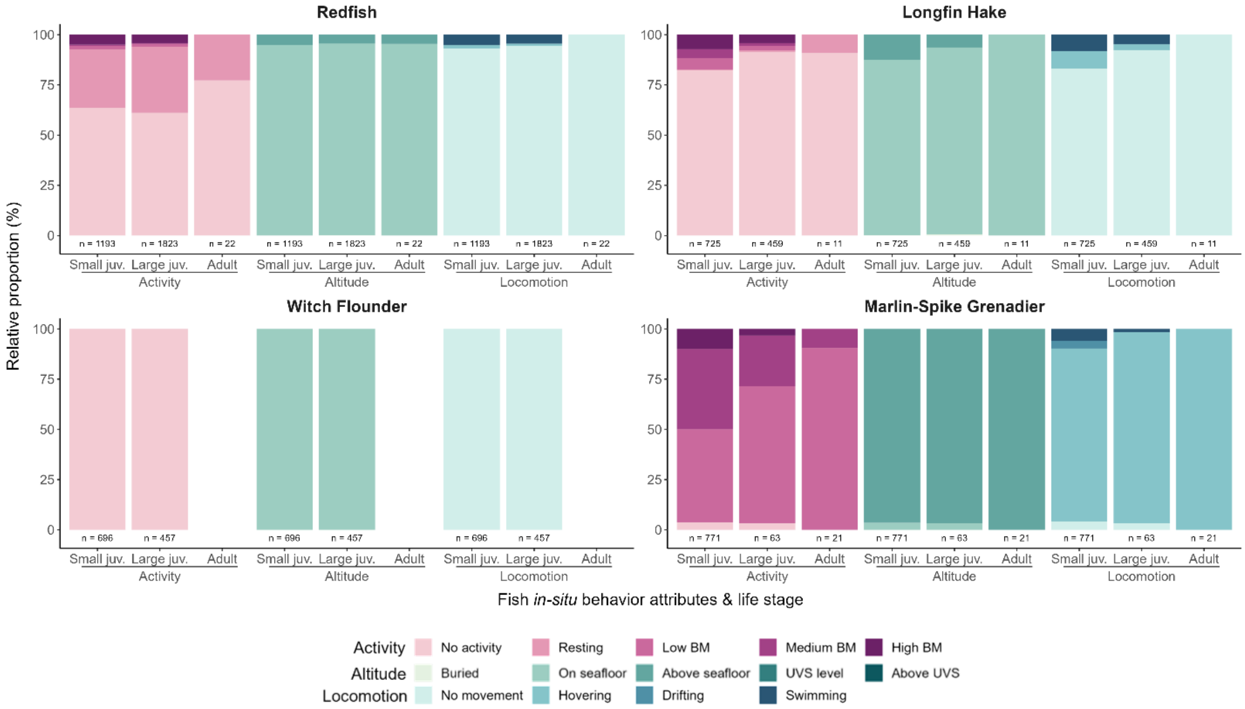


Fig. 4-8 | Variability of fish *in-situ* behavior per attribute and fish life stage.

'Avoidance' was the dominant reaction for one taxon, Skate sp1, occurring in 54% of observations of this taxon. Of all Skate sp1, 35% hid in a sediment plume they created and 20% of the taxon escaped the FoV. Additionally, 31% did not react and 11% displayed 'Minor reaction'.

'Attraction' was the dominant reaction for two taxa, Pollock and Atlantic Cod, in 56% and 54% respectively. Pollock displayed 'Major following' in 40%, 'No reaction' in 20% and was attracted to the UVSs in 16%. Atlantic Cod displayed 'Multi-reaction' behavior in 38%, was attracted to the UVSs in 16%, and was following the UVSs in 15%.

We considered fish response behavior described above as their reference behavior for this analysis. In this section below we present the predicted probabilities of the three reaction types ('Avoidance', 'Neutral' and 'Attraction') per factor for each fish taxon. The relative percentages of observed response behaviors per factor for each fish taxon are presented in Appendices 4-6 to 4-20. Model summary tables for each taxon are presented in Appendices 4-21 to 4-28. Too few Atlantic Cod were observed (n = 13) for model formulation. Nonetheless, the variability of the response behavior (type and magnitude) with factors described in Appendix 4-28 will be presented here. As the distribution of fish observed per factor category was often unbalanced, we focused on the categories where fish were the most observed to analyse patterns.

4-3.5.2 | Influence of technical factors on fish reactions to UVS

- **UVS type**

For six of the eight fish taxa for which we performed models, 'Neutral' was the most predicted reaction (average probability $\overline{P}$ = 90%) for both UVS types (**Fig. 4-9**). Skate sp1 had a higher probability of 'Avoidance' ('Escaping') towards ROPOS (P = 59%) and a higher probability of 'Neutral reaction' ('Minor') to CAMPOD (P = 62%). Pollock had a higher probability of 'Attraction' to ROPOS (P = 71%) and a higher probability of 'No reaction' to CAMPOD (P = 50%). Differences observed for those two taxa could be attributed to an unbalanced sampling effort between the two surveys, with an average of 80% of the two taxa observed during the ROPOS survey. It should be noted that there were slight changes in probability of reactions to UVS type for Marlin-Spike Grenadier. Marlin-Spike Grenadier had a higher probability of 'Avoidance' ('Escaping') towards ROPOS (P = 10%) than towards CAMPOD (P = 3%).

- **UVS speed**

For six fish taxa, 'Neutral' was the most predicted reaction ($\overline{P}$ = 95%), and for five of them we did not see any influence of UVS speed (**Fig. 4-10**). We observed a slight increase of 'Avoidance' ('Escaping') and 'Attraction' reactions for high UVS speeds for Black Dogfish (17 and 33% respectively). Skate sp1 had a higher probability of 'Avoidance' ('Hiding') for low and medium UVS speeds ($\overline{P}$ = 55%) and a higher probability of 'Neutral' reaction ('No reaction') for high UVS speeds (P = 67%). Differences observed for those two taxa could be attributed to an unbalanced distribution of fish observed, with most fish observed at low UVS speeds. Pollock showed high probabilities of 'Attraction' for all UVS speed categories where the taxon was mostly observed.

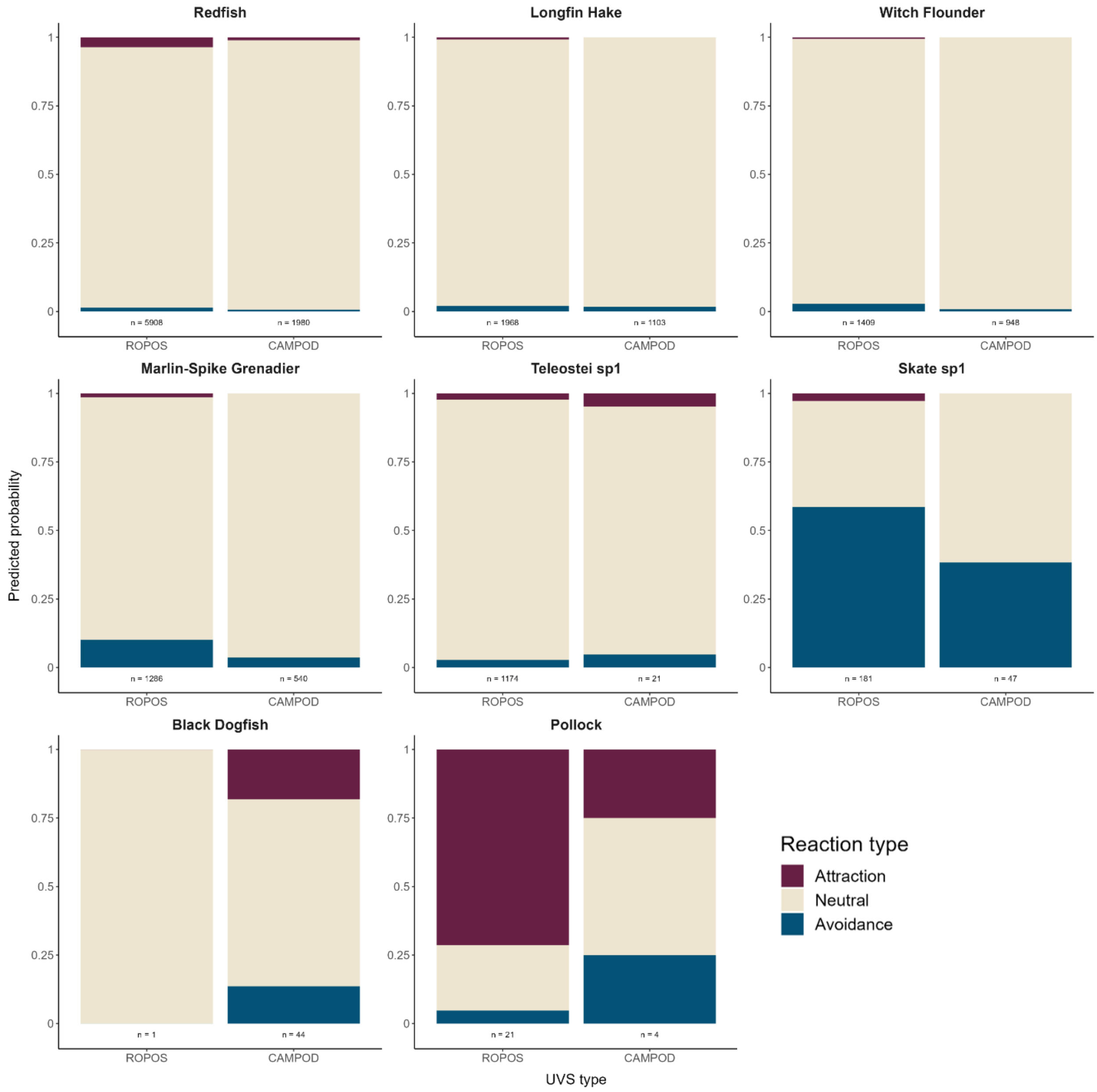


Fig. 4-9 | Predicted probabilities of fish reaction types in relation to UVS type per fish taxon. n = number of fish observed per category. See Table 4-2 for details of fish reactions.

- **UVS altitude**

For six fish taxa, ‘Neutral’ was the most predicted reaction ($\overline{P}$ = 95%) and we did not find any influence of UVS altitude (**Fig. 4-11**). Skate sp1 had a higher probability of ’Avoidance’ when UVS was on bottom of just above the seafloor ($\overline{P}$ = 55%) where the taxon was mostly observed (88%). Pollock had a higher probability of ‘Attraction’ when UVS was on bottom or just above the seafloor ($\overline{P} = 74\%$) and a higher probability of ‘Neutral’ reactions associated with medium UVS altitudes ($P = 50\%$).-Differences observed for Pollock could be attributed to an unbalanced distribution of fish observed, with most fish observed at low UVS altitudes.

- **Survey operation**

For five fish taxa, ‘Neutral’ was the most predicted reaction ($\overline{P} = 94\%$) and we did not find any influence of survey operation (**Fig. 4-12**). Skate sp1 had a higher probability of ‘Avoidance’ (‘Escaping’) associated with transect and transit survey modes, where it was most commonly observed (73 and 21% respectively), although we found a higher probability of ‘Neutral’ reaction associated with transect survey mode ($P = 46\%$). Pollock had a higher probability of ‘Avoidance’ associated with investigation and transit survey modes, where it was most commonly observed (68 and 26% respectively), although we found a slight increase of ‘Neutral’ reaction associated with transit survey mode ($P = 33\%$). Differences observed for those two taxa could be attributed to an unbalanced distribution of fish observed between survey modes.

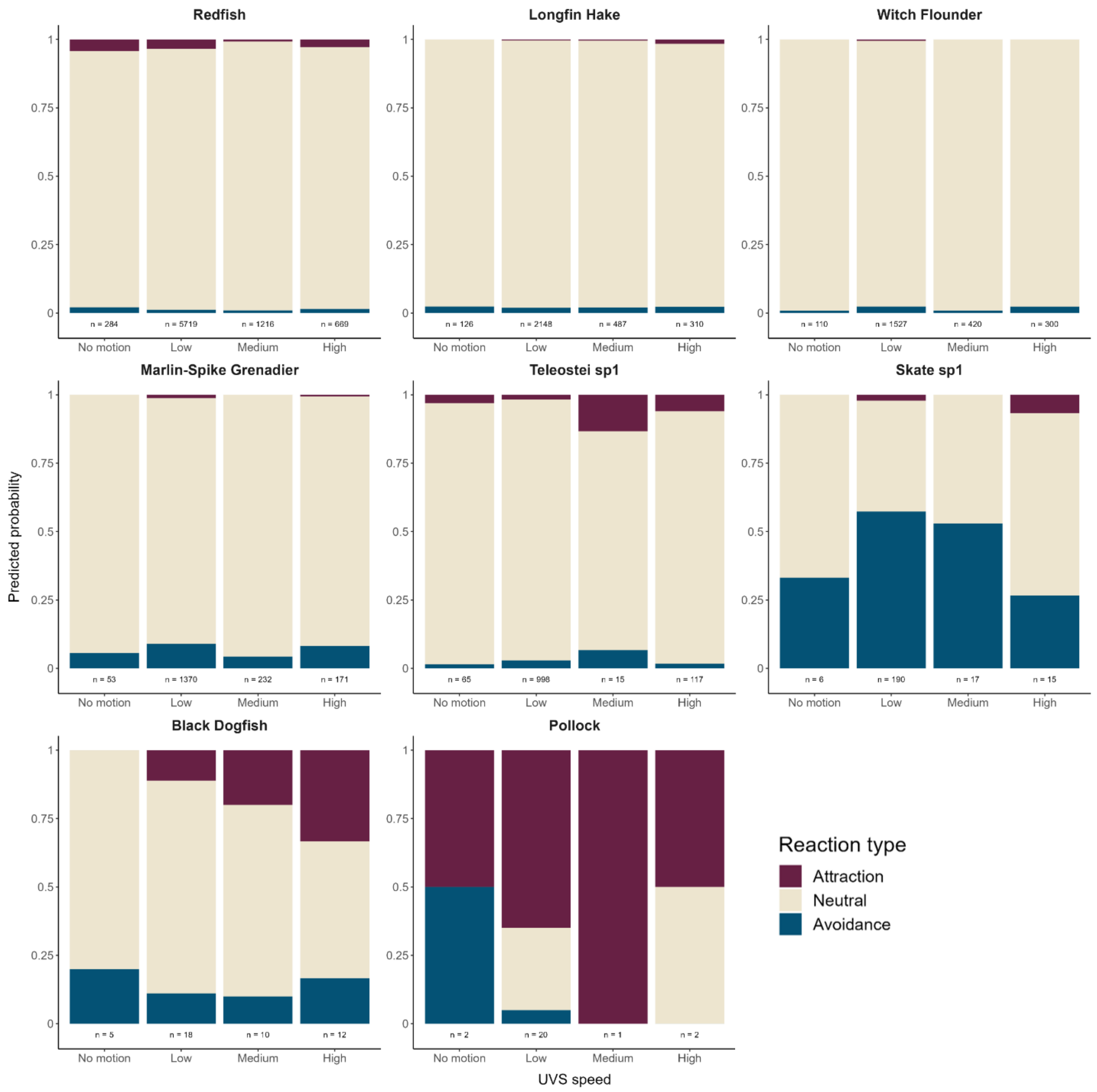


Fig. 4-10 | Predicted probabilities of fish reaction types in relation to UVS speed per fish taxon. n = number of fish observed per category. Table 4-2 for details of fish reactions and Table 4-3 for UVS speed categories.

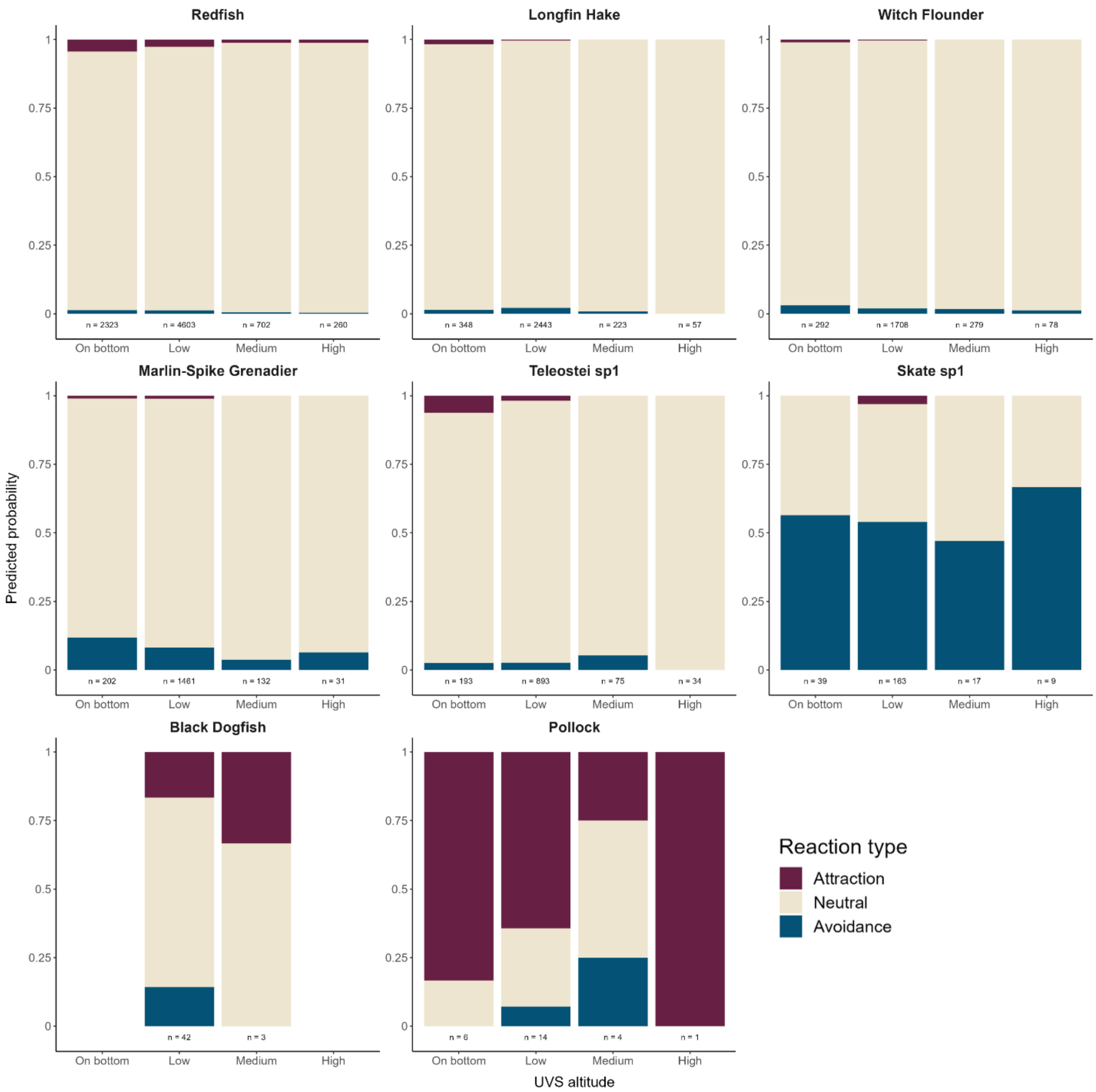


Fig. 4-11 | Predicted probabilities of fish reaction types in relation to UVS altitude per fish taxon. n = number of fish observed per category. See Table 4-2 for details of fish reactions and Table 4-3 for UVS altitude categories.

Fig. 4-12 | Predicted probabilities of fish reaction types in relation to survey operation per fish taxon. n = number of fish observed per category. No model was performed for Black Dogfish as the taxon was only observed during transect operations. See Table 4-2 for details of fish reactions and Table 4-3 for UVS altitude categories.

4-3.5.3 | Influence of environmental variables on fish reactions to UVS

- **Depth**

For six fish taxa, ‘Neutral’ was the most predicted reaction ($\overline{P}$ = 96%) and we did not find any influence of depth on fish reaction (**Fig. 4-13**). Skate sp1 had a higher probability of ‘Neutral’ reactions between 300 and 400 m deep ($\overline{P}$ = 56%) and a higher probability of ‘Avoidance’ (‘Escaping’) in the 400-455 m depth range (P = 66%). Pollock showed high probabilities of ‘Attraction’ in all depth ranges where this taxon was mostly observed.

- **Time of day**

For six fish taxa, ‘Neutral’ was the most predicted reaction ($\overline{P}$ = 93%) and we did not find any influence of time of day on fish reactions (**Fig. 4-14**). Both ‘Attraction’ and ‘Neutral’ were the most predicted reactions for Skate sp1, although we found an increase of ‘Avoidance’ (‘Escaping’) at night (P = 47 to 65%). Additionally, we found a higher percentage of ‘No reaction’ during the day for this taxon.

- **Benthic habitat type**

For six fish taxa, ‘Neutral’ was the most predicted reaction ($\overline{P}$ = 94%) and we did not find any influence of benthic habitat type on fish reactions (**Fig. 4-15**). Skate sp1 had a higher probability of ‘Avoidance’ (‘Hiding’) in ‘Sclerac-Anthop-Kopho’ (P = 64%) and a higher probability of ‘Neutral’ reaction (‘No reaction’) in ‘Flab-Penna’ (P = 54%). We also found higher probabilities of ‘Avoidance’ (‘Hiding’) in ‘Barren’ and ‘Kopho-Acti-Ceriant’ (P = 65 and 69% respectively), though fewer fish were observed in both habitats (23 and 16 individuals respectively). Pollock showed high probabilities of ‘Attraction’ (‘Following’) in every benthic habitat type where this taxon was mostly observed.

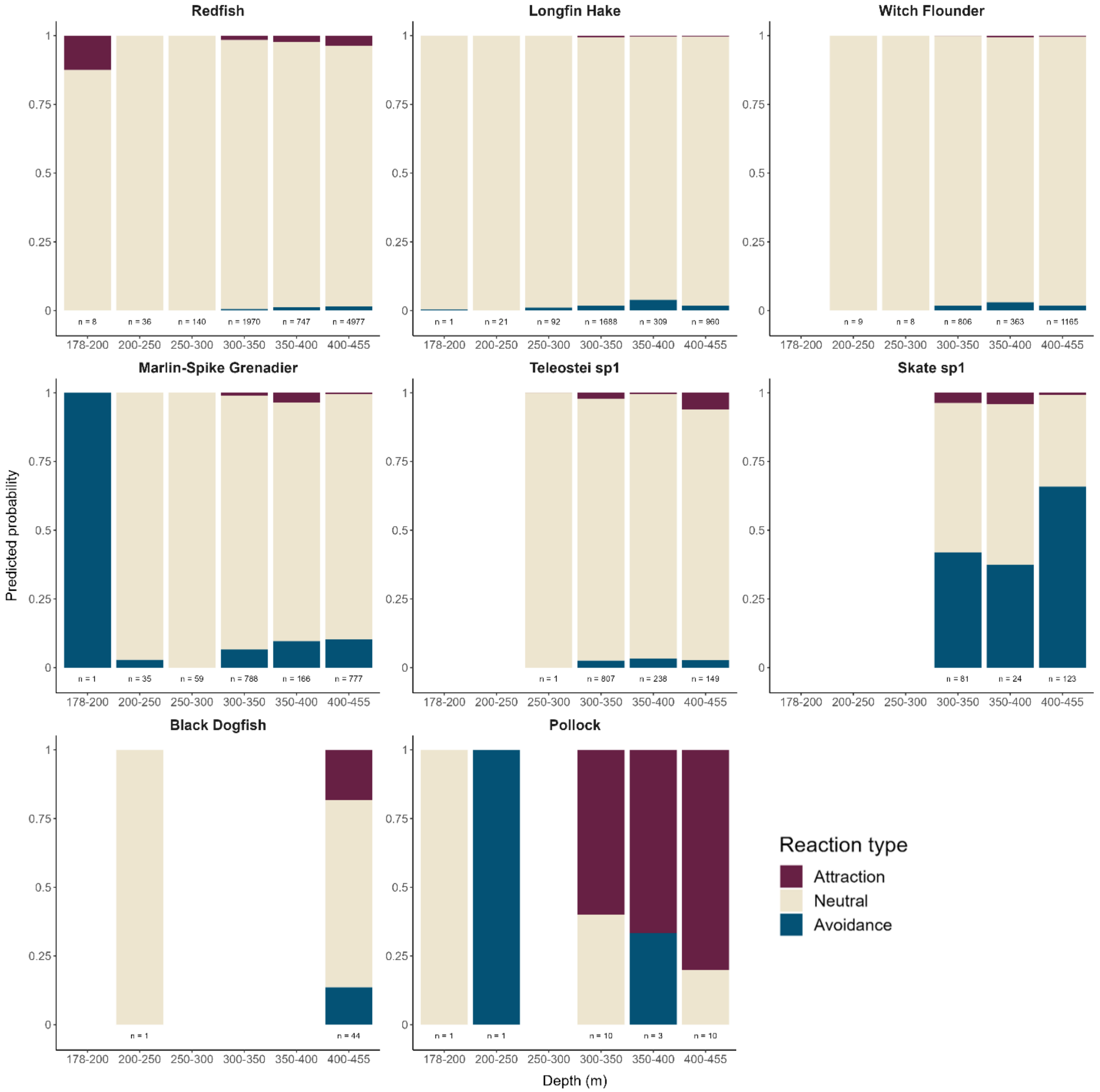


Fig. 4-13 | Predicted probabilities of fish reaction types in relation to depth per fish taxon. n = number of fish observed per category. Table 4-2 for details of fish reactions.

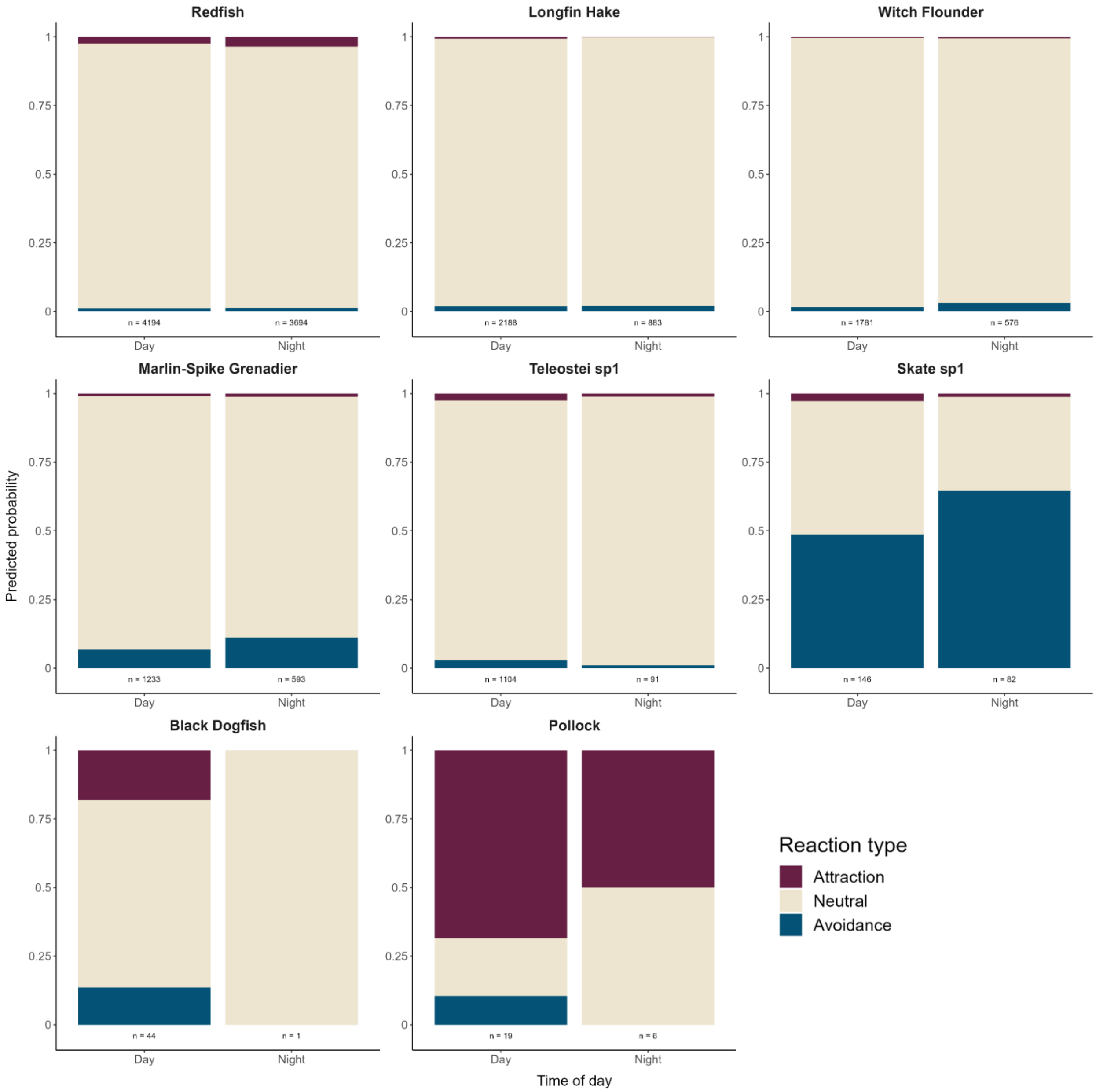


Fig. 4-14 | Predicted probabilities of fish reaction types in relation to time of day per fish taxon. n = number of fish observed per category. See Table 4-2 for details of fish reactions.

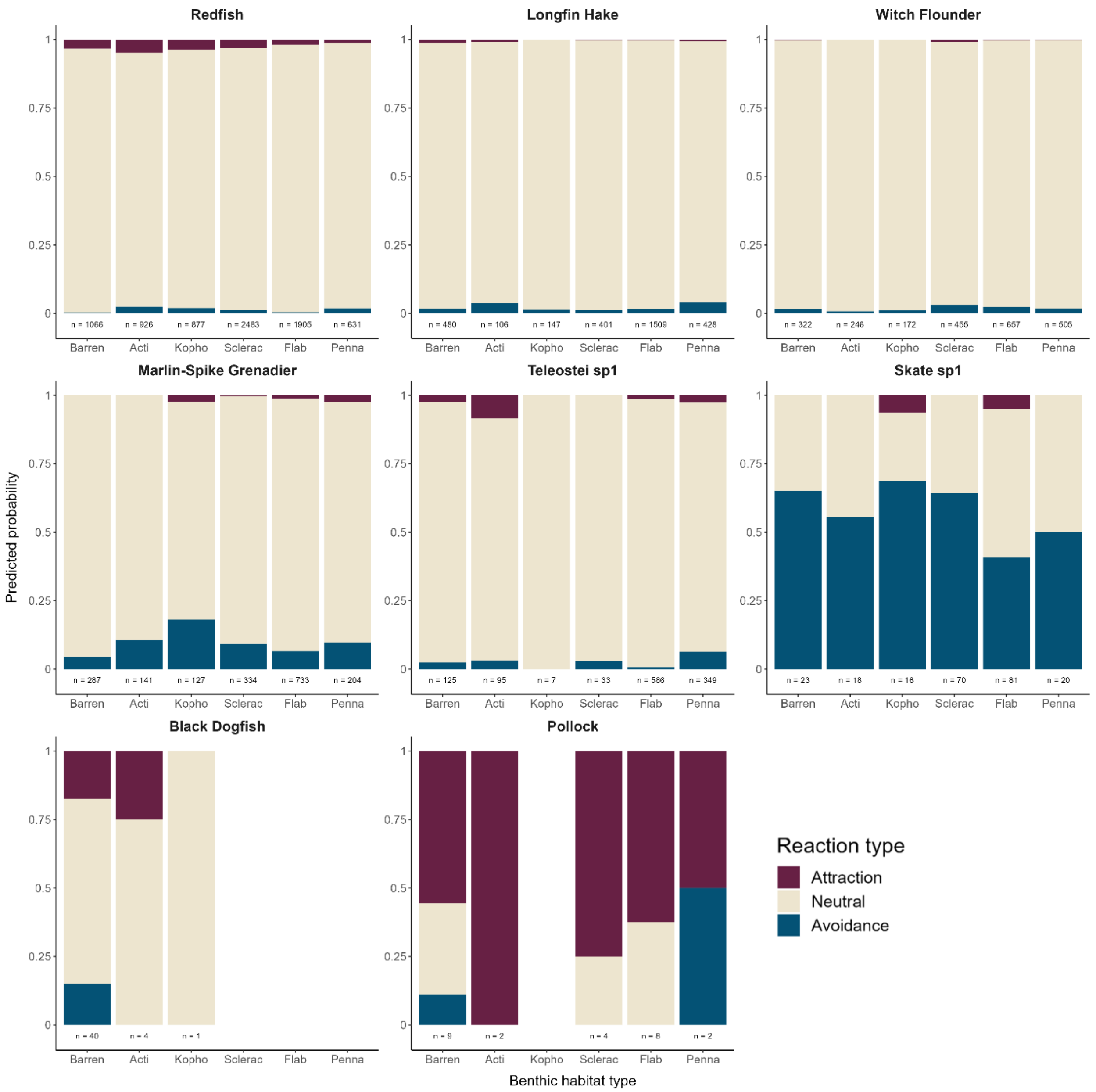


Fig. 4-15 | Predicted probabilities of fish reaction types in relation to benthic habitat type per fish taxon. n = number of fish observed per category. See Table 4-2 for details of fish reactions and Table 4-3 for benthic habitat types.

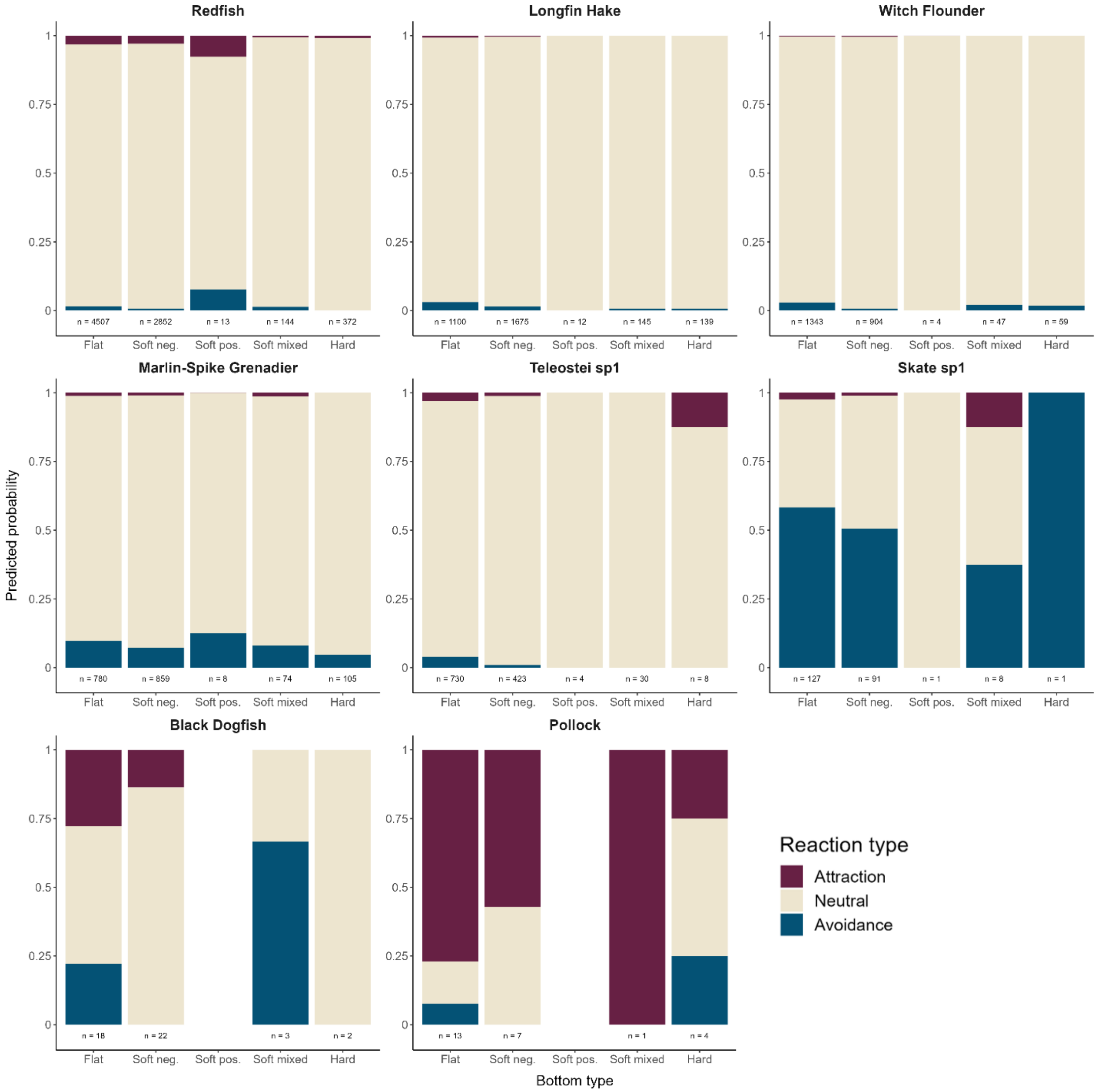


Fig. 4-16 | Predicted probabilities of fish reaction types in relation to bottom type per fish taxon. n = number of fish observed per category. See Table 4-2 for details of fish reactions and Table 4-3 for bottom types.

- **Bottom type**

For six fish taxa, ‘Neutral’ was the most predicted reaction ($\overline{P}$ = 94%), and for five of them we did not find any influence of bottom type on fish reactions (**Fig. 4-16**). Black Dogfish had a higher probability of ‘Neutral’ reaction (‘No reaction’) associated with ‘Soft negative’ bottom type than in ‘Flat’ bottom type (P = 86 and 50% respectively). Skate sp1 had a higher probability of ‘Avoidance’ (‘Hiding’) in both ‘Flat’ and ‘Soft negative’ bottom types ($\overline{P}$ = 54.5%). Although, we found an increase of ‘Neutral’ reaction associated with the ‘Soft negative’ bottom type (P = 39 to 48%). Pollock showed high probabilities of ‘Attraction’ in every bottom type this taxon was associated with ($\overline{P}$ = 67%), although we found an increase of ‘Neutral’ reactions associated with the ‘Soft negative’ bottom type (P = 15 to 43%).

4-3.5.4 | Influence of fish *in-situ* behavior attributes on fish reactions to UVS

- **Fish activity**

For six fish taxa, ‘Neutral’ was the most predicted reaction ($\overline{P}$ = 93%), and for all of them we did not find any influence of fish activity on their reactions (**Fig. 4-17**). Redfish and Longfin Hake had a higher probability of ‘Avoidance’ ($\overline{P}$ = 5 and 6% respectively) and a higher probability of ‘Attraction’ ($\overline{P}$ = 20% and 6% respectively) when displaying ‘Medium’ to ‘High’ body movements. Marlin-Spike Grenadier had a higher probability of ‘Attraction’ with ‘High body movements’ (P = 5.5%). Teleostei sp1 and Black Dogfish had a higher probability of ‘Avoidance’ when displaying no notable activity (P = 5% and 22% respectively) and a higher probability of ‘Attraction’ with ‘Medium’ to ‘High’ body movements (P = 3% and 23% respectively). Skate sp1 showed high probabilities of ‘Avoidance’ when displaying no activity (P = 57%), and Pollock showed high probabilities of ‘Attraction’ when displaying ‘High body movements’ (P = 70%).

- **Fish altitude**

For four fish taxa, ‘Neutral’ was the most predicted reactions ($\overline{P}$ = 93%) and we did not find any influence of fish altitude on their reaction (**Fig. 4-18**). Black Dogfish had a higher probability of ‘Neutral’ reaction when observed on the seafloor ($\overline{P}$ = 78%) and a higher probability of ‘Attraction’ when in the water column (P = 100%). Pollock showed increased probabilities of ‘Attraction’ with altitude in the water column ($\overline{P}$ = 44 to 89%). Differences observed for Pollock could be attributed to observations of too few individuals per altitude category (n = 1 to 9).

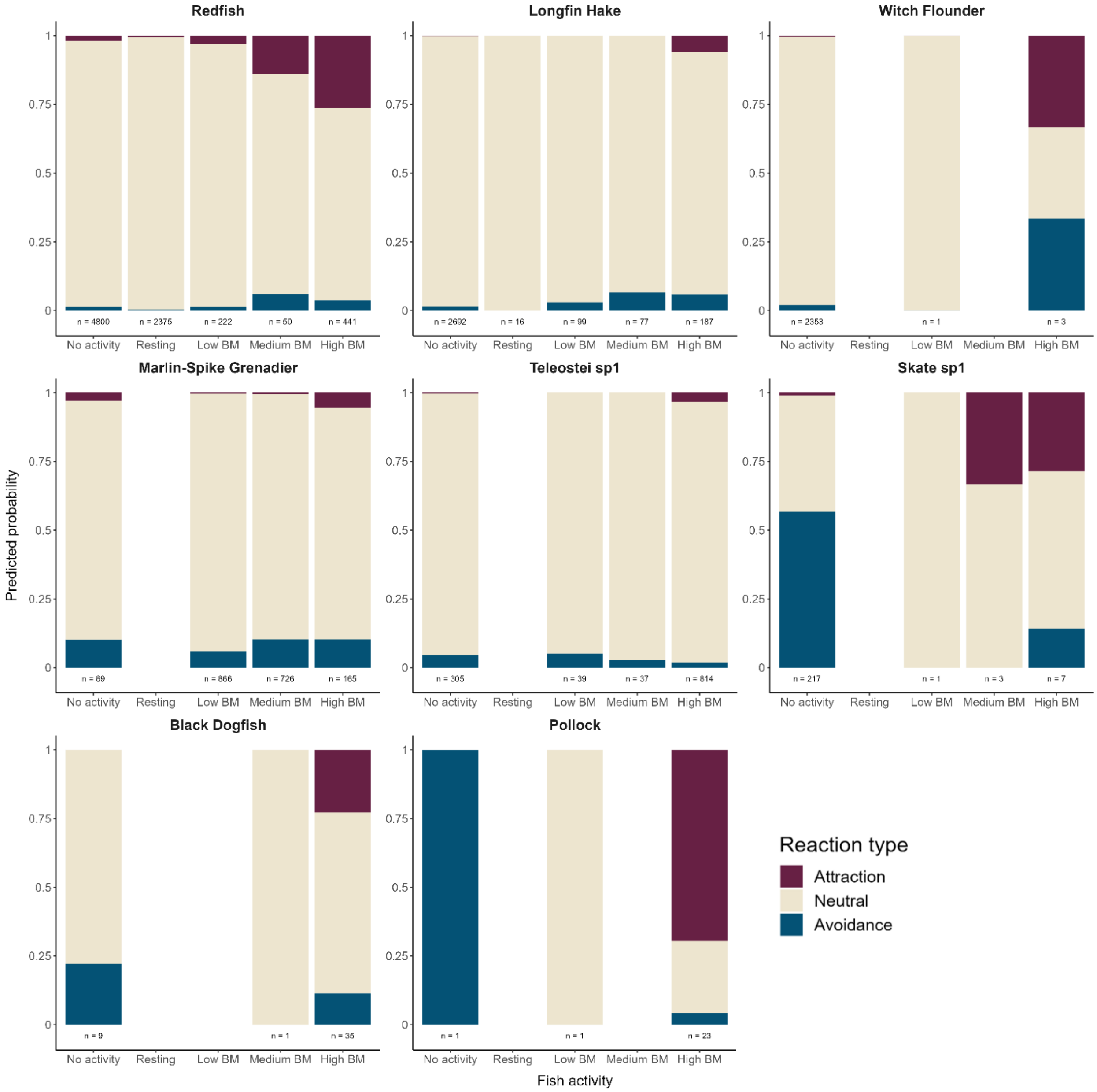


Fig. 4-17 | Predicted probabilities of fish reaction types in relation to fish activity per fish taxon. n = number of fish observed per category. See Table 4-2 for details of fish reactions and Table 4-3 for fish activity categories.

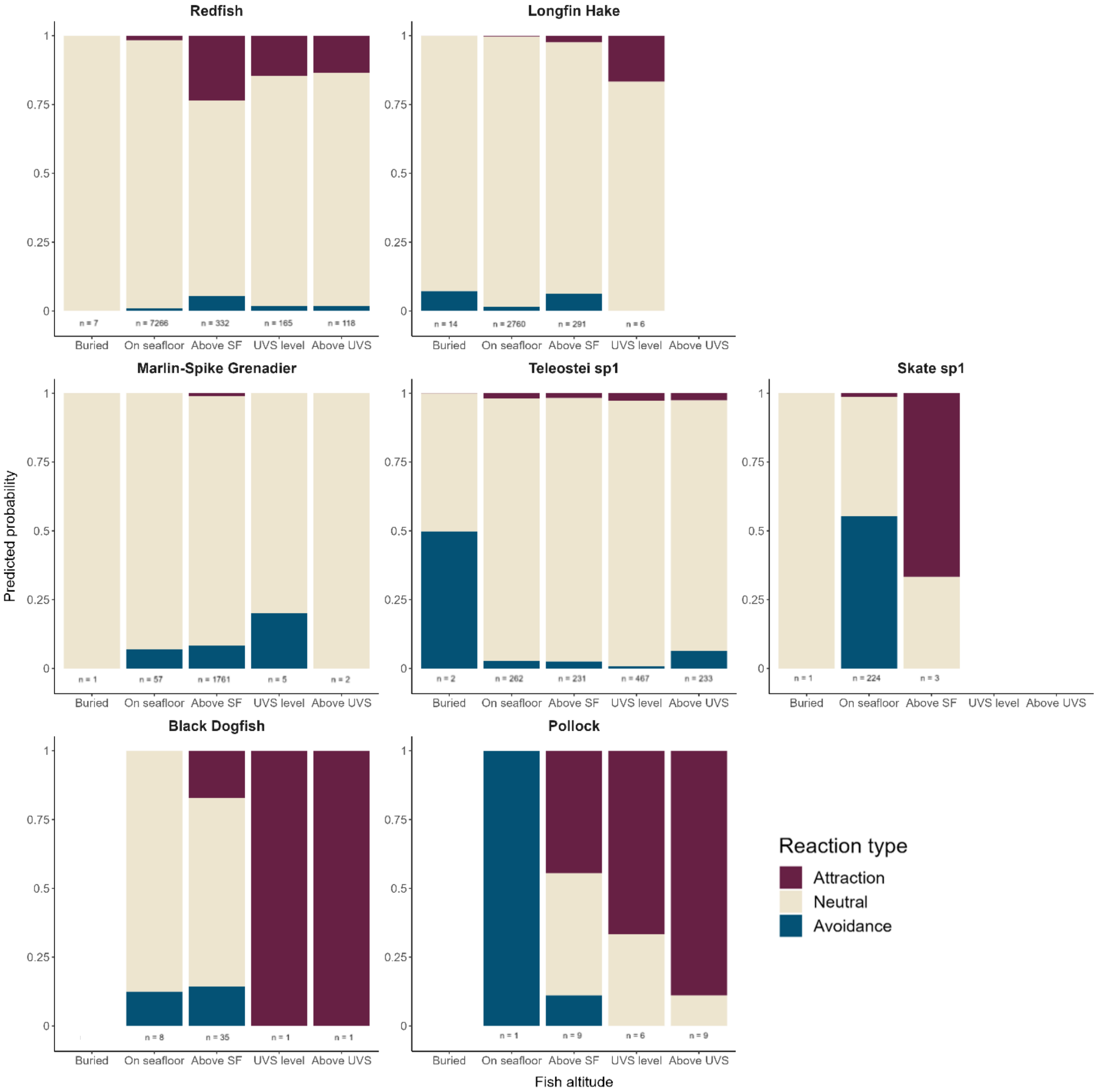


Fig. 4-18 | Predicted probabilities of fish reaction types in relation to fish altitude per fish taxon. n = number of fish observed per category. No model was performed for Witch Flounder as the taxon was only observed on the seafloor. Table 4-2 for details of fish reactions and Table 4-1 for fish altitude categories.

- **Fish locomotion**

For six fish taxa, 'Neutral' was the most predicted reactions ($\overline{P}$ = 94%), and for three of them we did not find any influence of fish locomotion on their reaction (**Fig. 4-19**). We found an increase of 'Attraction' reactions with active swimming for Redfish (P = <2 to

25%). We found an increase of 'Avoidance' and 'Attraction' reactions with active swimming for Marlin-Spike Grenadier (P = <10 to 17% and <3 to 8% respectively). We found a decrease in 'Avoidance' and 'Neutral' reactions, and an increase in 'Attraction' with active swimming for Black Dogfish (P = 22 to 11%, 78 to 67% and 0 to 22% respectively).

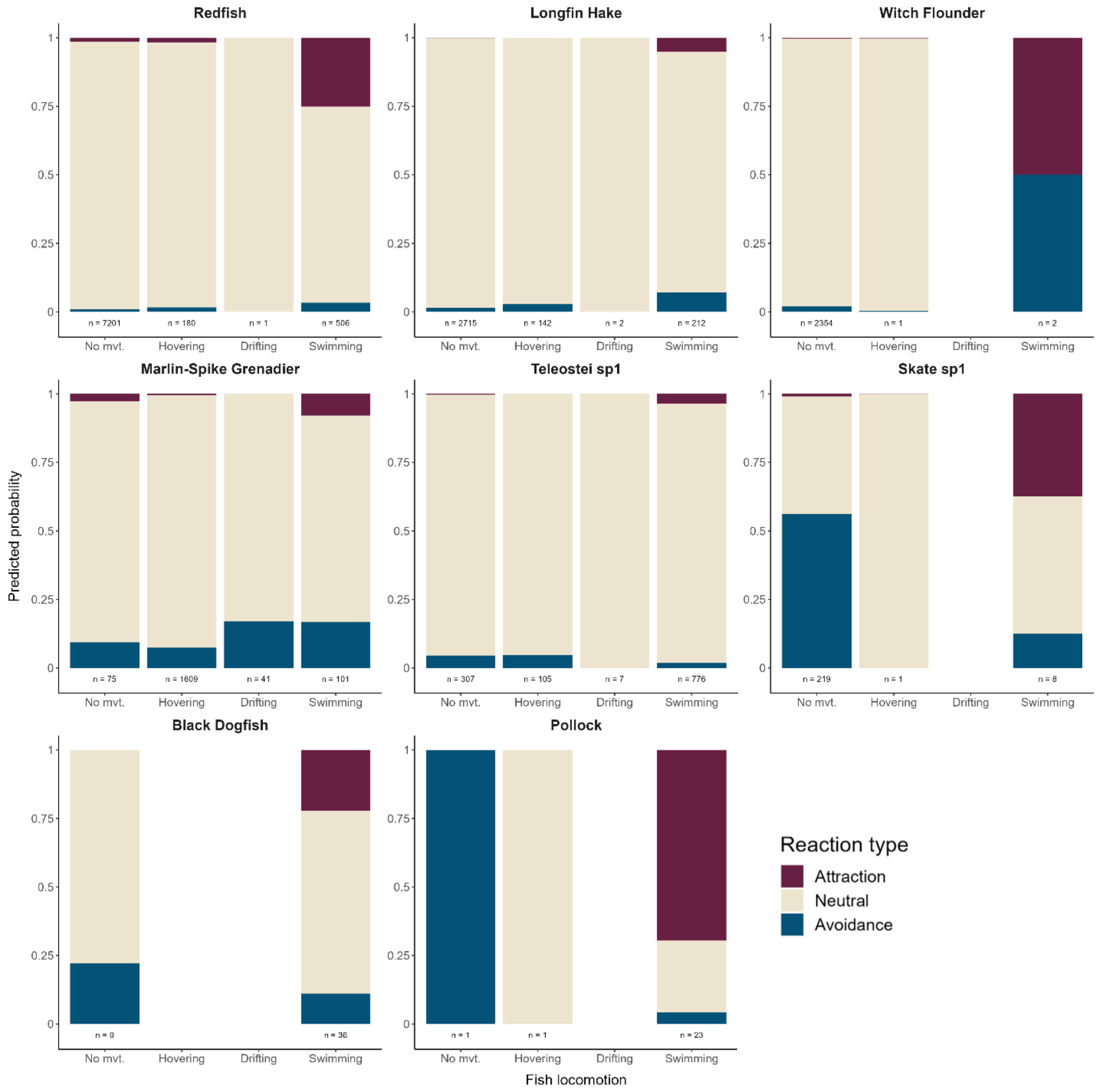


Fig. 4-19 | Predicted probabilities of fish reaction types in relation to fish locomotion per fish taxon. n = number of fish observed per category. See Table 4-2 for details of fish reactions and Table 4-1 for fish locomotion categories.

4-3.5.5 | Influence of fish-related factors on fish reactions to UVS

- **Fish total density**

For six fish taxa, ‘Neutral’ was the most predicted reactions ($\overline{P}$ = 92.5%) and we did not find any influence of fish total density on fish reaction (**Fig. 4-20**). Skate sp1 showed high probabilities of ‘Avoidance’ associated with every fish density category where this was taxon was mostly observed ($\overline{P}$ = 57%). Pollock showed high probabilities of ‘Attraction’ associated with every fish density category where this was taxon was mostly observed ($\overline{P}$ = 67%).

- **Fish life stage**

For all four fish taxa, ‘Neutral’ was the most predicted reactions ($\overline{P}$ = 96%) and we did not find any influence of fish life stage on fish reaction (**Fig. 4-21**).

- **Distance to the UVS**

For six fish taxa, ‘Neutral’ was the most predicted reaction ($\overline{P}$ = 95%), and for five of them we found an influence of fish distance to the UVS on fish reaction (**Fig. 4-22**). We found an increase of ‘Avoidance’ and ‘Attraction’ associated with far distance to UVS for Redfish, Longfin Hake and Marlin-Spike Grenadier ($\overline{P}$ = 1.5 to 14.5% and 1 to 11% respectively). We observed an increase of ‘Avoidance’ reactions associated with close and far distances to the UVS for Black Dogfish ($\overline{P}$ = 8 to 19%). Skate sp1 had a higher probability of ‘Neutral’ reactions associated with lateral distance to the UVS (P = 54%) and a higher probability of ‘Avoidance’ reactions associated with close and far distance to the UVS (P = 61 and 78% respectively). Pollock showed high probabilities of ‘Attraction’ associated with all distance categories where this was taxon was mostly observed ($\overline{P}$ = 70%).

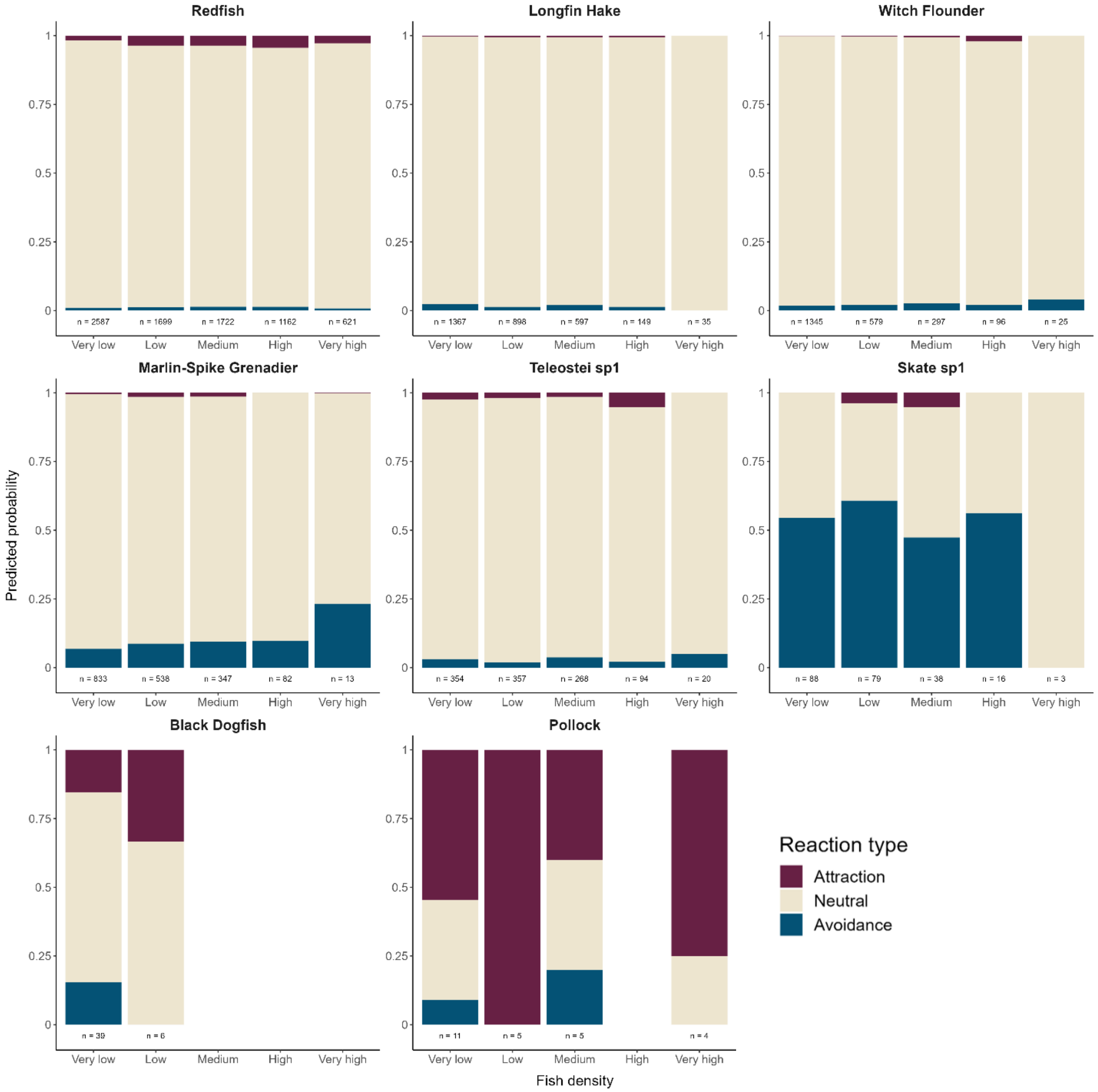


Fig. 4-20 | Predicted probabilities of fish reaction types in relation to fish total density per fish taxon. n = number of fish observed per category. See Table 4-2 for details of fish reactions and Table 4-1 for fish total density ranges.

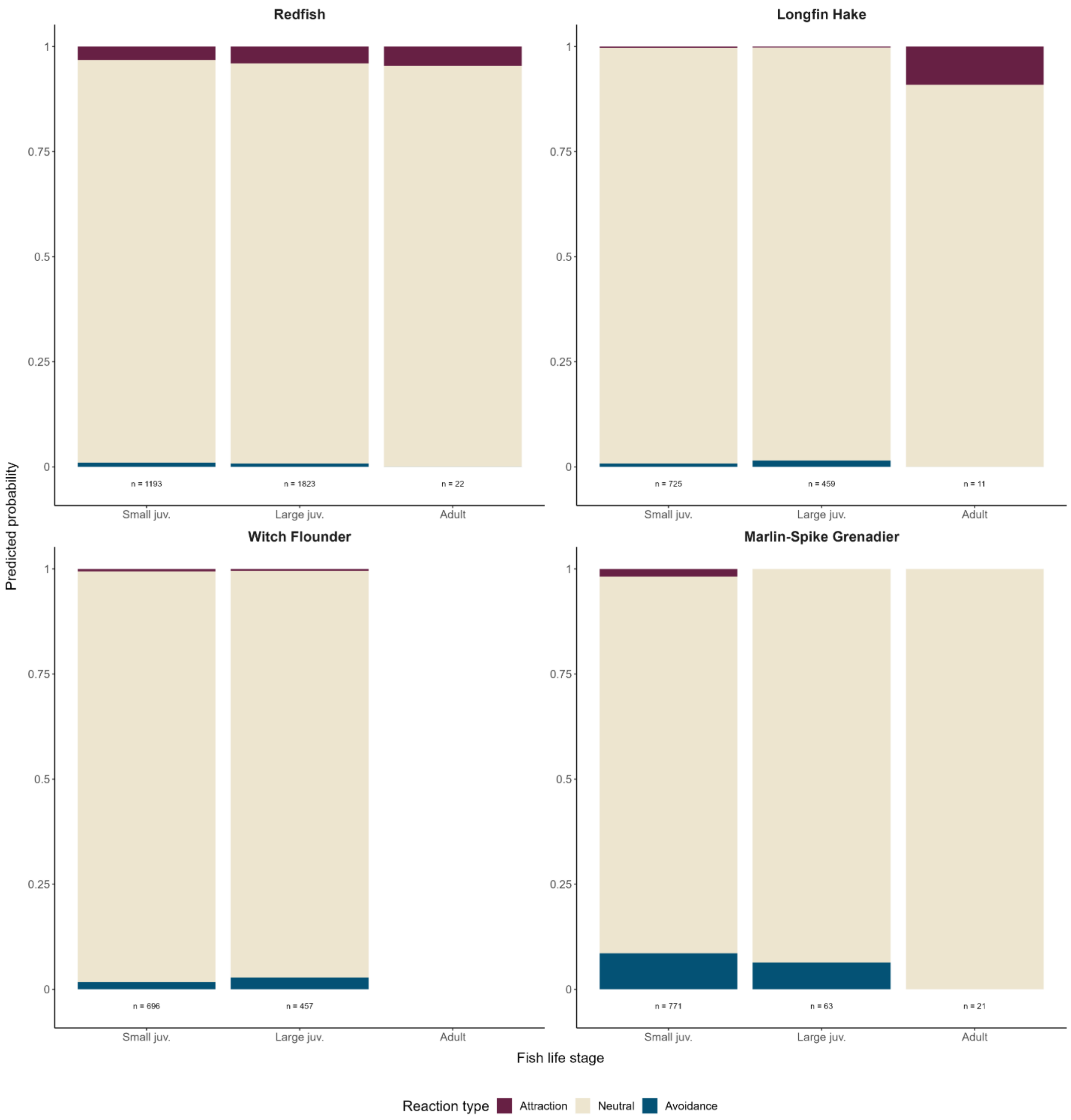


Fig. 4-21 | Predicted probabilities of fish reaction types in relation to fish life stage per fish taxon. n = number of fish observed per category. See Table 4-2 for details of fish reactions and Table 4-3 for fish life stage.

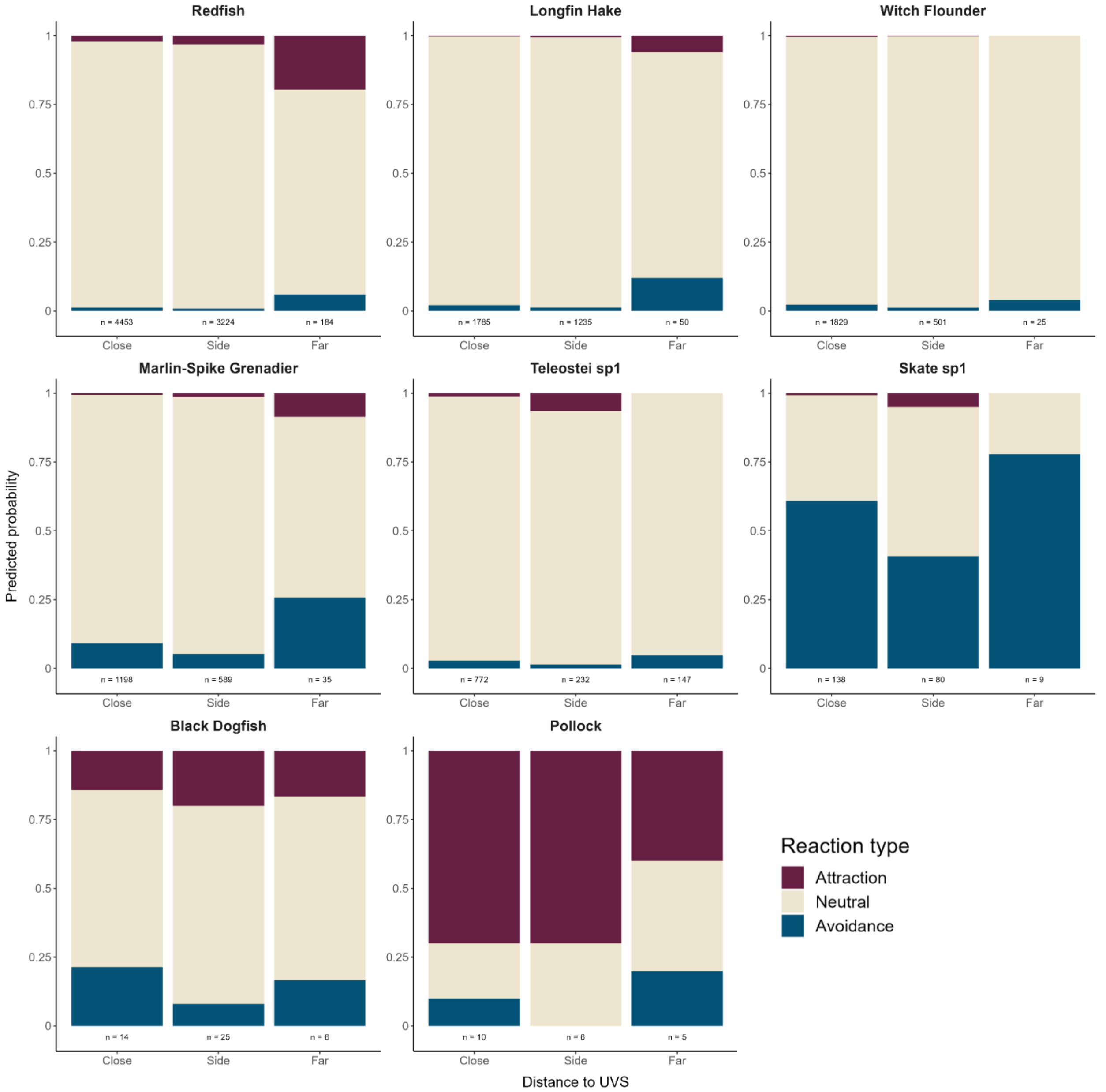


Fig. 4-22 | Predicted probabilities of fish reaction types in relation to fish distance to the UVS per fish taxon. n = number of fish observed per category. See Table 4-2 for details of fish reactions and Table 4-3 for distance to UVS categories.

- **Reaction timing**

To assess the relationship between fish reaction and the timing of their reaction, we only considered fish that displayed a noticeable reaction. Therefore, the reactions of 5,792 fish were analyzed, representing 35% of all fish observed. Here, ‘Neutral reaction’ then refers to ‘Minor’ and ‘Major reactions’ only.

Redfish had a higher probability of ‘Neutral’ reactions (‘Minor reaction’) during the UVS passage (P = 91%) and a higher probability of ‘Attraction’ before (‘Attraction’) and after (‘Following’) the UVS passage (P = 53 and 44% respectively) (**Fig. 4-23**). Of all Longfin Hake, 99% reacted during the UVS passage, and had a higher probability of ‘Neutral’ reactions (P = 94.5%). Witch Flounder and Marlin-Spike Grenadier had a higher probability of ‘Neutral’ reactions (‘Minor reaction’) during the UVS passage ($\overline{P}$ = 76%) and a higher probability of ‘Avoidance’ (‘Escaping’) before the UVS passage ($\overline{P}$ = 60%). Teleostei sp1 showed high probabilities of ‘Neutral’ reactions (‘Major reaction’) associated with all timing categories where this was taxon was mostly observed ($\overline{P}$ = 85.5%), but we found an increase of ‘Attraction’ reactions after the UVS passage (P = 22%). Of all Skate sp1, 90% reacted during the UVS passage, and had a higher probability of ‘Attraction’ reactions (P = 81%). Of all Black Dogfish, 95% reacted during the UVS passage, and had a higher probability of ‘Neutral’ reactions (P = 70%). Pollock showed high probabilities of ‘Attraction’ associated with all timing categories where this was taxon was mostly observed ($\overline{P}$ = 83%), but we found an increase of ‘Avoidance’ (‘Escaping’) and ‘Neutral’ reactions (‘Minor reaction’) during the UVS passage (P = 17 and 33% respectively).

Fig. 4-23 | Predicted probabilities of fish reaction types in relation to fish reaction timing per fish taxon. n = number of fish observed per category. See Table 4-2 for details of fish reactions and Table 4-3 for reaction timing categories.

4-4 | Discussion

In this study, we described and analyzed the variability of fish *in-situ* behavior and response behavior to UVSs during benthic multi-species surveys. We also provided detailed analysis of the influence of multiple factors on the reaction type and magnitude for nine groundfish taxa observed *in situ* in a deep-sea soft-bottom environment.

4-4.1 | Natural and response behavior in fish in the Laurentian Channel MPA

4-4.1.1 | Fish *in-situ* behavior

The fish assemblage we observed comprised three distinct groups of fish based on their *in-situ* behavior: inactive benthic, semi-active benthopelagic and active mesopelagic fishes. These groups are in accordance with assemblages described in other studies, and highlight the species-specific use of the habitat by fishes (**Lorance & Trenkel, 2006 | Devine *et al*., 2020**).

In our video footage, inactive benthic behaviour was the most observed behaviour type for most taxa. This sitting or resting behavior is common for groundfish taxa, and has been reported in low-current environments as an energy-efficient feeding strategy for ambush predators to hunt near-bottom prey (*i.e.*, a 'sit-and-wait' foraging strategy) (**Auster, 1985 | Krieger, 1993 | Uiblein *et al*., 2003 | Lorance & Trenkel, 2006**). In addition to being ambush predators, many taxa such as flatfishes and skates are also known to be cryptic species, using camouflage to hide (**Ryer, 2008 | Devine *et al*., 2020**).

Marlin-Spike Grenadier was the only species in this study described as 'semi-active benthopelagic', observed on or near the bottom and almost constantly on the move. This behavior has been reported in other studies focused on the NW Atlantic where this taxon was observed foraging near the seafloor (**Baker *et al*., 2012b | Devine *et al*., 2020**). Gartner *et al*. (**1997**) interpreted this hovering behavior above the seafloor as a way to conserve energy while foraging. This is in contrast to Uiblein *et al*. (**2011**) who observed active swimming behaviour among Marlin-Spike Grenadier in the NE Atlantic, highlighting the variability of fish behavior with local environmental factors (*e.g*., time of day) (**Stoner *et al*., 2008 | Uiblein *et al*., 2011 | Benoit-bird *et al*., 2023 | Williams *et al*., 2023**).

The last group mostly comprised large foraging predators (Pollock, Atlantic Cod and Black Dogfish) actively swimming in the water column (**Trenkel *et al*., 2004**). Another taxon present in this group was Teleostei sp1, comprising Sandlance and/or Barracudina species indistinguishable from each other in our video footage. Interestingly, nearly 30%

of this taxon were observed on or near the seafloor in the Laurentian Channel. Both Sandlance and Barracudina are fast swimmers with elongated bodies and are characterized as forage burial species. The two taxa are mostly found in the water column when they are feeding, but are also known to use soft-sediments burrows and depressions as a way to hide from predators (**Harry, 1953 | Bizzarro *et al.*, 2016**). Thus, differences in Teleostei sp1 behavior could reflect differences between these two taxa (Sandlance and Barracudina) and specific variability in habitat use with environmental factors (*e.g.*, diurnal vertical feeding migrations).

4-4.1.2 | Variability of fish *in-situ* behavior

Overall, we did not find any major influence of the ecological factors tested in this study on fish *in-situ* behavior, which is in contrast with most studies (**Table 4-7**). However, we did find species-specific variability for three fish taxa. Species-specific influence of ecological factors such as depth, fish size or benthic habitat has been reported in the NE Pacific, NE and NW Atlantic (**Lorance & Trenkel, 2006 | Uiblein *et al.*, 2011 | Stierhoff *et al.*, 2013 | Sward *et al.*, 2019 | Devine *et al.*, 2020**). Here, we observed a decrease in activity for Marlin-Spike Grenadier associated with all ecological factors and for Teleostei sp1 associated with depth and time of day. We also observed increased resting behavior for Redfish associated with one CWC habitat.

Table 4-7 | Influence of multiple ecological factors on deep-sea fish *in-situ* behavior variability reported in previous studies. Studies were conducted in the NE Pacific (green), the NE (blue) and NW Atlantic (purple).

Influence	**Ecological factors**			
	Depth	Time of day	Benthic habitat type	Fish life stage/size
No influence			Uiblein *et al.*, 2011	
Fish *in-situ* behavior	Uiblein *et al.*, 2003		Uiblein *et al.*, 2003, 2011	
Fish activity				
Fish altitude		Winslade, 1974 Meyer *et al.*, 1979		Adams *et al.*, 1995 Trenkel *et al.*, 2004 Sward *et al.*, 2019
Fish locomotion	Lorance & Trenkel, 2006			

Variability in fish *in-situ* behavior is highly representative of fish behavior plasticity and their adaptation to changes in local conditions (**Uiblein *et al*., 2011**). While it reflects differences in habitat use by different fish taxa, confounding effects of multiple factors makes it difficult to assess the direct influence of ecological factors on fish *in-situ* behavior. For instance, a number of studies have reported differences in fish altitude with fish size, with small juveniles observed on the seafloor while larger fish were found higher in the water column (**Adams *et al*., 1995 | Trenkel *et al*., 2004 | Sward *et al*., 2019**). This is the case with Redfish, where all life stages have been reported to feed at night in the water column and to rest during the day on the seafloor in the NW Atlantic (**Rodriguez-Marin *et al*., 1994 | Gauthier & Rose, 2005**). In our study, we only measured fish from the downward-looking camera, and therefore were not able to test the influence of fish size on fish altitude as they were all measured on or near the seafloor. Nonetheless, we found a slight decrease in activity and locomotion between juveniles and adults for Marlin-Spike Grenadier. More data would need to be collected as little is known about the ecology of this species. It is likely though that variability in *in-situ* behavior of Marlin-Spike Grenadier is linked to differences in habitat use between feeding and resting, at different life stages.

Differences in behavior for Teleostei sp1 with depth could reflect differences in behavior between the two fish taxa it represents. Sandlance and Barracudina are known to occur in the studied depth range, but their distribution areas overlap (**Post, 1990 | Robards *et al*., 2000 | Mundy, 2005 | Chapter 2**). While vertical migrations have not yet been reported for Barracudina, Sandlance is known to display diel feeding migrations, and is commonly found actively swimming and foraging in the water column during the day – depending on prey availability (**Rofen, 1966 | Winslade, 1974 | Meyer *et al*., 1979**). At night Sandlance burrow into preferred soft sediment to seek refuge from predators (*e.g.*, Flatfish, Haddock, Pollock) who may 'prey on them as they begin to burrow' (**Hobson, 1986 | Jensen, 2001 | Temming *et al*., 2004**).

Except for a few taxa, our results showed no evidence of differences in fish habitat use in the Laurentian Channel MPA. Our results and the lack of variability in fish *in-situ* behavior could reflect the low or lack of variability in the factors tested (*e.g.*, small depth range, low habitat complexity level, dominance of juvenile fish over adults). Moreover, the inconsistencies between our results and those of other studies suggest that fish *in-situ* behavior may differ with geographic location, combined with broader ranges of observed values for the factors tested in these studies compared to what we measured in the MPA.

4-4.1.3 | Fish response behavior

Most fish and most fish taxa did not react to the presence of UVSs or showed minor reactions that did not induce any bias in observed abundance estimates (as fish did not leave the FoV). There were, however, some taxon-specific reactions to the presence of UVSs. These results are consistent with many studies that assessed fish response behavior to UVSs in the NE and NW Atlantic (**Trenkel *et al*., 2002, 2004 | Uiblein *et al*., 2003, 2011 | Lorance & Trenkel, 2006 | Porteiro *et al*., 2013 | Devine *et al*., 2020**), the Gulf of Alaska (**Johnson *et al*., 2003 | Lauth *et al*., 2004 | Williams *et al*., 2023**), the NE & SE Pacific (**Raymond & Widder, 2007 | Bozec *et al*., 2011 | Pacunski *et al*., 2013 | Dunlop *et al*., 2020 | Benoit-Bird *et al*., 2023**) and the Mediterranean Sea (**Ayma *et al*., 2016**) (**Stoner *et al*., 2008**). As reported in other studies, we observed differences in fish reaction between and within fish groups (*i.e*., pelagic *vs*. benthic) (**Queirolo *et al*., 2010 | Robert *et al*., 2020**). However, generalization of fish response behavior is not possible as variability was also reported within taxa (*e.g*., flatfish, redfish) and with geographic location (**Krieger & Ito, 1999 | Trenkel *et al*., 2004 | Raymond & Widder, 2007 | Stoner *et al*., 2008 | Rountree & Juanes, 2010 | Laidig *et al*., 2013 | Stierhoff *et al*., 2013 | Ayma *et al*., 2016 | Devine *et al*., 2020 | Campbell *et al*., 2021 | Williams *et al*., 2023**).

Table 4-8 | Influence of multiple technical, environmental and fish-related factors on deep-sea fish response behavior variability reported in previous studies. Studies were conducted in the NE Atlantic (blue), the NW Atlantic (purple), the Gulf of Mexico (yellow), the SW Pacific (pink), the NE Pacific (green) and the Gulf of Alaska (orange).

Factor	**Influence on behavior variability**			
	No reaction	Unspecified reaction/ Reaction intensity	Avoidance	Attraction
Technical				
Multi	Adams *et al.*, 1995 Lorance & Trenkel, 2006 Williams *et al.*, 2023			
UVS type		Uiblein *et al.*, 2011 Laidig *et al.*, 2013 Somerton *et al.*, 2017	Stoner *et al.*, 2008 Dunlop *et al.*, 2020 Benoit-bird *et al.*, 2023	Campbell *et al.*, 2021 Williams *et al.*, 2023
UVS speed	Somerton *et al.*, 2017 Williams *et al.*, 2023	Trenkel *et al.*, 2004 Stoner *et al.*, 2008	Somerton *et al.*, 2017 Campbell *et al.*, 2021	Campbell *et al.*, 2021 Williams *et al.*, 2023
UVS altitude	Somerton *et al.*, 2017		Somerton *et al.*, 2017 Campbell *et al.*, 2021	Trenkel *et al.*, 2004
Survey operation	Lorance & Trenkel, 2006 Bold *et al.*, 2018		Stoner *et al.*, 2008	Trenkel *et al.*, 2004 Trenkel & Lorance, 2011 Uiblein *et al.*, 2011
Environmental				
Multi	Lorance & Trenkel, 2006			
Depth		Trenkel *et al.*, 2004 Uiblein *et al.*, 2002, 2003, 2011 Ryer *et al.*, 2009	Benoit-bird *et al.*, 2023	
Time of day	Williams *et al.*, 2023	Trenkel *et al.*, 2004 Uiblein *et al.*, 2002, 2003 Ryer *et al.*, 2009 Benoit-bird *et al.*, 2023		
Benthic habitat type	Lorance & Trenkel, 2006 Uiblein *et al.*, 2011	Lorance & Trenkel, 2006 Uiblein *et al.*, 2011 Campbell *et al.*, 2021		
Bottom type				
In-situ behavior				
Multi		Trenkel *et al.*, 2004 Uiblein *et al.*, 2003, 2011 Lorance & Trenkel, 2006 Porteiro *et al.*, 2013		
Fish activity		Johnson *et al.*, 2003		

		Ryer *et al.*, 2009 Williams *et al.*, 2023		
Fish altitude		Krieger & Ito, 1999 Adams *et al.*, 1995 Johnson *et al.*, 2003 Trenkel *et al.*, 2004 Laidig *et al.*, 2013 Stierhoff *et al.*, 2013 Sward *et al.*, 2019 Devine *et al.*, 2020 Williams *et al.*, 2023	Laidig *et al.*, 2013	Campbell *et al.*, 2021 Williams *et al.*, 2023
Fish locomotion		Uiblein *et al.*, 2011 Williams *et al.*, 2023		Campbell *et al.*, 2021 Williams *et al.*, 2023
Fish-related				
Total density	Lorance *et al.*, 2002 Uiblein *et al.*, 2003	Uiblein *et al.*, 2011 Laidig *et al.*, 2013 Stierhoff *et al.*, 2013		Campbell *et al.*, 2021
Life stage	Williams *et al.*, 2023	Adams *et al.*, 1995 Uiblein *et al.*, 2002, 2003, 2011 Lauth *et al.*, 2004 Trenkel *et al.*, 2004 Sward *et al.*, 2019	Laidig *et al.*, 2013 Stoner *et al.*, 2008 Rooper *et al.*, 2015	
Distance to UVS		Uiblein *et al.*, 2011 Laidig *et al.*, 2013 Porteiro *et al.*, 2013 Rooper *et al.*, 2015	Koslow *et al.*, 1995 Lorance & Trenkel, 2006 Uiblein *et al.*, 2011 Laidig *et al.*, 2013 Porteiro *et al.*, 2013 Rooper *et al.*, 2015	Raymond & Widder, 2007 Campbell *et al.*, 2021 Williams *et al.*, 2023
Reaction timing		Trenkel *et al.*, 2004 Lorance & Trenkel, 2006 Ryer *et al.*, 2009 Porteiro *et al.*, 2013	Somerton *et al.*, 2017	

4-4.1.4 | Variability of fish response behavior

Overall, our results did not show major variability in fish reaction type with the factors tested, although we did observe small variability of fish reaction magnitude. On the other hand, we observed more taxon-specific variability in fish reaction type and magnitude with fish *in-situ* behavior attributes, which was expected (**Lorance & Trenkel, 2006**). Moreover, taxa showing strong reactions to UVSs also showed the most variability in behavior. The reported influence of technical, environmental, fish *in-situ* and fish-related attributes on fish behavior and behavior intensity was variable among studies as it appeared to be taxon-specific and differed with geographic location (**Table 4-8**).

4-4.1.4.1 | Influence of technical factors

The influence of UVS attributes on fish behavior and behavior intensity has been previously demonstrated, but is difficult to assess because of confounding effects (**Campbell *et al.*, 2021**). In our study we observed a higher percentage of reaction towards ROV than the near-seabed camera. Differences in fish reactions between UVSs could be attributed to differences in lighting settings, vehicle tethers, vehicle size, vehicle noise or a combination of all of these (**Trenkel *et al.*, 2004 | Laidig *et al.*, 2013 | Somerton *et al.*, 2017**). Here, most of the reactions we observed occurred when UVSs were in motion and varied with UVS operational factors (*e.g.*, altitude and/or speed). For instance, Skate sp1 showed more avoidance when UVSs were on the seafloor, while when UVSs were in the water column Black Dogfish and Gadidae fish showed more attraction and Teleostei sp1 displayed less reaction overall.

4-4.1.4.2 | Influence of environmental variables

The influence of environmental factors on fish reaction type and magnitude has been previously demonstrated, but is difficult to assess because of confounding effects, especially in regard to fish *in-situ* behavior. Indeed, although environmental factors do not have an apparent influence on fish reactions, their influence on fish *in-situ* behavior could consequently affect fish reactions (**Uiblein *et al.*, 2003, 2011 | Lorance & Trenkel, 2006**). For instance, Uiblein *et al*. (**2002, 2003**) suggested that the influence of depth on fish reaction might be indirect, and could instead be attributed to the influence of fish size, food availability and/or ambient light which are all known factors correlated with depth (**Ryer *et al*., 2009 | Benoit-bird *et al*., 2023**).

4-4.1.4.3 | Influence of fish *in-situ* behavior attributes

Fish *in-situ* behavior attributes had the highest influence of all attributes tested on fish reaction type and magnitude. Overall, we observed an increase of reactions, specifically attraction, with increased fish activity, altitude and locomotion intensity. These results are in alignment with most studies (**Table 4-8**). Similarly to environmental factors, it is difficult to assess the influence of fish *in-situ* behavior on fish reactions because of confounding effects. For instance, studies that reported a positive correlation between fish size and fish altitude also reported an increase in fish reaction (**Adams *et al*., 1995 | Trenkel *et al*., 2004 | Sward *et al*., 2019**).

Here, in addition to finding differences between fish groups (*i.e*., benthic *vs*. pelagic fish) we also observed differences within groups and within taxa, which is consistent with other studies (**Krieger & Ito, 1999 | Laidig *et al*., 2013 | Campbell *et al*., 2021 | Williams *et al*., 2023**). When looking at the fish assemblage, swimming pelagic fish were strongly attracted to UVSs and would follow the vehicles (**Campbell *et al*., 2021 | Williams *et al*., 2023**), while inactive benthic fish showed no to low reaction (**Williams *et al*., 2023**). Conversely, Teleostei sp1 showed more disoriented reaction behavior when inactive on the seafloor than when swimming in the water column. Similarly, while most Redfish were observed inactive on the seafloor with no reaction to UVSs, we found an increase in response behavior from individuals in the water column (**Krieger & Ito, 1999 | Laidig *et al*., 2013**).

4-4.1.4.4 | Influence of fish-related factors

In our study, reactions to UVSs increased slightly with higher fish densities, especially for Redfish. Redfish was the densest taxon of the assemblage and was often observed in dense aggregations (up to 0.97 ind./m^2) (**Chapters 2 & 5**). Several studies reported or suggested that species-specific density could influence the behavior of this taxon (**Uiblein *et al*., 2011 | Stierhoff *et al*., 2013**). For example, Stoner *et al*. (**2008**) reported that multiple Redfish species were more likely to show attraction behavior and to follow a HOV when aggregated. Here we did not observe such behavior, but instead observed an increase in 'Minor reactions' as a result of a 'snowball' effect triggered by the initial reaction of a few Redfish individuals. This group behavior was occasionally observed for Teleostei sp1 as well, on or near the seabed, although this taxon presented lower densities.

Here our results and the lack of influence of fish size on fish reactions in our study could reflect the small range in fish size for the taxa measured. While most studies compare juveniles to adults, juveniles were the dominant life stage observed during the two video surveys (**Chapter 3**). It is also likely that no differences in behavior exist between small and large juveniles as large juveniles represent a 'transition' life stage. 'Large' juveniles mostly comprise individuals that are just starting to mature and some individuals more developed, thus displaying behavior of habitat use of both mature and immature fishes (**Chapter 3**).

Assessing when and where fish react in relation to UVSs is essential when assessing fish assemblages during video surveys. In our study, we observed increased reactions, both avoidance and attraction, in fish far from the UVS or on the sides of the transect. These reactions typically occurred before and/or after fish were detected in the close illuminated FoV rather than during the UVS passage. Escape behavior, demonstrated by fish prior to UVS detection is likely pursued in response to a perceived threat in predation (**Koslow *et al*., 1995 | Lorance & Trenkel, 2006 | Uiblein *et al*., 2011 | Laidig *et al*., 2013 | Porteiro *et al*., 2013 | Rooper *et al*., 2015**). After detection by the UVS, escape behavior might be explained again by predation avoidance or simply as an attempt to avoid collision with the vehicle (**Devine *et al*., 2020**).

4-4.1.5 | Fish behavior and ecology

Beyond elucidating the potential bias induced by UVSs on fish assessments, collecting data on fish behavior – both *in-situ* and response – can also inform on fish ecology

(**Uiblein *et al*., 2011 | Sward *et al*., 2019**). While studying fish *in-situ* behavior can give us insights on how fish use their habitat (*e.g*., feeding, resting grounds), fish responses to UVSs are likely more a reflection of their vulnerability and how they assess unfamiliar elements in their environment.

Many studies suggest that UVSs are perceived as a threat by groundfish, mainly due to the larger size of vehicles and their investigative predator-like behavior. Thus, fish reactions may reflect their assessment of the predation risk (**Frid & Dill, 2002 | Lorance & Trenkel, 2006 | Ryer *et al*., 2009 | Laidig *et al*., 2013**). Fish constantly make decisions and compromises regarding feeding, mating and survival. Similarly, they must make decisions regarding the UVS based on local environmental conditions and their life history (**Raymond & Widder, 2007 | Benoit-bird *et al*., 2023**). A lack of reaction from fish could mean that UVSs are not perceived as a threat (**Lorance & Trenkel, 2006 | Uiblein *et al*., 2011 | Ayma *et al*., 2016**). Cautiously, Trenkel *et al*. (**2004**) suggested that 'No reaction' could also be because other variables can have an influence on fish assessment. For instance, a lack of reaction from fish close to the bottom may be because habitat conditions are too good to leave and fish are in safe habitats and/or are relying on their camouflage to avoid detection (**Lorance & Trenkel, 2006 | Devine *et al*., 2020**). In these instances, movement could reveal their presence to potential prey or predators, whereas the same taxa could react differently in different habitats or at different altitudes.

Where reactions were observed in other studies, avoidance behavior, which is the most common response among fish to the threat of predation, was also reported as the most common reaction to UVSs (**Uiblein *et al*., 2003, 2011 | Trenkel *et al*., 2004 | Lorance & Trenkel, 2006 | Laidig *et al*., 2013 | Campbell *et al*., 2021**). Diverse avoidance strategies have been reported as a response to UVSs when they are perceived as a potential predator by the different fish taxa (**Ryer, 2008**). Ayma *et al*. (**2016**) described fish close to the bottom displaying short-distance 'escapes' or swim in fast short busts while remaining in the FoV. The authors reported fish swimming in zigzag patterns to confuse the 'predator', which is a behavior that we observed for taxa like Redfish and Marlin-Spike Grenadier and categorized as 'Minor reaction', or fish creating sediment plume and hiding or resettling further in another sediment plume, which was the most observed behavior for skates in our study. Ayma *et al*. (**2016**) qualified this behavior as being typical of ambush predators. According to Campbell *et al*. (**2011**) hiding is a common reaction for small (juvenile) fish as they do not have great swimming abilities to escape, therefore hiding (when possible) is more advantageous.

Conversely, there are also fish that may not perceive UVSs as a threat. Commonly reported, large pelagic fish tend to follow vehicles reflecting a ‘stalking’ or ‘investigating’ natural behavior and relative fearlessness in relation to UVSs, which is a behavior we observed for Pollock and Atlantic Cod (**Campbell *et al*., 2021**). Although it is difficult to assess if the attraction was direct (curiosity) or indirect, as large fish could be attracted to smaller prey (**Stoner *et al*., 2008**). For instance, Sandlance is a known prey for sharks, squids or other groundfish species including Pollock and Atlantic Cod, and many of our observations of these two predators occurred while they were chasing or preying on Teleostei sp1, especially when the taxon displayed a frenetic disoriented behaviour on or near the seafloor (**Robards *et al*., 2000 | Moteki *et al*., 2001 | Preti *et al*., 2008**). Though this natural hunting behavior has been described before (**Hobson, 1986**), here it seemed that Pollock and Atlantic Cod took advantage of the group confusion to enhance their chance to catch prey.

Differences in the intensity of reactions can be explained by different UVS operational factors combined with different fish *in-situ* behaviors. Indeed, one UVS moving at different speeds can be perceived as more or less suspicious for fish depending on fish altitude, thereby triggering different reactions (**Campbell *et al*., 2021**). For instance, Uiblein *et al*. (**2011**) showed that stationary UVSs might not be perceived as predators contrary to moving UVSs during transect operations. It is also possible that fish that are more naturally active are more detectable by potential predators, and are therefore more vulnerable (**Lorance & Trenkel, 2006**). Although the signals were weak, our results indicated that UVSs, especially ROV, could be perceived as a predator by Skate sp1 and Teleostei sp1, but that the threat is relative to UVS altitude (**Benoit-bird *et al*., 2023**). Indeed, Skate sp1 reacted more strongly when UVSs were closer to the seafloor (*i.e.*, closer to them), while Teleostei sp1 displayed their unique frenetic behavior when they were near the seafloor and the UVS was just above them. Inversely, this behavior decreased when Teleostei sp1 were higher than the UVS in the water column.

Similarly, differences in the intensity of reactions can be explained by differences in fish *in-situ* behavior combined with fish life history. It is expected that fish displaying different swimming ability and position in the trophic chain do not have the same vulnerability and anti-predation strategy, and therefore react differently (**Queirolo *et al.*, 2010 | Frid *et al.*, 2019**). For instance, small (juvenile) fish display an escape behavior more than larger fish (**Frid *et al.*, 2019**). Pelagic fish tend to display relatively more following behavior than other fishes, while benthic fish either hide or display following behavior, but only for short distances ('Minor following') (**Campbell *et al.*, 2021**).

Fish evaluate the threat posed by UVSs, an unknown element in their environment, and adjust their reaction accordingly over time (**Lorance & Trenkel, 2006**). When they react, this evaluation process can introduce lags in the timing and intensity of their reaction, which can ultimately result in a graded response. First, there is awareness, then short avoidance which can lead to fish swimming away and leaving the FoV (**Somerton *et al.*, 2017**). That is a behavior we commonly observed, especially for fish close to the bottom, and recorded as an 'After' reaction. Additionally, we observed 'Multi-reaction' behaviors where, for example, fish would show 'Minor reactions' at first before escaping the FoV. Another example is where we would observe fish being attracted to UVSs when stationary on the seafloor, before either settling and acclimating to the vehicle during its operation or leaving the FoV – a behavior also reported in other studies (**Moser *et al.*, 1998 | Trenkel *et al.*, 2004 | Lorance & Trenkel, 2006 | Trenkel & Lorance, 2011 | Uiblein *et al.*, 2011 | Boldt *et al.*, 2018**). This shows that the longer a UVS stays, the more interaction will likely happen, which may not happen during transect operations when UVSs are mobile. This highlights the importance of taking into account UVS operation when assessing fish behavior (**Trenkel & Lorance, 2011 | Uiblein *et al.*, 2011**) as well as how long a fish is seen in the FoV. The latter is rarely reported in existing studies, but should be assessed in relation to when fish reacts after its first observation, and the type and magnitude of the response behavior (**Sward *et al.*, 2019**).

4-4.2 | Considerations for UVS fish surveys

4-4.2.1 | Limitations to fish assemblage assessment

Fish catchability varies considerably between fishing gears, depends on gear characteristics, fish-related attributes and environmental factors, and can induce biased estimates of fish assemblages (**ICES, 2004**). This has been mostly demonstrated with fish trawls, which have been a long-established conventional tool to monitor fish stocks. For instance, fish species, size or swimming capacities can all influence response behaviour in fish, which has been demonstrated to affect catchability in trawl gears (**Michalsen *et al.*, 1996 | Casey & Myers, 1998 | Benoit & Swain, 2003 | Somerton, 2004 | Winger *et al.*, 1999, 2000**). Other factors that can influence on fish behavior and fish catch efficiency, include the size and type of trawl, sweep length, mesh size, trawl speed or transect duration (**Engas & Godø, 1989 | Suuronen & Millar, 1992 | Ehrich & Stransky, 2001 | Somerton & Weinberg, 2001 | Weinberg *et al.*, 2002**).

While our results strongly suggest a lack of bias in our assessment of the Laurentian Channel fish abundance and assemblage composition, our study was limited to the visible extent of the UVS FoVs. Indeed, the greatest bias in studying mobile fish *in situ* is the potential of attraction and avoidance behavior occurring outside of the FoV. This behavior cannot be recorded by camera systems, although it could be detected through the use of additional technology (*e.g.*, multiple UVSs, acoustic technology), this limitation can nonetheless bias fish assessment as observations then does not reflect natural fish behavior nor their initial reactions (**Stoner *et al.*, 2008 | Laidig *et al.*, 2013 | Stierhoff *et al.*, 2013 | Somerton *et al.*, 2017**). A potential bias in UVS-based fish assessments is that fish in movement in the water column may have already reacted to the camera system before entering the illuminated FoV (**Uiblein *et al.*, 2003 | Lorance & Trenkel, 2006**). For instance, during a ROV survey conducted in the NW Atlantic by Moser *et al.* (**1998**), fish attraction to the vehicle was observed while it was settled on the bottom for maintenance operations prior to beginning the video transect. Without a careful sampling strategy, this can lead to overestimation of fish abundances. Another example is that fish in the water column above the UVSs might have been missed, which could induce underestimation of fish abundances (**Stierhoff *et al*., 2013**).

The use of additional technologies can help mitigate these biases. For instance, Somerton *et al*. (**2017**) deployed three different camera systems concurrently during their surveys: one camera system to investigate fish, and two camera systems to record fish behavior outside the FoV of the first camera system. In their study, although fish were not observed on videos, fish were initially on the path of the vessel and left before being detected. Moreover, in another study using an echosounder system mounted on a ROV, fish were detected within 100 m ahead of the ROV and out of the illuminated FoV (**Benoit-Bird *et al*., 2023**). These authors demonstrated that fish displayed a wide range of behaviors outside of the illuminated FoV (avoidance to attraction) which varied in magnitude. The implications of this are that, despite all precautions taken to reduce bias during UVS surveys, we must acknowledge that there are biases inherent to fish surveys that are currently outside of our control.

One aspect that limited our study was the low number of fish observed for some species or taxa. Indeed, for some of the fish selected for detailed analysis we observed less than 30 individuals (*e.g*., Atlantic Cod, Pollock) and/or observed less than 30 specimens per category tested (*e.g*., Skates, Black Dogfish). Following other studies that opted to focus their statistical analyses on taxa with numerous observations (*e.g*., >19 fish per transect), we limited our analysis of taxa with few observations to qualitative assessments of behavioural patterns (**Uiblein *et al*., 2011**). One way to increase the number of fish per category is by reducing the number of variables tested. This approach would enable a more balanced distribution of fish between categories and reduce the complexity of the study (**Uiblein *et al*., 2011**). Alternatively, grouping fish species that are close in taxonomy and anatomy is another possibility, though, this approach must be chosen when only necessary and when there are high levels of confidence in taxonomic identifications (**Uiblein *et al*., 2011**).

As we concluded and as many studies have previously proven, fish behavior is highly variable between and within taxa, and so grouping fish taxa could cause researchers to miss unique and significant patterns. For instance, during one ROV survey conducted in nearshore waters of southeastern Alaska, several *Sebastes* species were displaying different *in-situ* behaviors. One species was observed more in the water column, while another was more observed inactive on the seafloor (**Johnson *et al.*, 2003**). As *in-situ* behavior is the variable most likely to influence fish response behavior, it could be reasonably assumed that these different *Sebastes* species might react differently to the presence of UVSs. While most Redfish we observed in our study were inactive on the seafloor, 8% of them were observed in the water column. Here, we grouped three *Sebastes* species as one Redfish taxon, as we were unable to identify them to the species level based on visual morphological characteristics alone. Redfish identification from video footage is a common challenge and is even more difficult to attempt considering that the juveniles of the three species that co-occur in the Laurentian Channel are almost identical within this depth range (**Saborido-Rey, 1993**). This could explain the weak signals we assessed for this taxon and the differences in response behavior with those reported in other studies.

While the resolution of fish identification can limit fish behavior analysis, we also faced the inverse challenge, where fish behavior limited our ability to identify some taxa at a low taxonomic level. This was the case for Skate sp1 and Teleostei sp1. Skate sp1 whose main behavior consisted in escaping the FoV or hiding in sediment plumes it created, represented both Thorny Skate and Smooth Skate. Skates would leave the FoV too fast or too early, or remain hidden by sediment by the time UVSs were close enough for identification to be possible. This was detrimental as Smooth Skate is a species targeted by the conservation objectives of the Laurentian Channel MPA (**Lewis *et al.*, 2016**). Sandlance and Barracudina are two other morphologically and ecologically similar taxa which were both grouped as Teleostei sp1 in our study (**Robards *et al.*, 2000 | Moteki *et al.*, 2001 | Preti *et al.*, 2008**). In addition to the taxon being relatively small compared to other groundfish (< 30 cm long, 2 cm wide), its disoriented behavior made it difficult, if not impossible to differentiate the two taxa. Expert taxonomists were consulted during this study to help distinguish Sandlance from Barracudina; however, an agreement could not be reached for many of the specimens assessed, which ultimately led to inconclusive results. These two examples highlight the importance of close collaboration work with taxonomists, as well as the need to collect more high-resolution imagery data.

Identification of these taxa was further complicated where the reactions of one fish would trigger many others to react as well. Whether or not fish would leave the FoV, UVSs were never close enough for identification to be possible. As we observed sometimes with Redfish and Teleostei sp1, the reaction of a minority of fish close to the UVSs would trigger the reaction of many others when found in dense aggregations. Despite this qualitative visual assessment, our models did not reveal any significant influence of fish density on fish response behavior. In order to reduce the number of variables tested in our study, we decided to test the influence of total fish density instead of testing specific fish density. Considering that fish reaction is taxon specific, we would expect to get a stronger signal from our models when using species/taxon density (**Laidig *et al*., 2013**). Similarly, considering fish prey-predator interactions, integrating presence/absence data and/or specific densities of known prey or predators of the fish of interest in the Laurentian Channel could reveal new patterns.

4-4.2.2 | Implications for fish surveys and monitoring

Despite the low percent of fish that reacted intensely to the UVSs, our results highlight the importance of relying on continuous videos instead of extracted images at regular intervals, to prevent the under- or overestimation of fish that were either attracted to the UVSs or escaping the FoV.

In most studies that assessed fish reactions and reported avoidance or attraction behavior, reactions did not necessarily induce a bias in fish assessments (**Stoner *et al*., 2008 | Ryer *et al*., 2009 | Laidig *et al*., 2013**). Any bias would depend on the intensity of the reactions, the proportion of fish reacting and the distance to which they react (*i.e*., outside the FoV) (**Stoner *et al*., 2008**). If not taking into account potential fish behavior that might have occurred outside the FoV during the UVS surveys, our fish assessment was relatively unbiased despite the reaction of a few taxa or individuals. In most instances, reactions were of low intensity while most fish did not leave the FoV. Our study suggests that our fish assemblage composition is representative of the Laurentian Channel fish assemblage, and supports the premise that UVSs are suitable substitutes for bottom trawls to conduct benthic fish surveys (**Ayma *et al.*, 2016**). UVSs are presently the best tool for direct observation of fish, but there is a need to continue assessing fish behavior to improve survey designs and reduce bias (**Stoner *et al.*, 2008**).

Fish reaction time is rarely recorded in studies but is very informative, especially when paired with fish response behavior (**Sward *et al.*, 2019**). How long a fish is seen in the FoV, how and when the UVS is detected, and the timing of the response behavior are variables that should be integrated in future dedicated studies (**Ryer *et al.*, 2009 | Sward *et al.*, 2019**).

The reported influence of survey operations on fish reactions were variable among studies, with reports of increased attraction with stationary operations, especially during manipulations (**Trenkel *et al.*, 2004 | Trenkel & Lorance, 2011 | Uiblein *et al.*, 2011**) while conversely it has been hypothesised that fish adjust their behavior over time and eventually acclimatize to stationary UVSs (**Lorance & Trenkel, 2006 | Boldt *et al.*, 2018**). Moser *et al.* (**1998**) reported that, while their ROV was positioned on the seafloor following deployment and prior to beginning the video transect, fish were initially attracted to the vehicle before eventually adopting a more neutral or dispersion behavior. Therefore, in order to reduce biased fish assessments during *in-situ* surveys, an ‘acclimation period’ where no data is collected at the beginning of a video transect is strongly advised. Similarly, slower UVS speeds and longer transects are also recommended to allow fish to acclimate to the presence of the UVSs (**Benoit-bird *et al.*, 2023**). Finally, following a standardized sampling approach between dives – and between surveys - is essential where possible to maximize unbiased and balanced assessments (**Uiblein *et al.*, 2011**).

4-5 | Conclusion

In this study we assessed the *in-situ* and response behavior of groundfish taxa in a low-relief soft-bottom deep-sea environment using two UVSs. Our results showed that most taxa and most fish did not react to UVSs, or did not react strongly enough to induce bias in our assessment. One challenge inherent to this type of study is the difficulty to test the influence of multiple factors as oftentimes the effects are confounding. Here, while we did not find a significant influence of the variables tested on fish reaction type, we observed variability in fish reaction magnitude, especially with fish *in-situ* behavior. Most patterns we observed were inconsistent with previously reported fish behavior, as responses are taxon-specific and differ with survey conditions, local conditions and especially geographic locations. In addition to improving UVS assessments, studying fish behavior – both *in-situ* and response – and its variability with ecological factors can inform on fish habitat use/biology and ecology, which is especially challenging in deep-sea environments. This highlights the importance of taking into account all biotic and abiotic factors, as well as separating natural behaviors from responses to disturbances. Finally, our results support the use of UVSs as an effective, non-destructive approach to conduct *in-situ* fish surveys, and as a valuable tool for fish assemblage assessments.

Chapter 5

Comparing deep-sea groundfish diversity, abundance and population size structure captured by a bottom trawl, a Remotely Operated Vehicle and a near-seabed drift-camera system in a deep-sea soft-bottom environment[3]

Abstract

The development of non-invasive monitoring alternatives to bottom trawling as a means of assessing fish populations in a Marine Protected Area (MPA) can reduce disturbance in epibenthic and associated fish communities. In this study we present a comparison between remotely operated vehicle (ROV), a near-seabed drift-camera system and a bottom-trawl sampling methods for assessing the diversity, abundance and local size structure of deep-sea groundfish in the Canadian Laurentian Channel MPA.

Near 250,000 fish were sampled by Underwater Video Systems (UVS) and bottom trawls within the 1070 ha study area, comprising 86 taxa. A higher fish diversity was captured by bottom trawls compared to both UVSs, as a result of a much larger seabed area covered. However, a similar species richness was expected to be observed on the ROV if sampling increased, which was not the case with the drift-camera. Relative abundances of fish were similar between surveys, with similar dominant fish taxa identified by each video and trawl survey. Highest dissimilarity percentages were found between fish assemblages of trawl surveys conducted in April/May and the trawl survey conducted in August, as well as the UVS surveys. High-abundance fish taxa and multispecies morphotypes contributed most to the dissimilarity. Higher total and specific fish densities were assessed with UVSs than with trawls, specifically with the ROV. In addition, different patterns of distribution were assessed from the trawl surveys and the UVS surveys.

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[3] A modified version of this chapter was submitted as a DFO contract report as: **Boulard M., Lawton P., Edinger E.** (in review). ‘Comparing deep-sea groundfish diversity, abundance and population size structure captured by a bottom trawl, a Remotely Operated Vehicle and a near-seabed drift-camera system in the Laurentian Channel Marine Protected Area’. *DFO Contract Report*. 103 p.

Redfish local size structure was similar between surveys across habitats, although the ROV identified more ‘Small juveniles’ than the drift-camera or trawls.

Our results highlighted significant fish-specific, seasonal and interannual variability in the metrics assessed between surveys, as well as variability related to survey gear. We therefore recommend the combination of UVS and bottom-trawl be deployed in trawlable habitats, during dedicated surveys in the Laurentian Channel MPA to calibrate the assessments. Nonetheless, our results suggest UVSs are effective alternatives to bottom trawling and can meet long-term non-destructive MPA management and monitoring objectives to assess fish populations.

5-1 | Introduction

The Laurentian Channel Marine Protected Area (MPA), designated in 2019, aims to protect the highest-known sea pen densities and sea pen species richness of the Newfoundland and Labrador Shelves bioregion, as well as the biodiversity associated with sea pen habitats and other several at-risk species (**Lewis *et al.*, 2016**). In spite of this, the Laurentian Channel MPA ecosystem is not well-studied, and several knowledge gaps have been identified in the understanding of the nature of the associations between sea pens and fishes. Key gaps include the diversity and abundance of fish occurring in sea pen habitats, as well as fish species occupying sea pen habitats at different life stages. While sea pens are a primary conservation target for the MPA, there is little known beyond correlative observations (*e.g.*, higher diversity of fish in trawl sets associated with high bycatch of sea pens) in terms of understanding the ecological and functional role of sea pen assemblages as biogenic habitat for fish (**Auster, 2007**). Previous studies of the associations between fish and soft-bottom invertebrates in the Laurentian Channel have showed evidence of fish-sea pen association with groundfish larvae and juveniles observed within diverse sea pen habitats which were presumably used as nurseries (**Baillon *et al.*, 2012 | Chapters 2 & 3**).

Additionally, Fisheries and Oceans Canada (DFO) is seeking to understand these ecological relationships more fully as well as to identify non-invasive means of monitoring

MPAs, as alternatives to bottom trawling (**Lewis *et al*., 2016**). Traditionally, surveys of demersal fish species are conducted with mobile or fixed bottom-tending gear, especially bottom trawls. In Atlantic Canada, data on commercial and non-commercial fish and invertebrate species are collected during annual multispecies trawl surveys, yielding information on fish distribution and abundance, population dynamics, community structure, habitat associations (**Stoner *et al*., 2008 | DFO, 2015a**). Although this approach provides valuable data, its use in MPAs is controversial due to the impacts on the habitat being conserved (*e.g*., habitat destruction, resuspended sediment, fauna removal) (**Auster, 2005**). Moreover, because trawl sets sample a coarse spatial scale (*e.g*., 1.5 km per tow in the Northwest Atlantic), small-scale processes to which fish respond (~m to 100 m scale) are often masked (**Edinger *et al*., 2007 | Baker *et al*., 2012a**), which can lead to knowledge gaps or misinterpretation of results.

Underwater video systems (UVSs), such as remotely operated vehicles (ROVs), towed cameras, drift-cameras or baited cameras are non-destructive, non-extractive monitoring tools that can be deployed in both trawlable and non-trawlable areas and can assist in reducing those knowledge gaps (**Graham *et al*., 2004 | Pacunski & Palsson, 2008 | Stoner *et al*., 2008 | Sward *et al*., 2019**). The use of video-based surveys enables additional *in-situ* observations on fish habitat use, community composition and behaviour in structurally complex habitats and at a finer scale (**Trenkel *et al*., 2004 | Lorance & Trenkel, 2006 | Ross & Quattrini, 2007 | Clark *et al*., 2016**).

Here we compared fish diversity, abundance and local size structure assessed by bottom-trawls, and two alternate seabed imaging systems used within the Laurentian Channel MPA between 2015 and 2019, to evaluate the relative effectiveness of survey gear in sampling fish assemblage characteristics. Our objectives were to determine 1) if UVSs can be substituted for bottom trawls and yield comparable results currently provided by trawl surveys, 2) if there is a systematic bias between UVSs and trawl data, and 3) if UVSs provide additional types of information not provided by trawls.

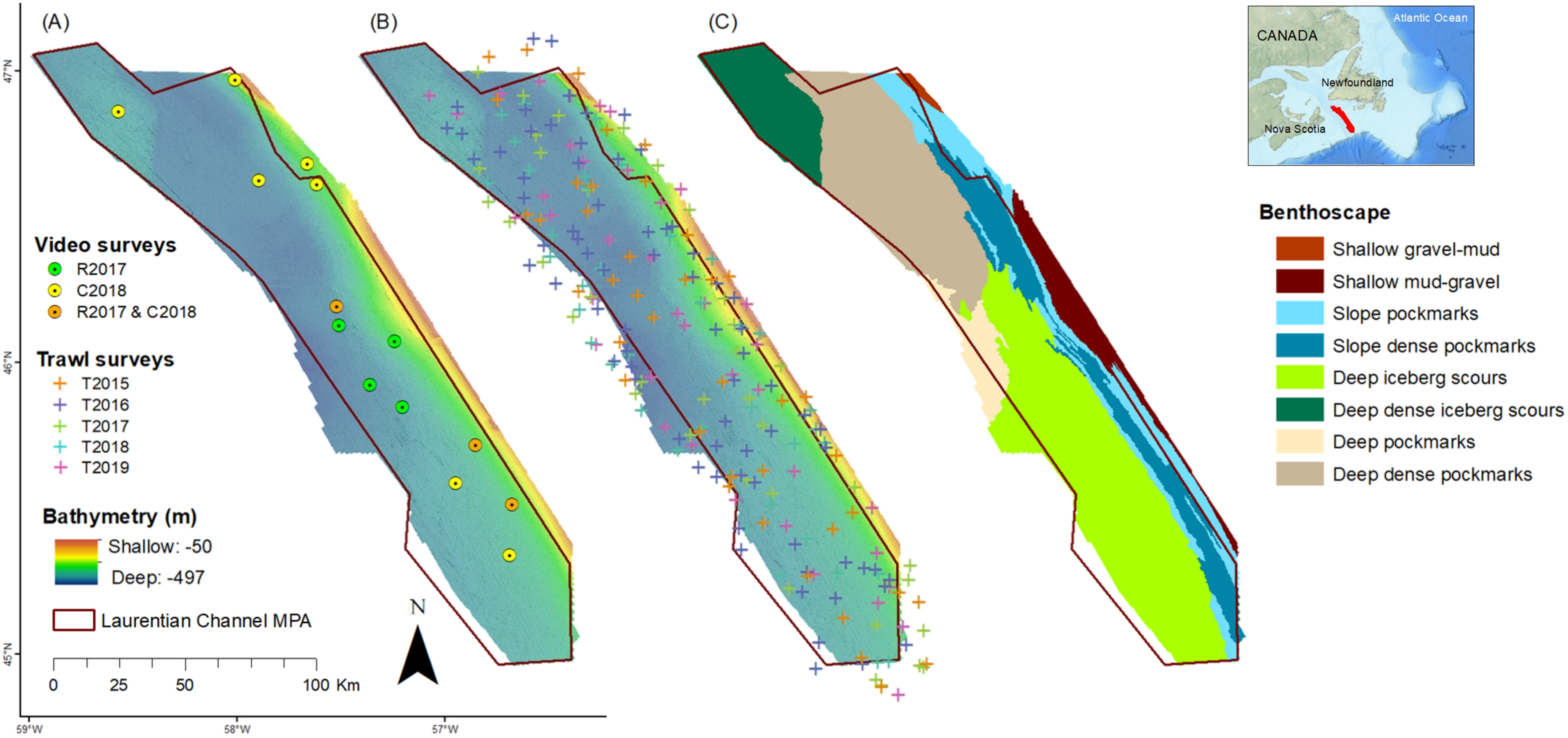

Fig. 5-1 | (A) Location of stations sampled during the two video surveys (R2017 and C2018), (B) location of stations sampled during the six DFO trawl surveys (T2015-T2019), (C) benthoscape distribution in the Laurentian Channel MPA (retrieved from Lacharité *et al.*, 2020).

5-2 | Methodology

5-2.1 | *In-situ* video surveys

5-2.1.1 | Fish density calculation

Based on the approach taken by Baker *et al.* (**2012**) and in Chapter 2, video data from both UVS surveys were divided into 10-m segments, which were used as sample units. For each snapshot extracted from the ROPOS' forward-looking camera, the width of the field of view was measured in the software ImageJ (**Schneider *et al.*, 2012**) using the lasers as a scale to estimate the width covered (total of 5200 snapshots, 1 to 5 per segment, with an average width of 5.3 m). We calculated 4.7 m as ROPOS' 'transect-mode' average field of view and used it as a proxy to estimate CAMPOD's field of view. The surface area of each segment was estimated as the segment length multiplied by the average field of view. Fish densities (ind./m^2) were calculated in each segment by dividing abundances by segment area. We also calculated fish total and specific densities per station by dividing abundance per area covered at each station.

5-2.1.2 | Redfish total length measurements

For both UVS surveys we extracted images from the downward-looking camera every time Redfish individuals were in the field of view. We took total length measurements (cm) of each individual in ImageJ using the lasers as a scale. Based on these measurements, Redfish were classified as 'Small juveniles', 'Large juveniles' or 'Adults', based on estimations of their life cycle stages (**Vaskov, 2005 | Wilhelms, 2013 | Brassard *et al.*, 2017**). We then used this typology to calculate fish abundance per life stage: 'Small juveniles' (1-20 cm), 'Large juveniles' (20-40 cm) and 'Adults' (40+ cm), and per size classes: 1-10 cm, 10-20 cm, 20-30 cm, 30-40 cm and 40+ cm.

5-2.2 | Campelen trawl surveys

Six surveys, following a stratified random sampling design, were conducted by DFO in the Laurentian Channel between April 2015 and April 2019 using a Campelen 1800 Shrimp trawl (**Fig. 5-1A & Table 5-1**). Bottom trawls were towed along 1.5 km-long transects for ~15 minutes (one transect per station). For our analysis we used Campelen headline distance as the width to calculate area covered per transect, rounded to 30 m (**McCallum & Walsh, 1996**). The surface area of each transect was estimated as the transect length multiplied by the Campelen headline. Fish densities (ind./m^2) were calculated in each transect by dividing abundances by transect area. Redfish abundance was calculated at each station per life stage and per size class, as it was for UVS video analysis.

Table 5-1 | Sampling effort of Campelen trawl, ROPOS and CAMPOD surveys with number of stations surveyed, cumulative distance on bottom, cumulative time on bottom, cumulative area covered and depth range surveyed.

Survey	Sampling gear	Year	Month	Number of stations	Distance (km)	Time (h)	Area (ha)	Depth range (m)
R2017	ROPOS	2017	September	7	49.4	69.5	25.4	330-450
C2018	CAMPOD	2018	July	10	37.3	25.8	17.5	179-455
T2015	Campelen Trawl	2015	April-May	41	60	10	178	63-483
T2016$_{Ap}$	Campelen Trawl	2016	April	35	52	9	154	146-483
T2016$_{Au}$	Campelen Trawl	2016	August-September	38	55	9	164.5	205-494
T2017	Campelen Trawl	2017	April-May	39	60	10	175	90-490
T2018	Campelen Trawl	2018	May	39	60	10	174	120-480
T2019	Campelen Trawl	2019	April	39	60	10	181	68-488

5-2.3 | Statistical analysis

First, we calculated fish relative abundances per survey as the percentage of total number of fish caught by trawl or observed on video. For all statistical analyses we compared trawl, ROPOS and CAMPOD data within benthoscapes. Benthoscapes are broad biophysical features of the seafloor derived from surficial geomorphological features and geology (**Brown *et al.*, 2012**). Eight benthoscapes were defined according to depth, slope and density of iceberg scours and pockmarks (**Fig. 5-1B & Appendix 1-1**) (**Lacharité *et al.*, 2020**). Of the eight benthoscapes identified (within the Laurentian Channel MPA), five were sampled during both trawl and UVS surveys; just these five were selected for analysis (**Table 5-2**). All statistical analyses were performed in R (**R Core Team, 2019**).

5-2.3.1 | Sampling effort and fish diversity

We produced species accumulation curves using the 'iNEXT' package for the six trawl surveys and the two UVS surveys (**Hsieh *et al.*, 2016**). We calculated fish species richness in relation to area covered per benthoscape. We set the diversity order of Hill number (q) to zero, and the maximum sample size for all surveys (endpoint) to 4000. We used the incidence frequency datatype (incidence_freq), defined as species incidence frequencies for each survey. We also explored the diversity of fish assemblages assessed during each survey and compared fish species/taxa relative abundances.

Table 5-2 | Number of stations surveyed per benthoscape and per survey. Total_B: total number of stations surveyed per benthoscape. Total_S: total number of stations sampled per survey.

Benthoscape	**Survey**								**Total_B**
	T2015$_{\text{Ap}}$	T2016$_{\text{Ap}}$	T2016$_{\text{Au}}$	T2017$_{\text{Ap}}$	T2018$_{\text{Ap}}$	T2019$_{\text{Ap}}$	R2017$_{\text{Sp}}$	C2018$_{\text{Jl}}$	
Shallow gravel-mud	1	0	1	0	0	1	0	0	3
Shallow mud-gravel	4	3	2	4	4	3	0	0	20
Slope pockmarks*	6	5	4	5	8	6	0	2	36
Slope dense pockmarks*	4	6	7	4	3	7	3	3	37
Deep iceberg scours*	13	9	11	9	10	10	4	3	69
Deep dense iceberg scours*	0	3	1	1	1	2	0	1	9
Deep pockmarks	3	2	4	6	4	3	0	0	22
Deep dense pockmarks*	10	7	8	10	9	7	0	1	52
Total_S	41	35	38	39	39	39	7	10	248

*Benthoscapes selected for statistical analysis

5-2.3.2 | Fish assemblages

We conducted a multivariate analysis on fish densities to visualize the differences between trawl and UVS fish assemblages within benthoscapes. We first fourth-root transformed fish densities to reduce the weight of abundant species. Then we ran a non-metric multidimensional scaling (NMDS) analysis using a Bray-Curtis similarity matrix from the 'vegan' package (**Oksanen *et al.*, 2020**). We ran permutational multivariate analyses of variance (PERMANOVA) per benthoscape on the fourth-root transformed fish densities, using a Bray-Curtis distance, to test for differences on fish assemblages between surveys. We ran Adonis pairwise mean comparisons between surveys when significant differences were found. We then used the SIMPER (similarity percentages) analysis from the 'vegan' package to identify which fish species/taxa contributed the most to dissimilarities between surveys within benthoscapes. We explored the contribution to dissimilarity of seven fish taxa sampled during at least one trawl survey and one UVS survey. We selected those seven taxa based on their high relative abundance, their conservation status or their commercial importance in Atlantic Canada.

5-2.3.3 | Fish specific densities

We ran analyses of variances (ANOVA) on the square-root transformed fish densities calculated per transect/station of the seven selected taxa (Redfish (Sebastes spp.), Longfin Hake (*Phycis chesteri*), Witch Flounder (*Glyptocephalus cynoglossus*), Silver Hake (*Merluccius bilinearis*), Marlin-Spike Grenadier (*Nezumia bairdii),* Black Dogfish (*Centroscyllium fabricii*) and Atlantic Cod (*Gadus morhua*)) to test for significant differences between surveys within benthoscapes. We used the square-root transformation to reduce the weight of abundant species in the analysis. We verified data independence, homoscedasticity and normality to ensure compatibility with the assumptions of ANOVA analyses by plotting the model diagnostics. Then, we performed Tukey tests as a post-hoc analysis to run pairwise mean comparisons between benthoscapes and surveys when significant differences were found.

5-2.3.4 | Redfish size structure

As we could not measure all taxa, we selected Redfish as an example to compare fish local size structures assessed by trawls and the two UVSs. We summed Redfish abundances per size class per benthoscape and explored Redfish size frequency distribution per survey, as the percentage of total abundance by size class.

For each benthoscape we performed multinomial logistic regression models ('multinom' function from the 'nnet' package) (**Venables & Ripley, 2002**). on Redfish size classes to assess their representation in each survey. Multinomial logistic regressions are adapted to model categorical response variables (*i.e.*, Redfish size class) and to predict probabilities of occurrence. The model calculated the probability that a given size class would be dominant in each survey, using the [1-10] class as the reference level. We verified data linearity, independence and non-collinearity, as well as the absence of outliers to ensure compatibility with the assumptions of multinomial logistic regression analysis by plotting the model diagnostics. We also tested if there was a relationship between residuals and specific predictors, by visually looking at the ‘Residuals *vs.* Fitted’ plot. We extracted the predicted probabilities of each size class associated with each survey and plotted them.

Additionally, we used ArcGIS (**Esri Inc., 2020**) to produce Redfish local size structure distribution maps. We calculated the relative abundance of each life stage per station as the percentage of Redfish abundance per station surveyed by trawl or UVS.

5-2.3.5 | Fish taxon distribution maps and Getis-Ord hot-spot analysis

We produced fish distribution maps of the seven selected fish taxa (see section 5-2.3.3). We calculated fish average density per station surveyed by ROPOS and CAMPOD. We created a hexagonal grid (100-km^2 cells) and calculated the average fish density of all trawl stations per cell. We determined the local spatial Getis-Ord Gi* statistic using ArcGIS to test for local spatial patterns in fish distribution assessed by UVS and trawls (**Ord & Getis, 1995**). The hot-spot analysis identifies the locations of statistically significant ‘hot-spot’ and ‘cold-spot’ clusters, by calculating the Gi* statistic in each station or cell based on fish densities. Hot spots are defined as statistically significant clusters of high fish density values compared to expected values given by a random distribution model, while cold spots are defined as significant clusters of lower values. We produced distribution maps for the seven fish taxa and represented stations or cells that presented either an aggregation pattern (hot spots or clusters of high fish densities), a dispersion pattern (cold spots or clusters of low fish densities) or a random distribution.

5-3 | Results

5-3.1 | Data summary

Five out of eight benthoscapes were sampled during at least one trawl survey and one UVS survey (**Table 5-2**). Four benthoscapes with more than 30 stations sampled were 'Deep iceberg scours', 'Deep dense pockmarks', 'Slope pockmarks' and 'Slope dense pockmarks'. 'Deep pockmarks' and 'Shallow mud-gravel' had between 20 and 30 stations surveyed. 'Deep dense iceberg scours' and 'Shallow gravel-mud' had less than 10 stations surveyed. Only one to three stations were sampled per survey in 'Deep dense iceberg scours', therefore this benthoscape was not included in some of the statistical analyses we performed.

Table 5-3 | Number of fish sampled per benthoscape and per survey. Total_B: total number of fish sampled per benthoscape. Total_S: total number of fish sampled per survey.

Benthoscape	**Survey**								**Total_B**
	T2015$_{Ap}$	T2016$_{Ap}$	T2016$_{Au}$	T2017$_{Ap}$	T2018$_{Ap}$	T2019$_{Ap}$	R2017$_{Sp}$	C2018$_{Jl}$	
Shallow gravel-mud	24	NA	557	NA	NA	1260	NA	NA	1841
Shallow mud-gravel	6002	5416	996	4216	4578	7540	NA	NA	28748
Slope pockmarks*	4970	4896	2983	6418	13551	37563	NA	1071	71452
Slope dense pockmarks*	2302	3395	3011	2129	3654	5241	6451	2258	28441
Deep iceberg scours*	4969	6445	3660	4528	5453	14044	10612	1069	7321
Deep dense iceberg scours*	NA	2325	327	995	491	2797	NA	386	50780
Deep pockmarks	1654	1440	668	1852	2267	7116	NA	NA	45899
Deep dense pockmarks*	6158	4440	1309	5746	4128	23479	NA	639	14997
Total_S	26079	28357	13511	25884	34122	99040	17063	5423	249479

*Benthoscapes selected for statistical analysis

A total of 249,479 fish were sampled between April 2015 and April 2019 across surveys (**Table 5-3**). Between 13,511 and 99,040 fish were caught per trawl survey (T2015 to T2019), while 17,063 and 5,423 fish were observed *in situ* during the ROPOS and CAMPOD surveys (R2017 & C2018), respectively.

5-3.2 | Species accumulation curves per survey and benthoscape

Of the five benthoscapes, only two were surveyed by both UVSs (‘Slope dense pockmarks’ and ‘Deep iceberg scours’). These two benthoscapes had the greatest area covered during both video surveys, although twice as many fish species were (and are predicted to be) observed by ROPOS (**Fig. 5-2A**). None of the interpolated species accumulation curves (SACs) for the ROPOS survey reached a plateau. The trajectory of extrapolated curves support this, with observed species richness expected to increase with survey coverage area (>25 species). While none of the interpolated SACs for the CAMPOD survey within the same benthoscapes reached a plateau, the extrapolated curves indicate that fish species richness is expected to plateau with increased covered area (<15 species). CAMPOD surveyed three other benthoscapes, but covered smaller areas (‘Slope pockmarks’, ‘Deep dense iceberg scours’ and ‘Deep dense pockmarks’). None of the interpolated SACs for those benthoscapes reached a plateau. Two interpolated SACs indicated intermediate fish species richness (~ 15 species) while the third curve indicated a species richness as high as that observed by ROPOS. As with the other CAMPOD SACs, however, extrapolated curve trajectories for these SACs suggest that species richness will likely plateau with increased survey area.

None of the interpolated SACs for the trawl surveys (T2015-T2019) reached a plateau, and they all indicated a fish species richness between 15 and 40 species for four benthoscapes surveyed (**Fig. 5-2B to 5-2E**). Trawl surveys revealed relatively high seasonal and annual species variability in all benthoscapes. Based on the trajectory of the extrapolated curves, in three benthoscapes all trawl surveys reached a plateau with increased area. In the fourth benthoscape (Deep dense pockmarks), the extrapolated curves of three trawl surveys kept increasing and predicted significantly higher fish diversity than the other trawl surveys. While both ROPOS and CAMPOD covered a smaller area than the trawls, the extrapolated SACs for ROPOS predicted similar fish species richness to that assessed during trawl surveys (**Fig. 5-2C & 5-2D**). On the other hand, all extrapolated SACs for CAMPOD reached a plateau and indicated lower predicted fish diversity observed on videos than caught by trawl (**Fig. 5-2B to 5-2E**).

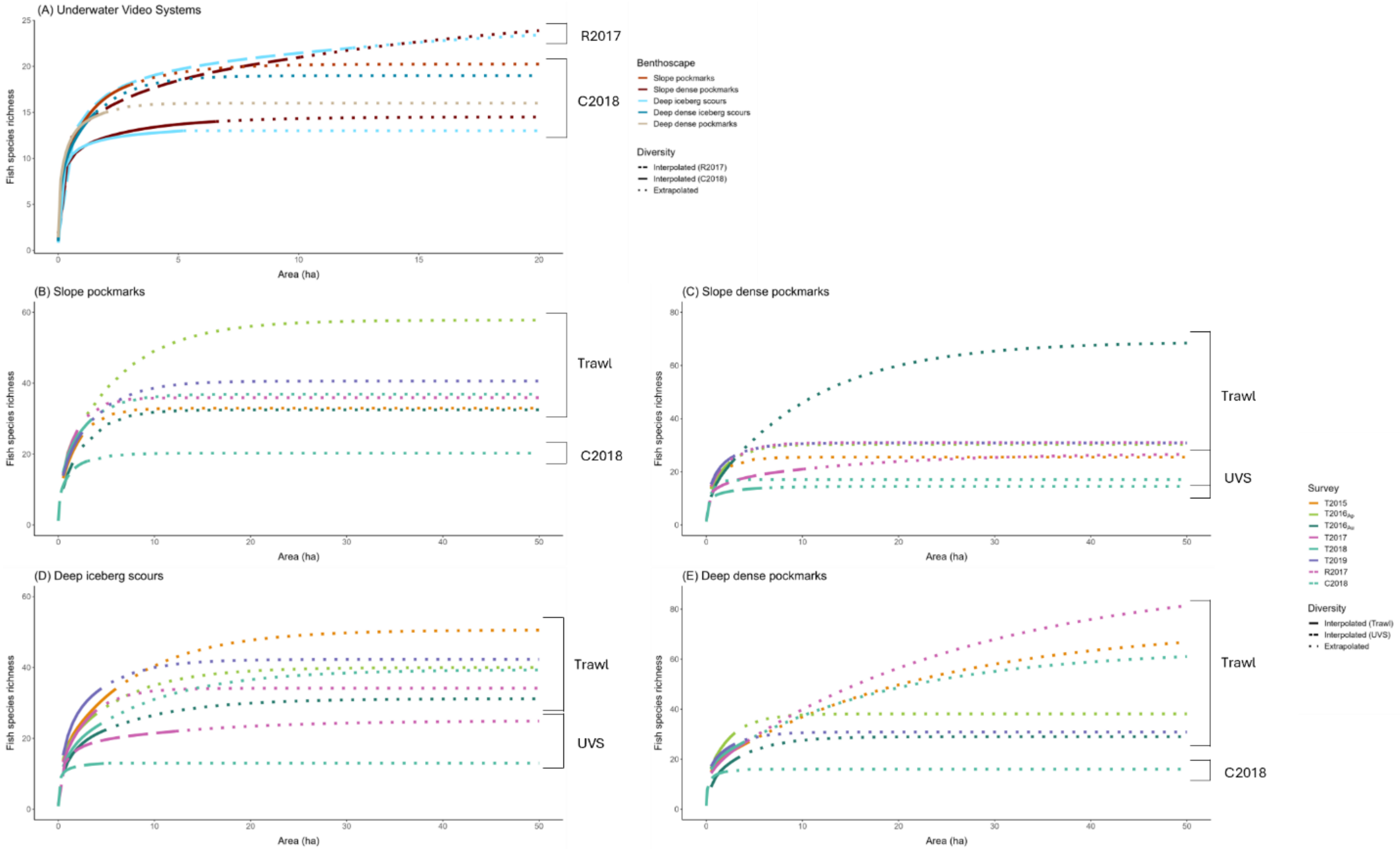

Fig. 5-2 | Fish species accumulation curves in relation to area covered (A) per benthoscape surveyed by ROPOS and CAMPOD, and for the six trawl surveys and the two UVS surveys in (B) Slope pockmarks, (C) Slope dense pockmarks, (D) Deep iceberg scours, (E) Deep dense pockmarks. T2015, T2016$_{Ap}$ and T2017-T2019 were conducted in April/May, T2016~~Au~~ was conducted in August, R2017 was conducted in September, and C2018 was conducted in July.

5-3.3 | Fish relative abundances per survey

A total of 75 fish species and 11 grouped fish morphotaxa were encountered across all surveys (**Appendix 5-1**). Trawls caught 81 fish species/taxa, with between 40 and 58 species/taxa were caught per trawl survey. Only 26 fish species/taxa were observed *in situ* by the UVSs; 24 on ROPOS videos and 21 on CAMPOD videos. A total of 22 common species/taxa were sampled by bottom trawls and UVSs. Moreover, 13 out of the 86 species/taxa each represented more than 1% of the total abundance (cumulated 94%); 10 of them were common to both survey types. Here we presented relative abundances of 11 abundant fish species and/or of commercial interest (**Fig. 5-3**).

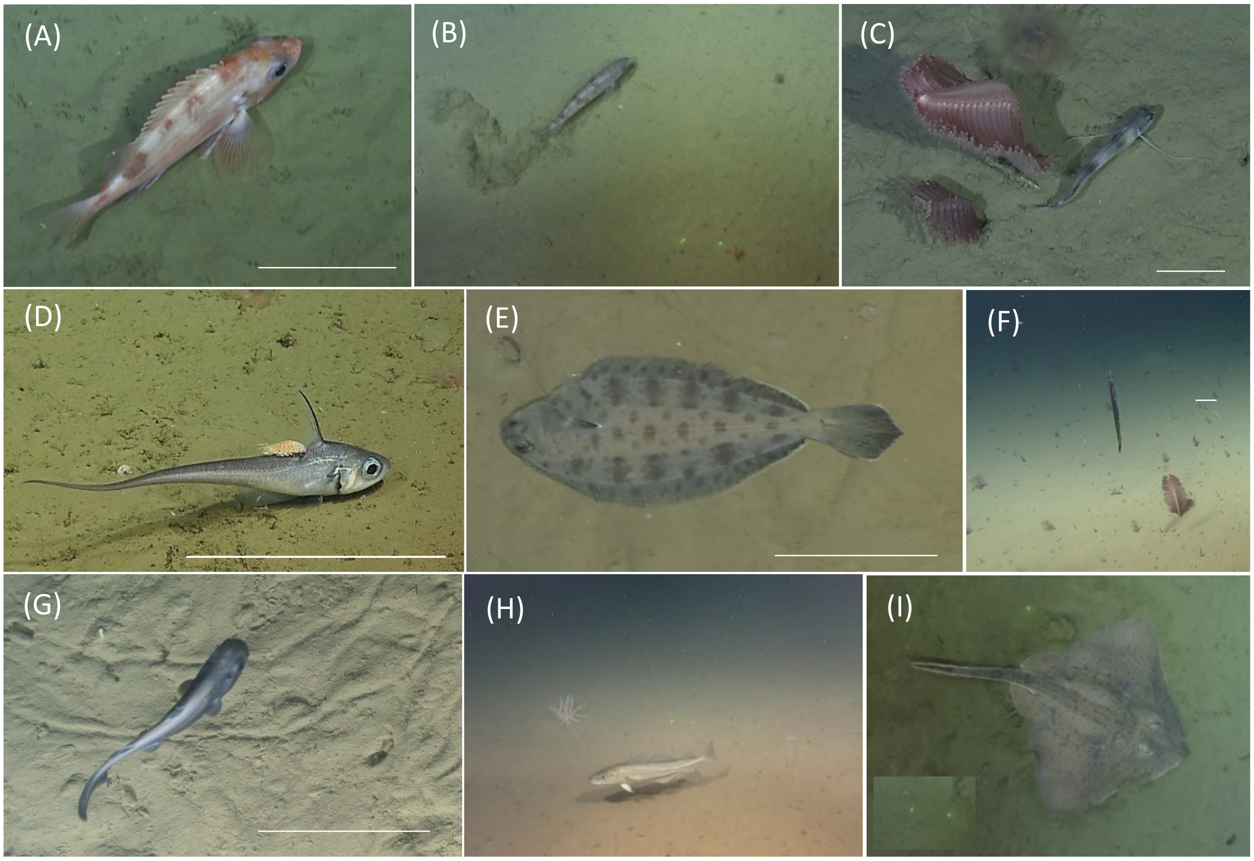

Fig. 5-3 | Frame captures from underwater video recordings of nine of the most dominant groundfish taxa across all DFO trawl and UVS surveys. (A) Redfish (*Sebastes* spp.), (B) Silver Hake (*Merluccius bilinearis),* (C) Longfin Hake (*Phycis chesteri*) near *Pennatula* sea pens, (D) Marlin-Spike Grenadier (*Nezumia bairdii*) with parasitic copepod behind the dorsal fin, (E) Witch Flounder (*Glyptocephalus cynoglossus*), (F) Teleostei sp1 (Sandlance (*Ammodytes* spp.) and/or Barracudina (*Arctozenus* sp. and/or *Paralepis* spp.)) in a *Pennatula* habitat, (G) Black Dogfish (*Centroscyllium fabricii*), (H) Pollock (*Pollachius*

***virens*), (I) Skate sp1 (Thorny Skate (*Amblyraja radiata*) or Smooth Skate (*Malacoraja senta*)). Pictures A, B, C, E, G and I were taken from the downward-looking camera. Pictures D, F and H were taken from the forward-looking camera. Scale bar and distance between lasers: 10 cm. Frame captures from underwater video of the other fish taxa observed in situ are provided in Appendix 5-2.**

Redfish was identified as the dominant taxon in all surveys (average 57%) (**Fig. 5-4**). Three Sebastes species are common to the area: *Sebastes mentella*, *S. fasciatus* and *S. norvegicus*. As they are difficult to differentiate without physical specimens of each individual, we grouped them as one Redfish taxon. Despite some annual variability in Redfish relative abundance among trawl surveys (36-78%), relative abundances from both UVS surveys were within the same range (38-58%), though higher in 2017 (58 *vs*. 37%), and similar in 2018 (38 *vs*. 37%). Silver Hake was identified as the second most dominant fish species encountered, representing 14% of the combined observations of all surveys. Silver Hake was caught in every trawl survey but showed significant variability in its relative abundance between surveys (4-27%). On the other hand, the species was only the 12th most dominant fish species observed during UVS surveys (0.5-2%). Longfin Hake, Witch Flounder and Marlin-Spike Grenadier were identified as the third to fifth dominant species of all surveys (3 to 6%), but second to fourth most dominant species identified during the UVS surveys. Their relative abundances were higher in the UVS surveys (8-20%) compared to those in the trawl surveys (1-11%) (an effect linked to Silver Hake being less observed *in situ*). Teleostei sp1 was the fifth most dominant taxon observed on video and showed significant variability between surveys (0.4-7%). Teleostei sp1 could represent either Sandlance (*Ammodytes* spp.) or two genera of Barracudina (*Arctozenus* sp. and *Paralepis* spp.). All three taxa are known to occur in the channel, but were difficult to reliably differentiate without detailed views or physical specimens of each individual.

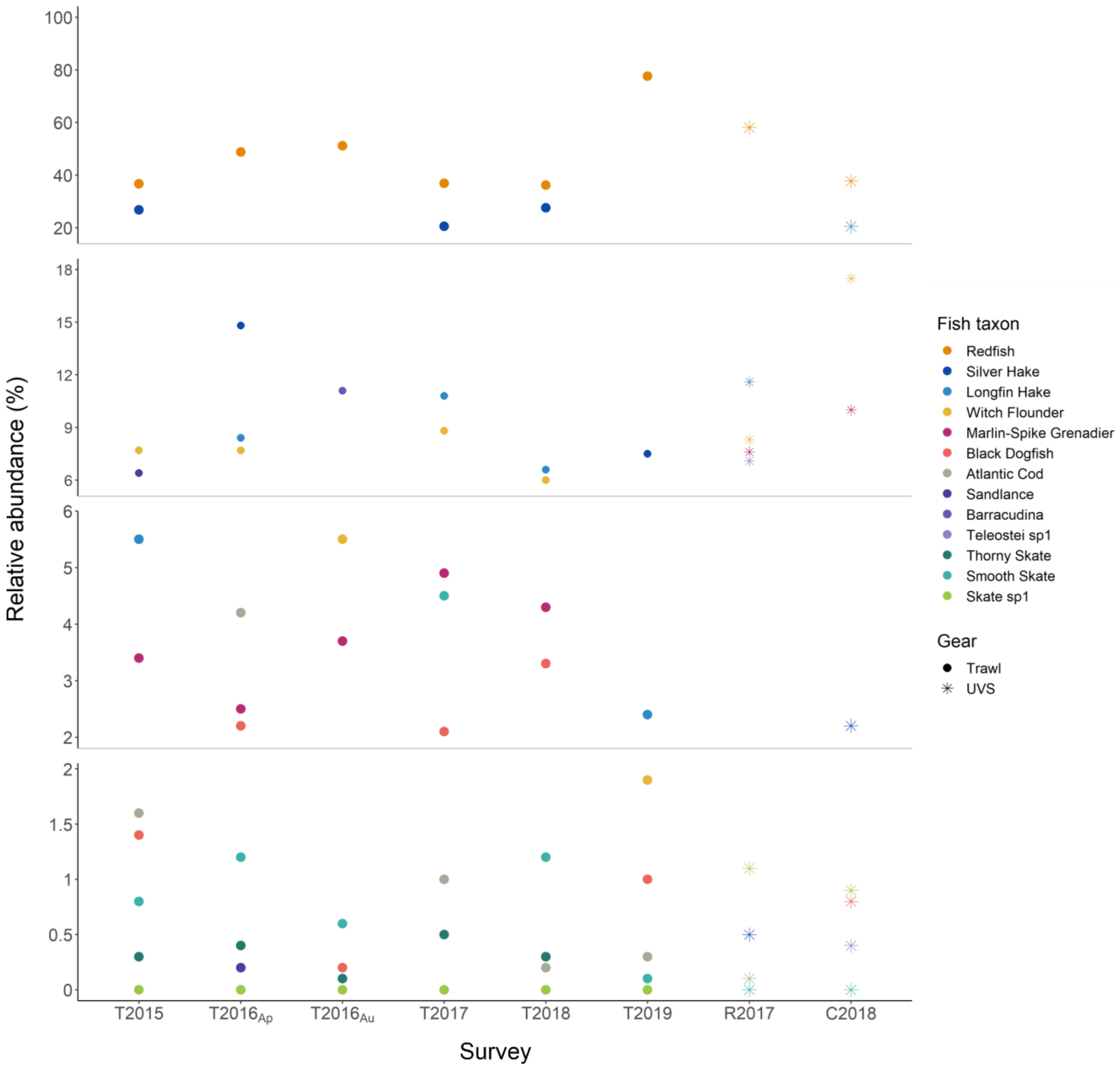

Fig. 5-4 | Relative abundances of eleven fish taxa and two fish morphotypes per survey. Each panel presents a different scale of percentages: 0-2, 2-6, 6-12 and 20-100%.

Comparatively, Sandlance and Barracudina were the 14th and 15th most dominant taxa (all surveys combined), and also showed variability in their relative abundance between trawl surveys (0.2-11%). The two taxa were identified as the third most abundant taxa in two of six trawl surveys. Black Dogfish (7th) and Atlantic Cod (13th) showed considerable variability in their relative abundance between all trawl surveys (0.2-3% and 0-4% respectively). Skate sp1 only represented 1% of the fish assemblage in each UVS survey. Thorny Skate (*Amblyraja radiata*) and Smooth Skate (*Malacoraja senta*) were the two species of skates we observed, but were difficult to differentiate without physical specimens of each individual. We grouped them as one Skate taxon. Comparatively, Thorny Skate (12th) represented 0.1-5% of the fish assemblages in the trawl surveys, and Smooth Skate (23rd) represented 0.1-1%.

5-3.4 | Fish assemblages per survey and benthoscape

The NMDS plot (**Fig. 5-5**), in addition to the PERMANOVAs (**Table 5-4 & Appendix 5-3**) performed on fourth-root transformed fish densities, revealed that the two 'Shallow' benthoscapes formed a cluster with a different fish assemblage than the other benthoscapes, as did the two 'Slope' benthoscapes (**Fig. 5-5A**). The two 'Deep iceberg' benthoscapes had a different fish assemblage than the two 'Deep pockmarks' benthoscapes. The PERMANOVAs revealed that assemblage characteristics observed during $T2016_{Au}$ were different from those from other trawls surveys in every benthoscape (**Fig. 5-5B to 5-5F, Table 5-4 & Appendix 5-3**). Annual differences were shown in two benthoscapes, with four trawl surveys yielding different results than the other trawl surveys. Finally, ROPOS and CAMPOD had observed similar fish communities, that differed only from the trawl fish communities in two benthoscapes.

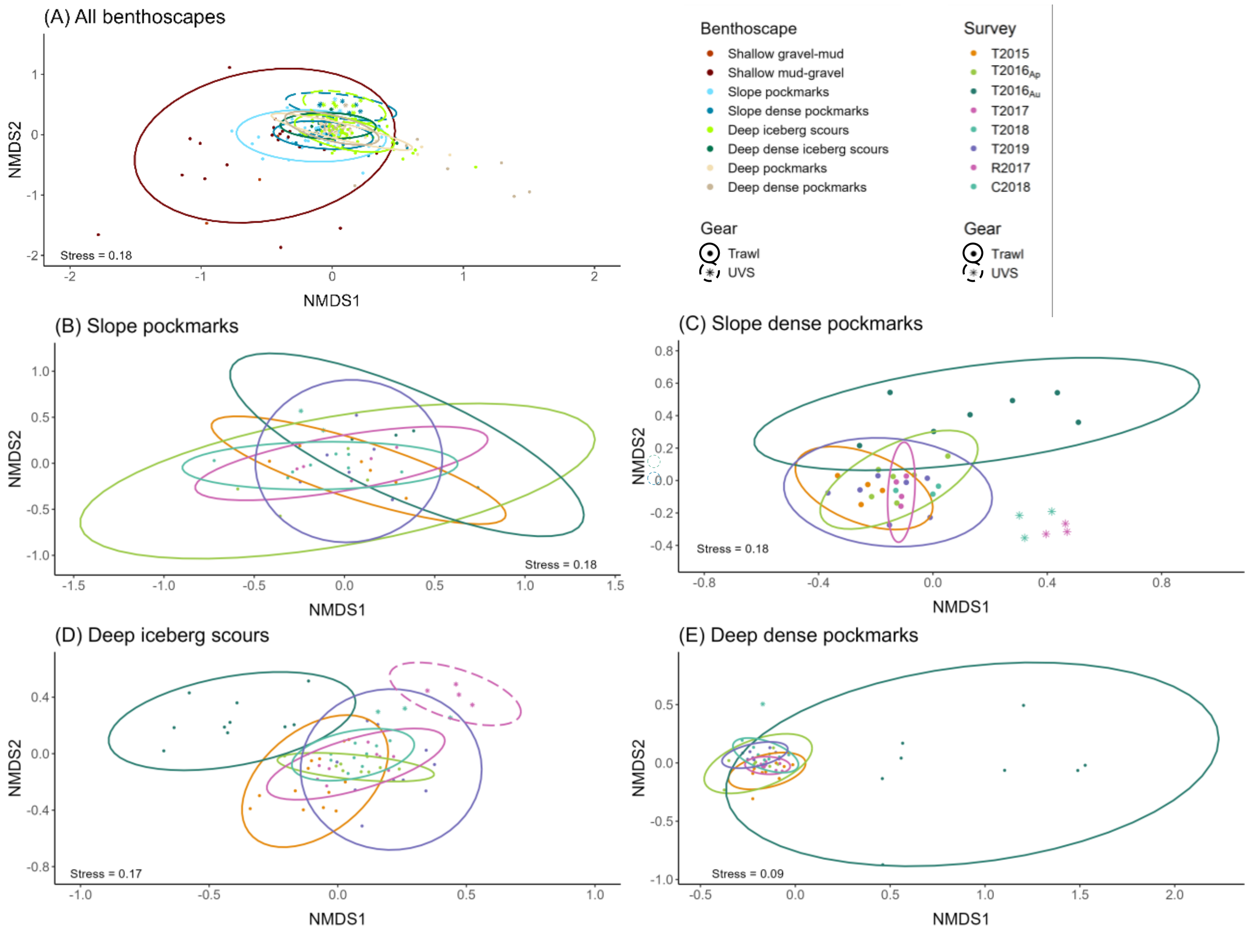

Fig. 5-5 | NMDS plots based on fourth-root transformed fish densities (A) per benthoscape, and assessed by survey in (B) Slope pockmarks, (C) Slope dense pockmarks, (D) Deep iceberg scours, (E) Deep dense pockmarks. Dots represent stations sampled during the different surveys. Not ellipses were produced for UVSs on plots B, C and E as not enough stations were surveyed per benthoscape.

The SIMPER analysis revealed that, on average, dissimilarity between trawl surveys and T2016$_{Au}$, and between trawl and UVS surveys was the highest (56 and 49.5% respectively) (**Table 5-5**). The lowest percentage of dissimilarity was found between the R2017 and C2018 surveys (28%). The detailed percentages of dissimilarity between surveys within benthoscapes is presented in Appendix 5-4. Dissimilarities between R2017 and trawl surveys were similar to dissimilarities between C2018 and trawl surveys (52 *vs.* 47% respectively). Additionally, dissimilarities between both UVSs and T2016$_{Au}$ surveys were higher than dissimilarities between both UVS and the other trawl surveys (58 *vs.* 49.5%).

Table 5-4 | PERMANOVA's post hoc Adonis pairwise comparisons performed on fish assemblages between trawl, ROPOS and CAMPOD surveys within benthoscapes. ✓ indicates no difference in fish assemblages between the paired surveys.

Benthoscape	Pairwise comparison					
	Trawls			ROPOS *vs.* Trawls	CAMPOD *vs.* Trawls	ROPOS *vs.* CAMPOD
All	T2016$_{\text{Au}}$	≠	All	R2017 & C2018 ≠ All		✓
Slope pockmarks	T2016$_{\text{Au}}$	≠	All	NA	C2018 ≠ All	NA
Slope dense pockmarks	T2016$_{\text{Au}}$	≠	All	R2017 & C2018 ≠ All		✓
	T2015	≠	T2018			
Deep iceberg scours	T2016$_{\text{Au}}$	≠	All	R2017 & C2018 ≠ All		✓
Deep dense iceberg scours	NA			NA	NA	NA
Deep dense pockmarks	T2016$_{\text{Au}}$	≠	All	NA	✓	NA
	T2015	≠	T2018 & T2019			
	T2017	≠	T2018 & T2019			
	T2018	≠	T2019			

Of the most abundant fish taxa (all surveys combined), 12 were among the 27 taxa that contributed to at least 1%, on average, of dissimilarity between surveys (**Table 5-6**). Silver Hake, Redfish and Teleostei sp1 were the taxa that contributed the most to dissimilarity between all surveys (5.2-6.4%), and between UVS surveys (7.7-10.5%). They were among the taxa that contributed the most to dissimilarity between the trawl and UVS surveys (4.9-6.4%), and between T2016$_{\text{Au}}$ and the trawl surveys (6.5-8.1%). Additionally, Silver Hake and Redfish were among the taxa that contributed the most to dissimilarity between trawl surveys (6.8-7.7%). Other notable fish taxa that contributed to dissimilarity between surveys were Longfin Hake, Marlin-Spike Grenadier and Witch Flounder (between trawl and UVS surveys, 5.1-5.6%), Hagfish, Lanternfish and Skate sp1 (between T2016$_{\text{Au}}$ and the trawl surveys, 5.9-7.1%), and Black Dogfish, Lanternfish, and Skate sp1 (between trawl surveys (5-6.1%).

Table 5-5 | Average percentage (min-max range) of dissimilarity between trawl, ROPOS and CAMPOD surveys within benthoscapes.

Benthoscape	Survey			
	Trawls *vs.* Trawls	T2016$_{\text{Au}}$ *vs.* Trawls	Trawls *vs.* UVSs	R2017 *vs.* C2018
All	38 (34.7-56.6)	56 (54.7-57.8)	49.5 (43.2-58.3)	28

Slope pockmarks	41 (39.3-53.6)	48 (45.9-53.6)	49 (44.8-56.1)	NA
Slope dense pockmarks	28.5 (26.3-30.6)	46 (44.4-47.7)	46 (39.1-52.4)	25
Deep iceberg scours	30 (24.6-37.3)	48 (46-50.5)	45 (34-55.6)	28
Deep dense pockmarks	26 (22-39.4)	66.5 (65-68.9)	44 (29-70.3)	NA

The detailed contribution to dissimilarity of seven fish taxa between surveys within benthoscapes is presented in Appendix 5-6. The seven taxa were selected as they were the most overall abundant taxa with representation in trawl and UVS surveys, while also making the most significant contributions to dissimilarity between surveys.

Table 5-6 | Average contribution (%) to dissimilarity between survey assemblages of fish taxa that contributed to at least 1% (all surveys combined). Fish taxa in bold represent the most abundant taxa (at least 1% of total abundance). Contributions of the other fish taxa are presented in Appendix 5-5. Total represents the average contribution of each fish taxon across all surveys.

Taxon	**Survey**				**Total**
	Trawls *vs.* Trawls	T2016$_{Au}$ *vs.* Trawls	Trawls *vs.* UVSs	R2017 *vs.* C2018	
Teleostei sp1	NA	NA	6	11.5	6.3
Silver Hake	7.2	7.7	4.5	7.3	6.3
Redfish	7.4	6.8	4.7	8.4	6.3
Verrill's Wolf Eel	0.4	0.3	7.5	4.2	6.2
Skate sp1	NA	NA	5.9	2.8	5.7
Barracudina	0.7	8.4	3.5	NA	5.2
Lanternfish	6.3	6.4	3.2	NA	5.1
Longfin Hake	4.0	4.9	5.2	4	4.6
Fourbeard Rockling	4.4	2.9	5.2	3.9	4.4
Marlin-Spike Grenadier	3.7	3.5	5.0	4.2	4.2
Atlantic Hagfish	3.4	7.9	3.0	4.2	4.1
Witch Flounder	3.1	4.0	4.7	1.9	3.8
Actino sp1	NA	NA	3.5	6.6	3.7
Black Dogfish	5	3.6	2.2	2.5	3.7
White Hake	3.3	4.3	3.4	5.8	3.6
American Plaice	4.3	3.6	2.6	NA	3.5
Atlantic Argentine	2.9	2	4.3	4.2	3.3
Thorny Skate	3	3.1	3.8	NA	3.3
Snipe Eel	NA	3.3	2	NA	3
Smooth Skate	3.1	3.4	2.7	NA	3
Scaled Lancetfish	4.2	2.4	1.8	NA	3
Greenland Halibut	3.4	3.1	2.1	NA	2.9
Atlantic Cod	3.7	2.3	1.8	3.9	2.8
Actino spp	NA	NA	2.6	4.4	2.7

Zoarcidae	NA	NA	2.4	4	2.5
Monkfish	3.2	2.1	1.8	3.4	2.5
Blacksnout Seasnail	3	1.7	1.3	NA	2.4
Pollock	1.6	0.9	2.8	5.7	2.2
Unidentified Grenadier	NA	NA	1.7	2.4	1.8
Sandlance	2.1	1.7	1.1	NA	1.8
Gelatinous Seasnail	1.2	0.8	2.5	3.9	1.8
Atlantic Snipe Eel	2.2	1.5	1.0	NA	1.6
Soft Eelpout	2.2	1.1	0.8	NA	1.6
Boa Dragonfish	2.3	1.5	1	NA	1.6
Offshore Silver Hake	1.9	1	0.8	NA	1.3
Spiny Dogfish	1	0.6	1.8	1.2	1.3
Atlantic Herring	1.9	1	0.7	NA	1.3
Atlantic Halibut	1.5	0.8	1	1.7	1.2
Esmark's Eelpout	1.9	0.6	0.4	NA	1.2
Viperfish	1.2	1.8	0.5	NA	1.1
Haddock	1.6	0.9	0.6	NA	1.1
Threebeard Rockling	1.5	0.9	0.6	NA	1.1
Northern Wolf Eel	1.6	0.7	0.5	NA	1.1
Eelpout	1.5	0.7	0.5	NA	1

5-3.5 | Variability of fish specific densities

5-3.5.1 | Fish densities per survey and per benthoscape

Fish total densities observed by ROPOS and CAMPOD were 3 and 1.5 times higher than the average fish total density caught by trawls (0.02135 ind./m^2), respectively (**Appendix 5-7**). Fish total density observed by ROPOS was two times higher than fish total density observed by CAMPOD (0.065 and 0.033 ind./m^2, respectively).

We ran ANOVAs to test for differences in fish specific densities between surveys within benthoscapes for the seven selected fish taxa (**Table 5-7 & Appendix 5-8**). We compared fish densities between surveys in 35 fish-benthoscape combinations (seven fish taxa and five benthoscapes). We did not find differences in fish densities between surveys in 11 of 35 combinations (31%). Densities assessed by ROPOS and CAMPOD differed in 3 of 14 combinations (21%) (ROPOS surveyed two of the five benthoscapes), with ROPOS estimating higher densities than CAMPOD. We found differences in densities between ROPOS and all trawls in 11 combinations (79%), and in 16 combinations between

CAMPOD and all trawls (46%). When differences were found, ROPOS and CAMPOD densities were mostly higher than trawl densities (8 of 14 (57%) and 14 of 35 (40%) combinations respectively). ROPOS and CAMPOD densities were the lowest in three and two combinations respectively (21 and 6%). We found differences in densities between trawls in 16 combinations (46%), which reflects interannual variability. In ten combinations densities assessed by $\mathrm{T2016_{Au}}$ were lower than the other trawl densities (29%), which reflects seasonal variability.

5-3.5.2 | Fish species distribution maps

Distribution maps for the seven taxa selected for the analysis are presented in Appendix 5-9. Each map represents the average fish density estimated from UVS data per station and the average fish density estimated from stations surveyed by trawls within 100-km^2 hexagonal cells. Using the Gi* statistic calculated on fish densities per station and per cell, we compared fish distribution patterns assessed by UVSs and trawls. Clusters with a positive z-score formed hot-spot clusters, representative of an aggregation pattern (high densities), and clusters of segments with a negative z-score formed cold-spot clusters, representative of a dispersion pattern (low densities) (**Fig. 5-6**).

We found differences in fish distribution pattern assessment according to trawl or UVS surveys between fish taxa. Hot-spot clusters identified by the trawl and UVS surveys were located in different areas for Redfish, Silver Hake and Atlantic Cod (**Fig. 5-6A, 5-6B & 5-6G**). Additionally for Silver Hake, cold spots assessed from the UVS surveys were localized near hot spots assessed from the trawl surveys (**Fig. 5-6B**). Several hot-spot and cold-spot clusters were assessed from the trawl surveys for Longfin Hake and Marlin-Spike Grenadier, while no specific distribution pattern was assessed from the UVS surveys for the two taxa (**Fig. 5-6C & 5-6D**). Cold-spot and/or hot-spot clusters assessed by the trawl and UVS surveys for Witch Flounder and Black Dogfish were located in similar areas, considering a medium spatial scale (17-20 km on average) (**Fig. 5-6E & 5-6F**).

Table 5-7 | Tukey's test pairwise comparisons of fish specific densities between trawl, ROPOS and CAMPOD surveys within benthoscapes.

Fish taxon	Benthoscape	Tukey test								
Redfish	Slope pockmarks	No difference								
	Slope dense pockmarks	All trawls	<	T2018, R2017 & C2018						
	Deep iceberg scours	All trawls & C2018	<	T2019	<	R2017				
	Deep dense iceberg scours	$T2016_{Au}$ & T2018	<	$T2016_{Ap}$, T2017 & C2018	<	T2019				
	Deep dense pockmarks	All trawls & C2018	<	T2019						
Silver Hake	Slope pockmarks	No difference								
	Slope dense pockmarks	No difference								
	Deep iceberg scours	$T2016_{Ap}$, $T2016_{Au}$, R2017 & C2018	<	All trawls						
	Deep dense iceberg scours	All trawls	<	C2018						
	Deep dense pockmarks	$T2016_{Au}$ & T2018	<	T2017 & T2019	<	$T2016_{Ap}$	<	T2015	<	C2018
Longfin Hake	Slope pockmarks	All trawls	<	T2017	<	C2018				
	Slope dense pockmarks	R2017 & C2018	<	All trawls						
	Deep iceberg scours	$T2016_{Au}$	<	T2015	<	All trawls	<	R2017 & C2018		
	Deep dense iceberg scours	$T2016_{Ap}$ & T2019	<	All trawls	<	C2018				
	Deep dense pockmarks	$T2016_{Au}$	<	All trawls	<	C2018				
Marlin-Spike Grenadier	Slope pockmarks	All trawls	<	C2018						
	Slope dense pockmarks	All trawls	<	T2018 & C2018	<	R2017				
	Deep iceberg scours	All trawls	<	R2017 & C2018						
	Deep dense iceberg scours	No difference								
	Deep dense pockmarks	$T2016_{Ap}$ & $T2016_{Au}$	<	All trawls	<	C2018				
Witch Flounder	Slope pockmarks	No difference								
	Slope dense pockmarks	All trawls	<	R2017 & C2018						
	Deep iceberg scours	All trawls	<	R2017 & C2018						
	Deep dense iceberg scours	All trawls	<	C2018						
	Deep dense pockmarks	$T2016_{Au}$	<	$T2016_{Ap}$	<	T2015 & T2018		T2017 & T2019	<	C2018
Black Dogfish	Slope pockmarks	No difference								
	Slope dense pockmarks	No difference								
	Deep iceberg scours	$T2016_{Au}$, R2017 & C2018	<	All trawls	<	T2019				
	Deep dense iceberg scours	No difference								
	Deep dense pockmarks	$T2016_{Au}$	<	$T2016_{Ap}$, T2015 & T2017	<	T2018, T2019 & C2018				
Atlantic Cod	Slope pockmarks	No difference								
	Slope dense pockmarks	No difference								
	Deep iceberg scours	All trawls & C2018	<	R2017						
	Deep dense iceberg scours	No difference								
	Deep dense pockmarks	$T2016_{Au}$, T2019 & C2018	<	All trawls	<	T2015				

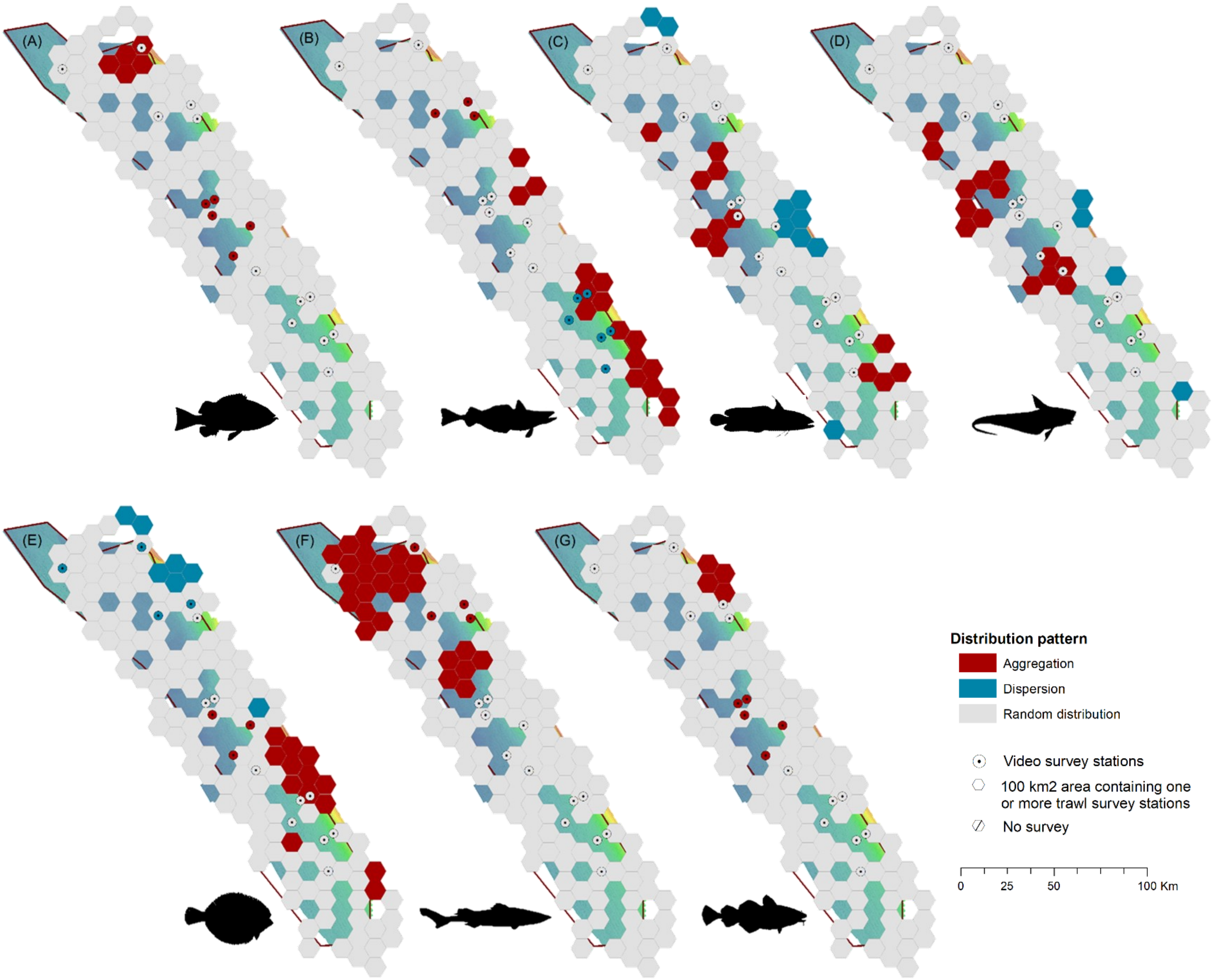
(A)
(B)
(C)
(D)
(E)
(F)
(G)
Distribution pattern
Aggregation
Dispersion
Random distribution
Video survey stations
100 km2 area containing one or more trawl survey stations
No survey
0
25
50
100 Km

Fig. 5-6 | Distribution patterns of (A) Redfish, (B) Silver Hake, (C) Longfin Hake, (D) Marlin-Spike Grenadier, (E) Witch Flounder, (F) Black Dogfish, (G) Atlantic Cod, based on the Getis-Ord hot-spot analysis ran on fish densities between stations surveyed by ROPOS and CAMPOD (⊙) and stations surveyed by trawls within hexagonal areas (⬡). Each cell contains one or more stations surveyed by bottom-trawl between 2015 and 2019.

5-3.6 | Redfish local size structure

A total of 36,832 Redfish individuals were measured from all surveys (**Table 5-8**). Between 611 and 7,406 fish were measured per survey, and between 374 and 23,830 fish were measured per size class. While all fish caught by trawl were measured, an average of 36% of Redfish observed during each UVS survey was measured. Redfish individuals measured from trawl samples ranged from 5 to 54 cm while Redfish individuals measured from the videos ranged from 8 to 47 cm. Overall, 'Large juveniles' dominated the surveys (73%), followed by 'Small juveniles' (26%), while 'Adults' only represented 1% of all fish measured. 'Large juveniles' were mostly represented by the 20-30 cm size class (67% of all fish), and dominated the T2017, T2018, T2019, R2017 and C2018 surveys (60 to 92% of survey abundance). 'Small juveniles' were mostly dominated by the [10-20] cm class (25% of all fish measured). 'Small' and 'Large juveniles' were co-dominant in T2015 and T2016 (44 to 53%).

Table 5-8 | Number of Redfish individuals counted per size class and per survey, and minimum and maximum of total lengths measured (cm) per survey.

Life stage	**Size class (cm)**	**Survey**							**Total**
		T2015	T2016	T2017	T2018	T2019	R2017	C2018	
Size range (min-max)		7-47	6-47	6-44	5-54	5-44	8-47	11-45	5-54
Small juvenile		**3091**	**3473**	**705**	**426**	**382**	**1433**	**31**	**9541**
	[1-10]	14	215	4	39	100	2	0	374
	[10-20]	3077	3258	701	387	282	1431	31	9167
Large juvenile		**2584**	**3872**	**4944**	**5962**	**6753**	**2225**	**566**	**26906**
	[20-30]	1845	3423	4333	5429	6504	1794	502	23830
	[30-40]	739	449	611	533	249	431	64	3076
Adult	[40+]	118	61	77	70	13	32	14	385
Total		5793	7406	5726	6458	7148	3690	611	36832

‘Small juveniles’ were the dominant life stage in the two ‘Shallow’ benthoscapes (55 and 64%), while ‘Large juveniles’ dominated the assemblages in the other six ‘Slope’ and ‘Deep’ benthoscapes (67-84%) (**Appendix 5-10**). The [20-30] size class was the most dominant class in all five benthoscapes explored (58-80%), followed by the [10-20] class (15-31%). Distribution maps of Redfish size structures across and within stations are presented in Appendix 5-11.

We found an increase in average body size for Redfish between 2015 and 2019 in all five benthoscapes, from the trawl surveys (17.4 to 24.5 cm). Similarly, we found an increase in average body size between 2017 and 2018 in the two benthoscapes surveyed by both UVSs (19.3 to 25.5 cm). In comparison the increase in body size between 2017 and 2018 according to the trawl surveys was smaller (22.3 to 24 cm) (**Fig. 5-7**, left panel).

Multinomial model summary tables are presented in Appendix 5-12, and relationships between Redfish size classes and surveys per benthoscapes as predicted in the models are presented in Appendix 5-13. ‘Small juveniles’, mainly comprised of the [10-20] size class, were the dominant (average predicted probability $\overline{P}$ = 71%) or co-dominant ($\overline{P}$ = 45%) life stage in the T2015 and/or T2016 assemblages in four benthoscapes (**Fig. 5-7**, right panel). ‘Large juveniles’, mainly comprised of the [20-30] class, were the dominant life stage in the T2015 and T2016 assemblages in one benthoscape ($\overline{P}$ = 65.5%), and in all the other trawl assemblages ($\overline{P}$ = 85%) in all five benthoscapes. ‘Small juveniles’ were the dominant (52%) or co-dominant ($\overline{P}$ = 44%) life stage of the R2017 assemblage in both benthoscapes. In comparison, the average probability of ‘Small juveniles’ associated with the T2017 survey was 12.5%. ‘Large juveniles’ were the dominant life stage of the C2018 assemblage in all five benthoscapes ($\overline{P}$ = 78%). We found a higher probability of ‘Small juveniles’ in the C2018 benthoscape than in the T2018 assemblage in one benthoscape (16 and 6.5% respectively), and a higher contribution of larger fish (>30 cm) in two benthoscape ($\overline{P}$ = 19.3 and 7.6% respectively).

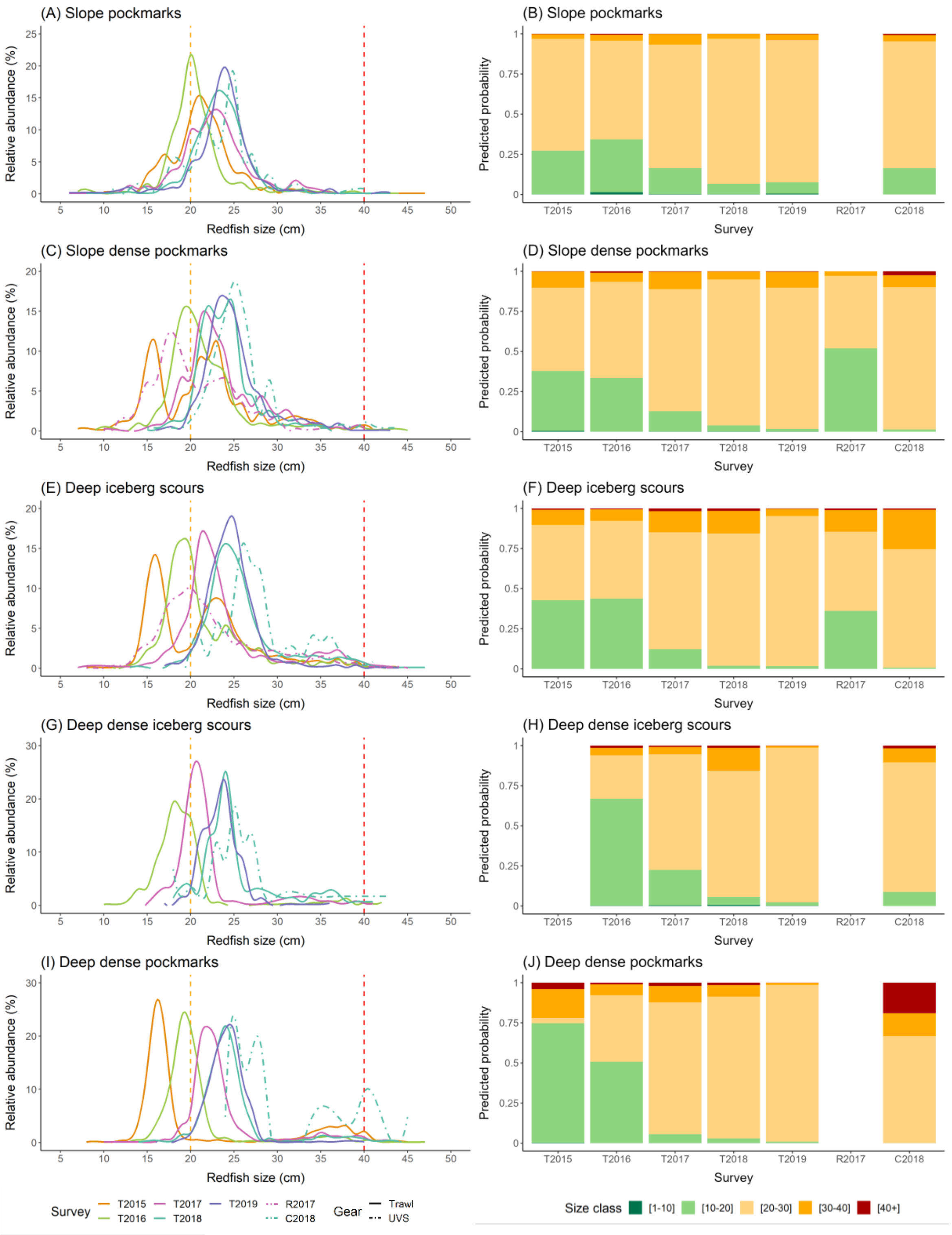

Fig. 5-7 | (Left) Redfish local size structure (as relative abundance per size class (cm)) per survey, (Right) predicted probability of representation of size classes (cm) per survey in (A & B) Slope pockmarks, (C & D) Slope dense pockmarks, (E & F) Deep iceberg scours, (G & H) Deep dense iceberg scours, (I & J) Deep dense pockmarks. The vertical dashed

lines represent the estimated transition threshold to the 'Large juvenile' (orange) and 'Adult' (red) life stages of the taxon.

5-4 | Discussion

In this study we compared fish diversity, abundance and local size structure within various benthoscapes, as assessed by bottom trawls and two UVSs, to evaluate the relative effectiveness of survey gear in sampling fish assemblage characteristics. Though, UVS and trawl surveys were conducted over different months and years. To address this, special attention was given to annual and seasonal variability when assessing potential gear-selectivity-induced bias.

5-4.1 | Fish species richness and accumulation curves

As a result of their capacity to cover relatively large areas, trawl surveys consistently detected a higher fish species richness than that observed by UVSs. We also found seasonal variability in fish species richness between the trawl surveys. Following SAC trends for ROPOS, we might expect this system to observe similarly high fish species richness to trawl surveys with an equal survey extent. On the other hand, for most benthoscapes surveyed by CAMPOD, SACs plateaued more rapidly than for ROPOS or trawl surveys. In addition, half as many fish species were observed by CAMPOD than by ROPOS. These results suggest that gear selectivity is likely to explain differences in species richness between trawls and UVSs, though the potential influence of seasonality cannot be ignored. Based on existing knowledge, it is difficult to differentiate the influence of seasonal and annual variability from gear selectivity to explain differences in species richness between the two video systems.

5-4.2 | Fish relative abundances

Although between 10 to 20 times fewer fish were observed by UVSs (due to a smaller survey area covered), fish relative abundances were globally similar between surveys, with similar dominant species identified by both trawls and UVSs. A notable difference between video and trawl assemblages was the discrepancy observed between abundances of Silver Hake. Indeed, while being the second most dominant taxon in the trawl surveys, only a few specimens were observed in the *in-situ* video footage. While these differences might be explained by seasonality and/or gear selectivity, geographic survey location may also bias observations as some fish species have very localized areas of distribution within the channel. Here, Silver Hake seemed to be more concentrated in the shallower areas of the MPA, which were not sampled as intensively during the two video surveys compared to the trawl surveys.

5-4.3 | Fish assemblages

Distinct fish assemblage compositions based on fish densities were found between benthoscapes, and between surveys in almost all benthoscapes. Assemblages collected in April-May by trawls were different from the August assemblage and both UVS assemblages grouped together. Additionally, more dissimilarity was found between the trawl and UVS assemblages than among the trawl assemblages. The results suggest that seasonality has a higher influence on fish assemblage differences between trawls than interannual variability. No difference was found between the fish assemblages from the two video systems, suggesting that seasonality, interannual variability or gear-selectivity did not influence those surveys. Differences in fish assemblage composition between trawls and UVSs is likely to be explained by gear selectivity and potentially seasonality. Most of the dissimilarity between assemblages was attributed to high-abundance taxa such as Redfish and Silver Hake, or two taxa such as Teleostei sp1 and Skate sp1 which we were not able to identify to the species level. Dissimilarity attributed to Redfish and Silver Hake is likely due to differences in density assessed for these taxa between the trawl and UVS surveys. The high-level Teleostei sp1 and Skate sp1 classifications were only used to identify taxa on the video footage and represent multiple species collected during the trawl surveys. In the trawl assemblages, the corresponding species - Sandlance and Barracudina, and Smooth and Thorny Skates - contributed to a similar cumulative dissimilarity.

5-4.4 | Fish densities and distribution patterns

Differences in total and specific fish densities were found between benthoscapes, and between surveys in almost all benthoscapes. Overall, both UVSs recorded higher fish densities than the trawls. We found larger differences in fish densities between trawls and UVS (especially with ROPOS) than between trawls, or than between the August survey and the April/May surveys. For five of seven taxa selected for analysis, UVS and trawls observed different patterns of distribution at a medium spatial scale (120 km) across the MPA based on fish densities. These results suggest that gear selectivity is likely to explain differences in fish density between trawls and UVSs, but that seasonality and geographic survey location cannot be ignored. Similarly, based on existing knowledge, it is difficult to differentiate the influence of seasonal and annual variability from gear selectivity to explain differences in fish density between the two video systems.

5-4.5 | Redfish local size structure

We observed an increase in Redfish body size over years in both trawl and UVS surveys. Assuming a consistent growth rate among Redfish, we expected to observe an increase in average size from T2017, R2017, T2018 to C2018 (April 2017, September 2017, April 2018, July 2018) (**Chapter 3**). Instead, we found a higher representation of 'Small juveniles' in 2017 in the ROPOS survey than in the trawl survey in every benthoscape. Additionally, we found higher representations of 'Small juveniles' and 'Adults' in 2018 in the CAMPOD survey than in the trawl survey in every benthoscape. Further, bottom trawls seemed to under-represent 'Adults' compared to CAMPOD and 'Small juveniles' compared to ROPOS, despite the small mesh size of the net's codend (12.5 mm) (**McCallum & Walsh, 1996**). These results highlight size-selectivity for both types of survey gear.

5-4.6 | Fish assessment from UVS surveys

Fish are mobile species that can react to the presence of sampling gear. Underestimation of fish abundance by trawls can be explained by small fish not being retained, or by the capacity of individual fish to swim away and avoid being caught. Fish are also known to display a range of reactions to UVSs which can induce *in-situ* observation bias (**Trenkel *et al*., 2004 | Stoner *et al*., 2008 | Sward *et al*., 2019**). In Chapter 4 we demonstrated that most fish observed during the two video surveys did not react to the UVS presence or displayed minor reactions, and that reactions observed did not induce notable bias in estimating observed abundances.

Compared to extracting snapshots from videos or using still images, watching underwater videos continuously is a superior method for assessing fish abundance as it can reduce overestimation of highly mobile fish individuals. Moreover, continuously watching videos increases the probability that rare species will be detected. Utilizing this approach by itself is not, however, without risk. Operating a UVS at a too high speed and/or altitude above seafloor enhances the risk of missing individual specimens, and especially small, hidden, camouflaged or low mobility specimens. In this scenario, still images are often better for detecting those individuals and provide higher-quality material for fish identification. Still images and continuous videos are complementary methods and should be used together to improve fish assessment. For instance, a standardized image sampling protocol could consist of single photos automatically taken in 10-second intervals, continuous recording, and photos taken manually when deemed necessary.

UVS surveys are characterized by a series of compromises around speed and altitude above seafloor, while consistency across these variables ensures a good quality and quantity of data are collected. High UVS speeds ensure a longer distance can be covered during dedicated time on bottom but increase the risk of scaring fish away. On the other hand going too slow would reduce the distance covered, resulting in the underestimation of fish abundance and diversity. Similarly, operating the UVS at high altitudes ensures that a larger area is covered due to a larger field of view but reduces the viewer’s ability to observe small specimens while negatively affecting image quality. Meanwhile operating UVSs too close to bottom can facilitate detection of camouflaged specimens, but at the expense of lost contextual information due to the smaller area covered. Difficulties in keeping a constant speed and altitude during the ROPOS and CAMPOD missions could explain the differences in diversity and density assessed with each UVS. Both ROPOS and CAMPOD are remotely operated from the surface by human pilots. In the case of an ROV system such as ROPOS, the vehicle has sophisticated on-board propulsion and depth-maintenance capabilities that are more comprehensive than the depth-keeping ability of a seabed drift camera such as CAMPOD. While CAMPOD height off the seabed can be remotely controlled, the current system does not have a heave-compensating winch system and so is much more sensitive to surface wave conditions causing difficulty to maintain a consistent height off-bottom.

Moreover, the use of imagery to identify fish at low taxonomic levels from imagery can be challenging due to image quality issues (*e.g.*, resuspended sediment in a sedimentary environment, fish behavior). For instance, we observed 216 skates during the two video surveys, but could not identify them lower than the family level. This was due to the skates displaying a high avoidance behavior towards both UVSs and ‘hiding’ in a sediment plume they created to camouflage themselves, rendering their identification impossible (**Chapter 4**).

Both UVSs are equipped with sensors that can monitor *in-situ* environmental data that can be linked to fish assemblages at a very fine-scale and be used to explain fish distribution. In addition, ROPOS is equipped with sampling tools such as two manipulator arms, a suction sampling system, as well as storage boxes and push cores, used to collect biological and geological samples. Conversely, UVSs similar to CAMPOD are primarily designed to acquire georeferenced digital still and digital video data and typically are not capable of conducting detailed physical sample collections. Using ROPOS, for example, specific sediment samples can be acquired to inform on soft sediment granulometry and invertebrate infauna for instance, as well as detailed *in-situ* stationary imaging and/or collection of sea pens to inform on sea pen size, which are parameters known to influence fish distribution (**Henderson *et al.*, 2020 | Miatta and Snelgrove, 2021**).

5-4.7 | UVS limitations and caveats

This study was based on single missions with two Canadian near-seabed imaging systems that have been used in a number of other similar surveys in Atlantic conservation areas over the past 20 years. As such, our comments on UVS setup and image quality considerations are based on the specific survey setups used in 2017 and 2018. Subsequent technical developments in these UVSs, and specific survey design considerations for new surveys will provide considerable flexibility into the future.

In this study, ROPOS covered 40 km during the 2017 survey in 60h, where CAMPOD covered the same distance in 36h and trawls in 7h. The ROPOS survey time is longer due in part to the complex seabed survey design with four sets of paired transects rather than two to three replicated linear transects (as with CAMPOD). This suggests that the use of a survey based on a near-seabed drift or towed camera system would be more efficient in terms of deployments, somewhat similar to deploying trawls at one station for 15 minutes and resetting elsewhere. In general, ROVs are harder to deploy and visit fewer stations, but record higher resolution imagery, in comparison to drift-camera systems.

We only had laser imaging capabilities available in the forward-looking video system with ROPOS. Further, the only forward-looking camera on the CAMPOD was the system navigation camera, and not a fully dedicated science camera. As such we were not able to derive comparable average transect width estimates for the CAMPOD forward-looking camera used in 2018.

There were differences in the digital image recording formats between those used by ROPOS and CAMPOD. CAMPOD video files were of a larger size and thus required more storage space (**Appendix 5-14**). Those files were also more difficult to manipulate in the video annotation software. For ongoing considerations in the implementation of non-destructive seabed survey approaches using UVSs it will be important to consider both survey system technical specifications and capabilities (*e.g.*, camera field of view, laser scaling), as well as both the at-sea imagery data management and the subsequent set-up of image analysis facilities.

ROPOS and CAMPOD surveys targeted multiple stations in the MPA, located in a specific sub-set of benthoscapes. Although both UVSs could be used in all of the benthoscapes, three out of the eight benthoscapes were not surveyed by either UVS in 2017 and 2018 (*i.e.*, ‘Shallow mud-gravel’, ‘Shallow gravel-mud’ and ‘Deep pockmarks’), compared to trawls having surveyed seven to eight benthoscapes during each survey.

5-4.8 | Recommendations for fish survey monitoring

We observed both annual and seasonal variability between trawl surveys that influenced all fish attributes assessed. Notably, the August trawl survey ($T2016_{Au}$) showed different patterns than all the other trawl surveys, which were conducted in April-May. As both UVS surveys were conducted in different months (September 2017 and July 2018), it is difficult to determine if differences in fish attributes between ROPOS, CAMPOD and trawl surveys are related to differences in sampling gear or to seasonality. In order to better compare trawl and UVS effectiveness in assessing fish assemblage characteristics, it would be useful to conduct additional UVS surveys during the months that DFO trawl surveys are most active (*i.e.*, April-May) to reduce the seasonality bias. UVS surveys through summer and early fall may still be considered; however, these should not be used as benchmarks to compare survey methods, but rather for time-scaled monitoring fish-habitat associations following the Laurentian Channel MPA establishment. Seabed surveys with UVS, and particularly with larger ROVs such as ROPOS, require calmer oceanographic conditions than those in which trawl surveys can be conducted. Sea state conditions in the summer, particularly when hurricane occurrences are low, tend to be more conducive to performing UVS surveys than those in winter or spring periods.

Following the Laurentian Channel MPA long-term monitoring strategy (**Warren *et al.*, in prep.**), we recommend UVS benthic surveys to be conducted in all benthoscapes for a better assessment of fish distribution within the MPA from multiple survey gear types.

Fish are a common target of multispecies benthic surveys, and require more precise management measures than sessile epifauna, due to their mobility. Indeed, fish mobility can impact their catchability (*i.e.*, possibility to escape survey gear), but also induce variability in fish assessments as fish can undertake daily or seasonal migrations. Based on our results, we suggest that to better assess fish distribution and habitat use during UVS surveys, the monitoring tool should consider following a straight-line trajectory, across depth, and survey a wide range substrates or habitats as much as possible. Further, we recommend a constant speed of 0.5 m/s and an altitude of 1-2 m above seafloor (**Sward *et al.*, 2019**). Moreover, the monitoring tool should be equipped with a forward-looking pair of lasers, useful to calculate the field of view, and appropriate lighting, suitable for fish estimates. Finally, we recommend the sampling protocol should integrate automated still images and continuous video.

5-5 | Conclusion

In our study, underwater video systems have been proven to collect similar ecological data to trawls, and can inform MPA and fishery managers on fish assemblage characteristics, fish distribution, and fish size structure. We were able to collect valuable *in-situ* data from both UVSs to assess small-scale distribution of fish as well as local size structure without any fish removal and population perturbation. Our results support the use of seabed video systems to substitute scientific bottom-trawls for fish assessments.

General Conclusion

This study was one of the largest-known *in-situ* video surveys 1) to assess the small-scale linkages between fish, biological and physical habitat features in a soft-sediment low-heterogeneity deep-sea environment and 2) to assess the bias and relative effectiveness of underwater video systems (UVSs) compared to bottom-trawls in sampling fish assemblage characteristics. A total of 17 UVS dives were completed during two research cruises conducted in September 2017 and July 2018 in a Canadian Marine Protected Area (MPA). The surveys captured 95h of cumulated seabed video spanning a depth range of 179-455 m, covering 87 km in total linear extent and an area of approximately 44 ha within the study area.

6-1 | Fish assemblage and habitat characterization of the Laurentian Channel MPA

I characterized the Laurentian Channel fish assemblage diversity and relative abundance, and assessed fish taxon-specific density, distribution and local size structure. A total of 22,486 fishes were observed, comprising 26 morphotypes. Of all fish observed, 91% were identified to 17 species and 5 genera. The Laurentian Channel MPA fish assemblage was mostly dominated by five taxa: Redfish, Longfin Hake, Marlin-Spike Grenadier, Witch Flounder and Teleostei sp1 – comprising Sandland and Barracudina - which represented 86% of all fish observed (**Chapters 2 & 3**). The fish assemblage composition assessed by the two UVSs was really comparable to that assessed by scientific bottom trawls (**Chapter 5**). I was able to measure fish from all dominant taxa except Teleostei sp1, with 99% of individuals identified as juveniles (**Chapter 3**).

I characterized habitat diversity and heterogeneity based on biological and physical features, and mapped their small-scale distribution within multiple transects across the MPA. I defined six benthic habitat types based on the presence of nine epibenthic invertebrate taxa, and five bottom types based on the presence of soft- and hard-bottom micro-habitat features. Only 6% of the study area covered was identified as non-structural (*i.e.,* no physical or biological attributes) and 87% of the area surveyed was categorized as having epibenthic megafaunal invertebrate species presence. However, invertebrates of medium size (5-25 cm tall) and small size (<5 cm tall) were the most dominant. The tallest invertebrates observed were mostly *Anthoptilum* sea pens (25-100 cm tall), which only represented 5% of the assemblage. The Laurentian Channel was also characterized by no-relief soft sediments with or without the presence of small-scale depressions (**Chapters 2 & 3**).

6-2 | Fish-habitat associations in a deep-sea low-relief soft-bottom environment

Overall, the Laurentian Channel was characterized by micro-habitats provided by biological and physical attributes presenting low levels of heterogeneity, lending to the general assumption that they would not be significant drivers of fish distribution. Nonetheless, I provided evidence that low complexity biotic and abiotic habitat attributes have a taxon-specific influence on fish small-scale distribution.

Specifically, I showed that invertebrate assemblages and invertebrate taxa (*i.e.*, sea anemones, sea pens and other CWCs) have an influence on fish density for Redfish, Longfin Hake, Marlin-Spike Grenadier, Witch Flounder and Teleostei sp1. In the case of sea pens, I did not find a specific influence on fish density compared to other CWCs and sea anemones (**Chapter 2**). However, my results showed a consistent spatial relationship between sea pen fields and juvenile Redfish, Longfin Hake, Marlin-Spike Grenadier and Witch Flounder, which suggests these CWCs provide nursery habitats for multiple early-life-stage fishes of these taxa. Contrary to my expectations, my results did not suggest that juvenile fishes undergo ontogenetic shifts in benthic habitats provided by biological features, as both small and large juveniles co-occur in the same habitats. In fact, it would appear that fish juveniles are less habitat specific in soft-bottom ecosystems than expected, and may stay in the Laurentian Channel over multiple years (**Chapter 3**).

In chapter 3 I interpreted significant increases in fish size within habitats between the two years as signs of interannual growth. Considering that some of these taxa migrate vertically on a daily basis and that they showed signs of using multiple benthic habitats (**Chapters 2 & 3**), there remains uncertainty that they are tied to any specific benthic habitat or have specific site fidelity that would be necessary to link changes in growth to benthic habitat. Moreover, differences in fish size between the two years could also be interpreted as a change in the distribution of the fish population (i.e., fish moving as way to find good environmental conditions), and/or as low to no recruitment in the area, or in the habitats in 2018. The latter could also explain the low increase in fish size associated with barren habitats, where juvenile fish could experience a higher predation rate due to the lack of habitat structural complexity compared to other benthic habitats in the area.

I showed that soft-bottom micro-habitat features as well as hard-bottom substrates have a taxon-specific influence on fish density for Redfish, Longfin Hake, Marlin-Spike Grenadier, Witch Flounder and Teleostei sp1 (**Chapter 2**). My results also indicated that juvenile fish taxa undergo ontogenetic shifts in use and specialization of micro-habitats provided by physical attributes in a low-relief soft-sediment environment (**Chapter 3**).

In spite of the small depth range in the study area, depth was identified as a co-dominant factor of fish density and fish size (**Chapters 2 & 3**). I identified preferred depth ranges of distribution for some taxa, such as Redfish in the deeper parts of the channel and Teleostei sp1 in the shallower flanks of the channel (**Chapter 2**). Additionally, my results indicated that ontogenetic shifts in depth range occurred between small and large juveniles for Redfish and Longfin Hake, and suggested that shifts occurred between juveniles and adults for Marlin-Spike Grenadier and Witch Flounder (**Chapter 3**).

My results support the premise that micro- and meso-scale habitats are ecologically important for fish juveniles, as they provide smaller niches adapted to fish size (**Chapters 2 & 3**). However, fish associations with small physical and biological habitat attributes in a soft-bottom environment were not as strong as expected, compared to associations in hard-bottom deep-sea CWC ecosystems (**Chapter 2**). This suggests that 1) soft-bottom CWCs likely provide important, and perhaps preferred (but not exclusive), habitats for fishes, and 2) more factors would need to be considered to understand the links between fish and habitats, at different developmental stages (**Chapters 2 & 3**). Nonetheless, I provided evidence that deep-sea juvenile fish undergo ontogenetic shifts in habitats, and that those shifts occur before the adult life stage (**Chapter 3**).

Beyond elucidating the potential bias induced by UVSs on fish assessments, the data I collected on the behavior of nine taxa also provided insight on their ecology. For most taxa, most fish were observed inactive on the seafloor, reflecting either a resting behavior or a foraging/ambushing strategy. On the other hand, the behavior of pelagic fish such as Pollock and Atlantic Cod was more indicative of hunting predators. Additionally, except for a few taxa, my results showed no (**Chapter 4**) to low evidence (**Chapter 3**) of differences in fish habitat use in the Laurentian Channel MPA. This suggests that the Laurentian Channel provides resting and feeding grounds for multiple juvenile fishes (*e.g.*, Redfish), as well as for key species (*e.g.*, Sandlance and Barracudina) and commercially important fish species (*e.g.*, Redfish and Atlantic Cod).

6-3 | Implications for fish monitoring

A primary objective of this dissertation was to evaluate the effectiveness of UVSs as tools for deep-sea ecological research and MPA monitoring. Overall, the use of UVS surveys in the Laurentian Channel MPA contributed to the acquisition of new data on the distribution of groundfish taxa at local and regional scales, and fish-habitat relationships in a deep-sea soft-bottom environment. Here, UVSs proved to be an effective tool for capturing representative fish assemblage composition (**Chapters 2, 4 & 5**), representative fish local densities (**Chapters 2 & 5**) and representative fish local size structures despite fish mobility and the low subsample of fish measured (40% of fish observed) (**Chapters 3 & 5**). Additionally, UVSs yielded information on the influence of benthic macro-habitat attributes on fish small-scale distribution (**Chapters 2 & 3**).

In the same way that fish behavior can influence their catchability during bottom-trawl surveys, fish behavior can also bias their assessment during video-based surveys (**Trenkel *et al.*, 2004 | Lorance & Trenkel, 2006**). Here, most fish and most fish taxa did not react to the presence of UVSs, or showed minor reactions that, since fish did not leave the field of view, did not induce any bias in observed abundance estimates (**Chapter 4**). Though my results did not show large variability in fish reaction type, I observed more taxon-specific variability in fish reaction magnitude with fish *in-situ* behavior attributes. Moreover, taxa showing strong reactions to UVSs also showed the most variability in response behavior. Notably, Skate sp1 and Teleostei sp1 were the two fish taxa that avoided UVSs the most, which impacted my ability to identify them to a low taxonomic rank, while Pollock and Atlantic Cod were the two fish species that were attracted to UVSs the most. These results highlight the importance of collaboration with experts in taxonomic identification as well as the need to rely on continuous video to reduce risks of under- or over-estimation of fish abundances, which were minimized in this study.

To evaluate the relative effectiveness of survey gear in sampling fish assemblage characteristics, I compared fish diversity, abundance and local size structure as assessed by bottom trawls and the two UVSs taking into account annual and seasonal variability as surveys were conducted during different months over six years. My results suggest that for most metrics assessed 1) seasonality appeared to contribute more to differences between trawl surveys than interannual variability, 2) no difference was found between the fish assemblages observed by the two video systems, and 3) it was difficult to differentiate the influence of seasonal and annual variability from gear selectivity to explain differences between UVS and bottom trawl assessments. Nonetheless, my results support the premise that UVSs are a non-intrusive substitute to traditional scientific bottom trawls to conduct benthic fish surveys. Both UVSs were overall as robust as bottom trawls in assessing fish densities and highlighting differences in diversity and relative abundances of specific size classes.

6-4 | Implications for Laurentian Channel MPA and other conservation areas

6-4.1 | Fish species targeted by conservation objectives in the MPA

Conservation targets of the MPA include sea pens, Black Dogfish, Smooth Skate, Northern Wolffish and Porbeagle Shark (**Lewis *et al.*, 2016 & Table 6-1**). While I was able to provide information on the diversity, density and distribution of sea pens in the MPA, the four protected groundfish species were numerically too few to conduct most statistical analyses from the video surveys. Nonetheless, I was able to contribute information on the distribution of some taxa at local and regional scales. Northern Wolffish was not observed in any video survey, but UVSs observed one Porbeagle shark, 45 Black Dogfish and 228 undifferentiated skates.

6-4.1.1 | The case of Northern Wolffish

Little is known about the ecology and habitat requirements of Northern Wolffish, as the species has no commercial value and inhabits deep areas (500-1000 m). The species is generally found in steep slopes habitats, near edges of continental shelves and in channel banks, (**DFO, 2002 | Kulka *et al*., 2004 | Dutil *et al*., 2014**). It appears to be found over all bottom types, but is mostly associated with rocky substrates and coarse sand areas (**Kulka *et al*., 2004**). Northern Wolffish does not undergo large-scale migration, therefore all life stages generally live together in the same location (**DFO, 2002**).

Though I did not observe any Northern Wolffish in the video footage I analyzed, Atlantic Wolffish (*Anarhichas lupus*) were observed at station LC07, from a subsample of still images recorded during the same surveys, but not included in this study due to technical issues (**Fig. 6-1 & Command *et al*., 2024**). LC07 was characterized as a ‘Barren’ environment, and was mostly dominated by hard-bottom substrates (**Chapter 3**). Moreover, between 2015 and 2019, only 191 Northern Wolffish specimens have been caught in the Laurentian Channel MPA during the annual DFO multispecies trawl surveys and in very low densities (1 to 6 individuals per set) (**Fig. 6-1**). The closest UVS station to a trawl station where Northern Wolffish was collected was 3 km away. This suggests that future UVS surveys in the MPA need to target areas of known presence of Northern Wolffish from previous trawl surveys and/or to target preferred habitats (*i.e*., coarser sediments on the banks of the channel) (**Chapters 2 & 3 | Lacharité *et al*., 2020**).On the other hand, this might reflect that Northern Wolffish might not be a good candidate for conservation target taxa.

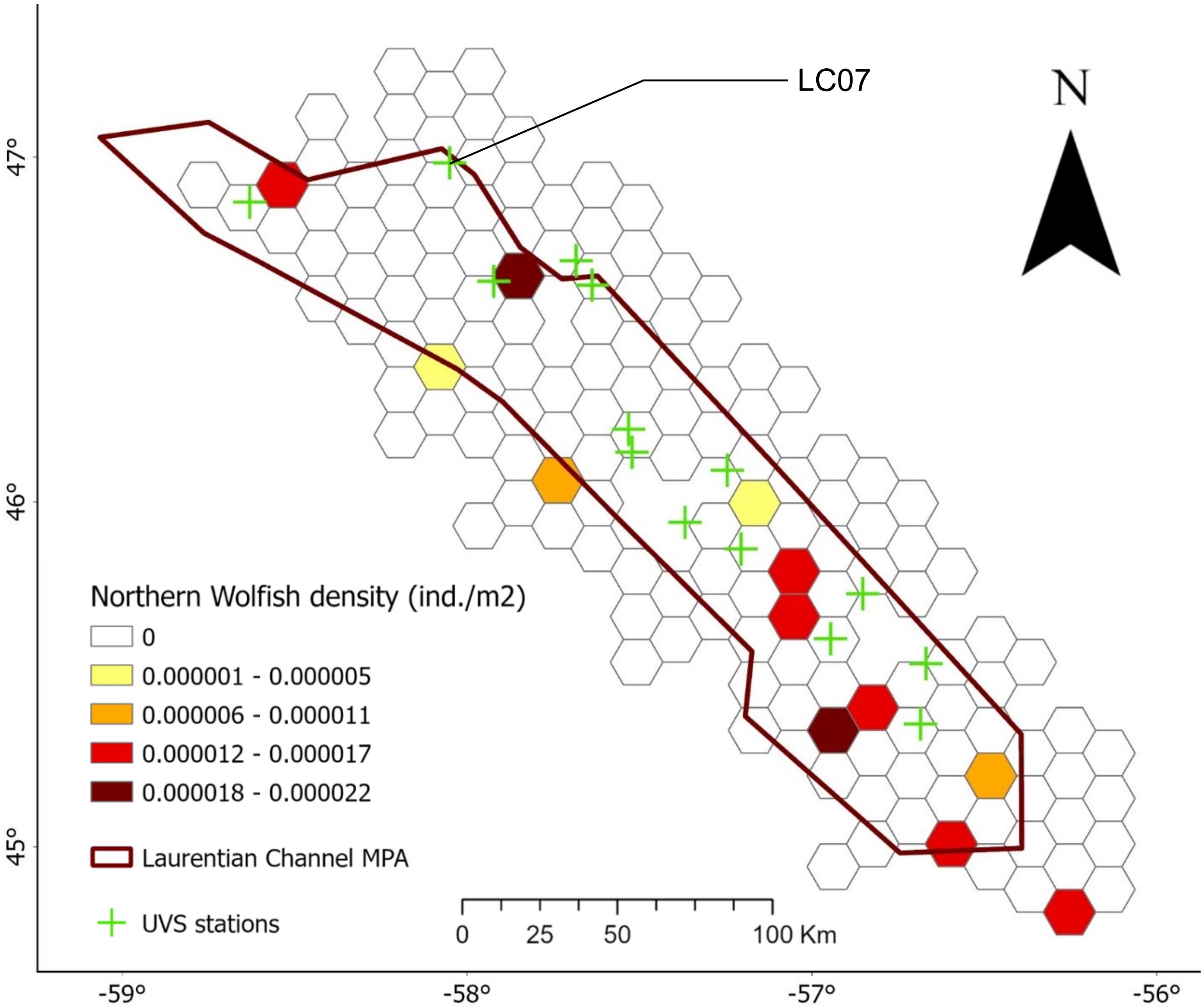

Fig. 6-1 | Average density (ind./m^2) of Northern Wolffish within 100-km^2 cell collected during DFO annual multispecies bottom trawl surveys between 2015 and 2019 in and around the Laurentian Channel MPA. Green symbols represent stations surveyed by UVS in 2017 and 2018. LC07 represents the only station where one Atlantic Wolffish individual was observed on video during the 2018 CAMPOD survey.

6-4.1.2 | The case of Black Dogfish

Black Dogfish was mostly observed during the 2018 survey and was mostly associated with the 'Acti-Ceriant' and 'Barren' habitats. This species displayed very high local densities in the northwest zone of the MPA, and was mostly found at depths of 450-455 m. I measured 11 individuals with total lengths between 16-39 cm. The known size at maturity for Black Dogfish was estimated from trawl survey data at 55 cm (**Kulka *et al.*,**

2022), indicating that all individuals measured from the video data were juveniles. This is consistent with previous reports of localized high densities of Black Dogfish in similar areas of the channel, while the presence of juveniles suggests that the channel is used as a nursery area by the species. However, these results are preliminary and more data need to be collected to determine the preferred areas of distribution of the species.

6-4.1.3 | Fish monitoring

Based on known distribution of Northern Wolffish and Black Dogfish in the MPA, it is likely that they were not observed during the UVS surveys because their preferred area of distribution was not sampled. As an alternative or as a complement to traditional UVSs, baited remote underwater video camera systems (BRUVs) have emerged as an efficient tool to monitor a wide range of marine species, including mobile benthopelagic fish species (**Stoner *et al.*, 2008 | Dalley *et al.*, 2017 | Coté *et al.*, 2019**). BRUVs are ideal to monitor mobile species as they are stationary camera systems. They can inform on benthic habitat characterization, faunal diversity and relative abundances, as well as organism sizes and behavior.

A first alternative or complementary tool to monitor protected fish taxa in the MPA would be acoustic tagging. Acoustic fish tags are used to monitor and track fish movements, and provide information on their distribution, behavior and habitat requirements at different life stages (**Kock *et al.*, 2013**). This tool is particularly advantageous as it can track migratory species (*e.g.*, Black Dogfish and Porbeagle Shark) and inform about their life history and ecology outside the boundaries of the MPA (**Meyer *et al.*, 2009**).

A second alternative or complementary tool to inform on conservation efforts is environmental DNA (eDNA); which is DNA collected from a variety of environmental samples, rather than from organisms (**Rodriguez-Ezpeleta *et al.*, 2020**). eDNA analysis has recently emerged as an effective method for the detection, monitoring, and characterization of faunal communities, including marine fish species. Previous studies have demonstrated that eDNA analyses can provide valuable data about fish communities, for a wide range of spatial scales, and across various depth gradients (**Port *et al*., 2016 | Andruszkiewicz *et al*., 2017 | Jeunen *et al*., 2019 | Jeunen *et al*., 2020 | Canals *et al*., 2021 | Lamy *et al*., 2021**). Indeed, eDNA metabarcoding can inform on the diversity and spatial patterns of fish communities, as well as fish abundance and biomass (**Rourke *et al*., 2021**). This is especially true when the eDNA approach is combined with traditional monitoring methods such as bottom trawl and UVS surveys (**West *et al*., 2020 | Gold *et al*., 2021 | Valdivia-Carrillo *et al*., 2021 | Liu *et al*., 2022**).

All three alternative approaches seem to be appropriate tools for monitoring conservation areas as they can be deployed in a wide range of habitats, while their deployment is minimally disruptive to the environment and the organisms (**Mallet & Pelletier, 2014 | Whitmarsh *et al*., 2016**). Additionally, as more data are collected on fish and their habitat, conducting small-scale distribution studies that integrate micro-habitat characteristics, fish density and fish local size structure will help understand how they use their habitat in the MPA.

6-4.2 | Fish taxa not targeted by conservation objectives in the MPA

In the early stages of the Laurentian Channel MPA designation process,13 groundfish species and taxa were identified in addition to sea pens as candidate conservation targets. Some of the fish taxa removed as MPA conservation targets following stakeholder consultations through the designation process include Atlantic Cod, Haddock, Monkfish, Pollock, Redfish, Thorny Skate, Spiny Dogfish and White Hake (**Muntoni *et al*., 2019**). All these taxa were observed during the two UVS surveys (**Chapters 2, 4 & 5**) and, despite their exclusion from the MPA conservation objectives, still appear to benefit from the protection measures within the boundaries of the MPA.

The five fish taxa on which I focused parts of this study were the most abundant taxa of the assemblage, yet are not key species targeted by the MPA protection measures. Despite having not found strong associations for all five fish taxa with CWC habitats, nor specifically with sea pen habitats, my results did reveal weak but measurable, though insofar unexplained relationships. (**Chapters 2 & 3**). Notably, I provided new evidence that other early-life stage fishes not targeted by the MPA conservation objectives occur in the channel and benefit from the protection of sea pens (**Chapter 3**).

6-4.2.1 | The case of Redfish

Redfish was the only abundant taxon of the fish assemblage observed during the UVS surveys that was both once considered as a MPA conservation target while also being the target of a commercial fishery in the Canadian Northwest Atlantic (**Muntoni *et al.*, 2019**). The most recent study of fish-sea pen association in the Laurentian Channel reported strong associations between Redfish larvae and diverse sea pen habitats, which were assumed to be used as spawning, nursery and shelter areas by early-life stage fishes (**Baillon *et al.*, 2012**). My results contributed new knowledge on the presence of Redfish early-life stages and close associations with CWCs in the Laurentian Channel MPA (**Chapters 2 & 3**), and support conclusions made by Baillon *et al*. (**2012**). While Redfish is not a targeted taxon by the MPA conservation objectives, early-life stages still benefit from protection measures within the boundaries of the MPA, where they can grow until they migrate to their adult habitat. This presumably will enhance their survival and recruitment, contributing to the maintenance of ecosystem processes and the provision of ecosystem services (**Holmlund & Hammer, 1999**), including sufficient Redfish stocks to sustain commercial fisheries into the future.

6-4.3 | Moving forward, moving outward

My study focused on a narrow time window and spatial range. Despite this constraint, my results highlighted patterns of ecological associations between groundfish and CWCs in the Laurentian Channel MPA. Yet, from these insights arose new questions.

1. What is the nature of the relationship between fish and their habitats? What is the ecological role of sea pens for fish beside providing nursery habitats?
2. Are the patterns of fish-habitat associations observed in the MPA specific to the Laurentian Channel, specific to sea pens or specific to CWC habitats in general?
3. How do we evaluate the ecological value and effectiveness of the Laurentian Channel MPA?

4. What are the implications for the Laurentian Channel MPA and other marine conservation areas in the Canadian Northwest Atlantic?

6-4.3.1 | Ecological role of CWCs for deep-sea groundfish

The ecological importance of CWCs for fish and other invertebrate species has been acknowledged worldwide (**Metaxas & Davis, 2005 | Baillon *et al.*, 2012 | Purser *et al.*, 2013 | Lewis *et al.*, 2016 | Gomes-Pereira *et al.*, 2017 | D'Onghia *et al.*, 2019**). While my results highlighted patterns of associations between fish and their habitat, the nature of the relationship with CWCs in the MPA is still unknown. There remains some uncertainty regarding how strong the associations are, as my results suggested facultative relationships between fish and CWCs. There is a need to collect more data to map the extent to which habitat-forming invertebrate taxa are distributed and the diversity of habitats within the MPA. Specifically, it will be important to investigate 1) what is the spatial extent of *Pennatula* fields in the channel and toward the St Pierre Bank, and 2) if there are other benthic habitat types distributed in the shallowest areas of the channel. Additionally, there is a need to collect more data to understand trophic interactions in the MPA and how they are related to the relationship between fish and CWCs. Based on the premise that most fish in the Laurentian Channel are juvenile zooplanktivorous benthic feeders, limited to feeding on small prey, it would be important to assess the meio- and macrofauna associated with CWC habitats and other benthic habitats in relation to known preferred prey of the fish taxa studied in this dissertation. This could help highlight the ecological contribution of sea pens to groundfish in the MPA.

6-4.3.2 | Fish distribution and habitat-associations outside of the MPA

Following my studies conducted within the MPA, some questions remained: where are the fish taxa of interest distributed outside of the MPA, and do they present similar densities? To answer this question, I looked at the density distribution of deep-sea fish taxa collected by DFO annual multispecies bottom trawl surveys in the southern and south-eastern waters of Newfoundland. I specifically focused on taxa observed during the UVS surveys and selected for analysis for parts of the study (**Fig 6-2**). Four taxa (Northern

Wolffish, Pollock, Atlantic Cod and Sandlance) presented low abundances in the MPA, and within the Channel in general, compared to the trawled area outside of the MPA. In contrast, all other seven taxa presented high densities within the MPA and within the Laurentian Channel in general. With the exception of Barracudina, these fish also presented high densities within the Hermitage Channel and/or along the edge of the Newfoundland shelf. Distribution of fish along the edge of the continental shelf is taxon-specific and varies between the Grand Banks and Flemish Cap (**Fig. 6-2A**).

The presence of deep-sea corals and sponges has been reported or predicted in or near the aforementioned areas (**Fig. 6-2M**) (**Kenchington *et al.*, 2016**), which has led to the designation of Significant Benthic Areas (SiBAs) and marine protected and conserved areas to protect them (**Kenchington *et al.*, 2016**). Warren *et al*. (***in prep.***) conducted a cluster analysis with surrounding ecosystems in the Newfoundland shelf to identify potential monitoring sites outside of the MPA, to perform an 'inside *vs*. outside' comparison, with the goal of assessing the MPA effectiveness. Based on their analysis, the Laurentian Channel was clustered with the Hermitage Channel and the south shelf of the Grand Banks based on oceanographic conditions and benthic fauna communities.

Although the distribution of deep-sea corals and sponges extends beyond the Hermitage Channel and the Grand Banks southeast slope, these areas appear to be suitable candidates to conduct a similar study to the one presented in this dissertation in order to assess small-scale fish distribution, size structure and habitat-associations with benthic attributes. Increasing the spatial extent of such a study would enable the assessment of whether the patterns I observed are unique to the Laurentian Channel MPA or occur in other similar ecosystems. Further, the study could be extended to other marine conservation areas, and other areas where 1) fish taxa of interest display high densities, whether or not CWCs have been reported, 2) fish taxa and sea pens are distributed (*e.g.*, Northeast Newfoundland Slope), or 3) fish taxa and other CWCs and structural sponges are distributed (*e.g.*, the edge of the Scotian Shelf).

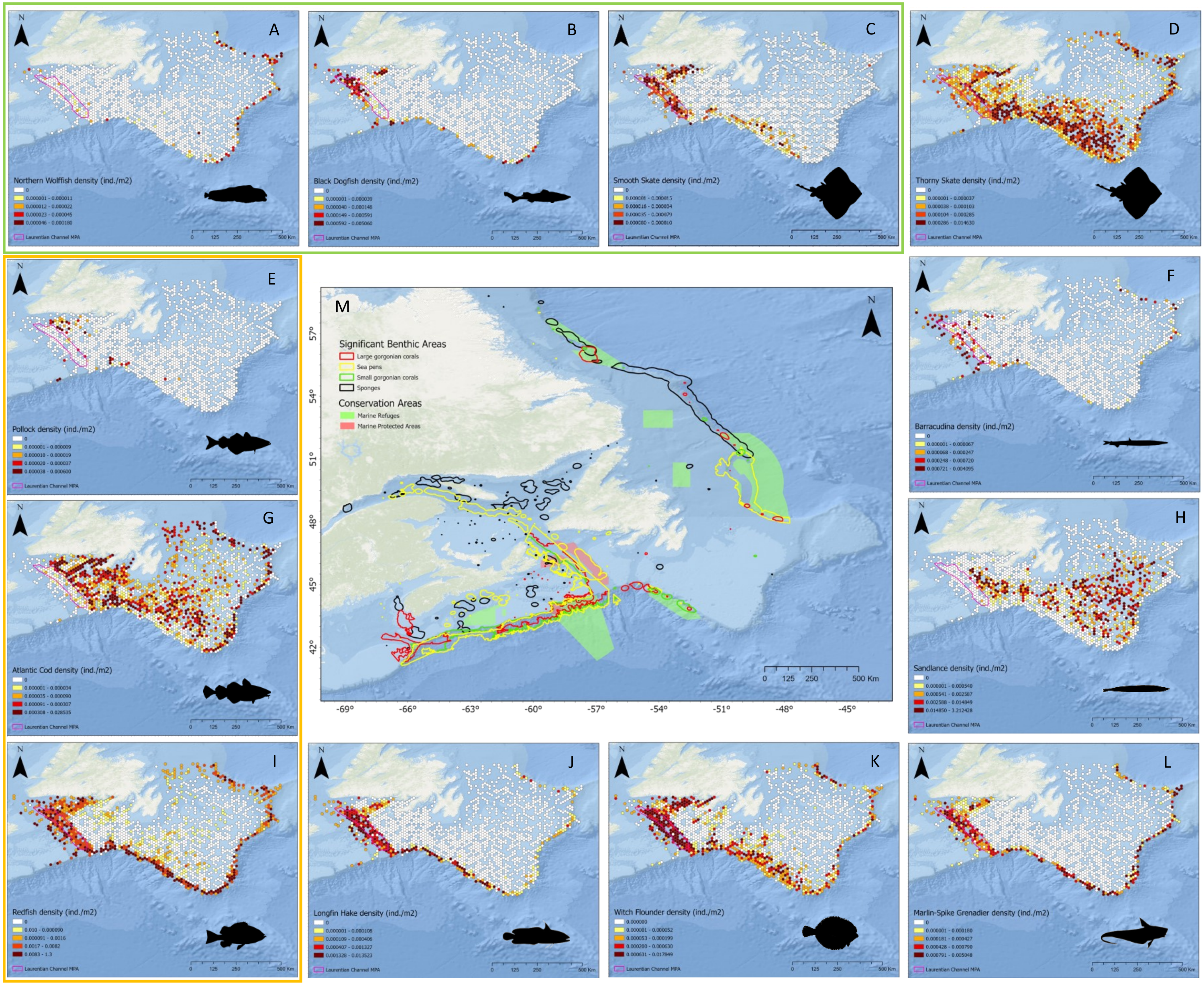
A
Northern Wolffish density (ind./m2)
0
0.000001 - 0.000011
0.000012 - 0.000022
0.000023 - 0.000045
0.000046 - 0.000180
Laurentian Channel MPA
B
Black Dogfish density (ind./m2)
0
0.000001 - 0.000039
0.000040 - 0.000148
0.000149 - 0.000591
0.000592 - 0.005060
Laurentian Channel MPA
C
Smooth Skate density (ind./m2)
0
0.000001 - 0.000015
0.000016 - 0.000034
0.000035 - 0.000079
0.000080 - 0.000810
Laurentian Channel MPA
D
Thorny Skate density (ind./m2)
0
0.000001 - 0.000037
0.000038 - 0.000103
0.000104 - 0.000285
0.000286 - 0.014630
Laurentian Channel MPA
E
Pollock density (ind./m2)
0
0.000001 - 0.000009
0.000010 - 0.000019
0.000020 - 0.000037
0.000038 - 0.000600
Laurentian Channel MPA
M
Significant Benthic Areas
Large gorgonian corals
Sea pens
Small gorgonian corals
Sponges
Conservation Areas
Marine Refuges
Marine Protected Areas
57°
54°
51°
48°
45°
42°
-69°
-66°
-63°
-60°
-57°
-54°
-51°
-48°
-45°
F
Barracudina density (ind./m2)
0
0.000001 - 0.000067
0.000068 - 0.000247
0.000248 - 0.000720
0.000721 - 0.004095
Laurentian Channel MPA
G
Atlantic Cod density (ind./m2)
0
0.000001 - 0.000034
0.000035 - 0.000090
0.000091 - 0.000307
0.000308 - 0.028535
Laurentian Channel MPA
H
Sandlance density (ind./m2)
0
0.000001 - 0.000540
0.000541 - 0.002587
0.002588 - 0.014849
0.014850 - 3.212428
Laurentian Channel MPA
I
Redfish density (ind./m2)
0
0.010 - 0.000090
0.000091 - 0.0016
0.0017 - 0.0082
0.0083 - 1.3
Laurentian Channel MPA
J
Longfin Hake density (ind./m2)
0
0.000001 - 0.000108
0.000109 - 0.000406
0.000407 - 0.001327
0.001328 - 0.013523
Laurentian Channel MPA
K
Witch Flounder density (ind./m2)
0.000000
0.000001 - 0.000052
0.000053 - 0.000199
0.000200 - 0.000630
0.000631 - 0.017849
Laurentian Channel MPA
L
Marlin-Spike Grenadier density (ind./m2)
0
0.000001 - 0.000180
0.000181 - 0.000427
0.000428 - 0.000790
0.000791 - 0.005048
Laurentian Channel MPA
N
0
125
250
500 Km

Fig. 6-2 | (A-L) Average density (ind./m^2) for 12 fish taxa within 100-km^2 cell collected during DFO annual multispecies bottom trawl surveys between 2015 and 2019 in the Laurentian Channel and the south to southeast area of the Newfoundland shelf. All fish taxa were observed during the two UVS surveys in the Laurentian Channel MPA. Green-bordered maps (A-C): fish taxa targeted by conservation objectives of the MPA. Orange-bordered maps (E, G & I): fish taxa that were original candidate conservation targets not included at the end of the selection process. (M) Distribution of MPAs, Marine Refuges and coral and sponge significant benthic areas (SiBAs) in Canadian Atlantic.

6-4.3.3 | Ecological value and effectiveness of the Laurentian Channel MPA

In the long-term, MPAs can contribute to conservation of biodiversity, the maintenance of ecosystem processes and the sustainable provision of ecosystem services (**Holmlund & Hammer, 1999 | Claudet *et al.*, 2008**). Thus, when well-managed, MPAs can be an efficient tool to support fisheries management by increasing fish diversity, density, size and biomass (**Botsford *et al.*, 2001| Claudet & Guidetti, 2010 | Guidetti & Claudet, 2010 | Russ & Alcala, 2011 | Rice *et al.*, 2012**). Despite their exclusion from the conservation objectives, the Laurentian Channel MPA hosts many commercial groundfish taxa (*e.g.*, Atlantic Cod, Redfish, Witch Flounder) that appear to benefit from the protection measures within the boundaries of the MPA (DFO commercial fisheries in the Canadian Northwest Atlantic). These fish species are mobile and likely migrate outside the boundaries of the MPA, whether for feeding or breeding purposes, or to settle to their adult habitats. Therefore, the MPA provides safe benthic habitats where fish can grow, which will ultimately enhance their survival and recruitment outside of the MPA (*e.g.*, passive movements of eggs and larvae, or active movements of juveniles and adults ('spillover' effect)) (**Di Lorenzo *et al.*, 2016**). Common approaches to assess spillover effect from deep-sea marine conservation areas include assessing fish connectivity between fish populations inside and outside marine conservation areas, by either tagging adult fish and recording their movements, or by measuring fish gene flow (**Brockstedt Olsen Huserbråten *et al.*, 2013 | Di Lorenzo *et al.*, 2016**). There is a need to assess connectivity among fish populations in the Canadian Northwest Atlantic to understand the ecological contribution of the Laurentian Channel MPA to other ecosystems and ecosystem services.

6-4.3.4 | Deep-sea marine protected and conserved areas in the Canadian Northwest Atlantic

There are currently two types of marine protected and conserved areas that legally protect corals and sponges in Canadian waters: MPAs and Marine Refuges. In the eastern Canadian Atlantic and Arctic, three MPAs and twelve Marine Refuges have been designated in the deep sea whose protection measures target either deep-sea corals and sponges SiBAs, Atlantic Cod and associated benthic habitats, or biodiversity (**Fig. 6-1 & Appendix 6-1**). All three MPAs aim to protect CWCs, benthic habitats and communities, including groundfish. Three of twelve marine refuges specifically target groundfish and their benthic habitats for conservation, while the remainder were designated to protect CWCs and sponges from destructive fishing practices (**Table 6-1**). While MPAs operate within a legal framework and with clear conservation objectives and monitoring strategies (**DFO, 2010c | Kenchington, 2014 | Lewis *et al.*, 2016**), marine refuges do not have equivalent strategies yet.

All marine protected and conserved areas targeting corals and sponges acknowledge that they serve as ecologically important benthic habitats for many species, including invertebrates and fish, and all recognize that associated fauna benefit from indirect protection within the boundaries of the conservation areas. Yet, CWCs in these deep-sea MPAs are protected as species and not as habitats and, as a result, MPA monitoring indicators do not include the ecological component of CWCs and sponges. For instance, direct CWC and sponge protection indicators selected in MPAs include taxa diversity, abundance, biomass, size and spatial distribution (**DFO, 2010c | Kenchington, 2014 | Lewis *et al.*, 2016**), but indirect indicators are limited to associated fauna diversity (**Lewis *et al.*, 2016**). Similarly, direct targeted fish-related indicators include abundance, biomass, size and spatial distribution, and indirect indicators include trophic structure and prey-predator biomass (**DFO, 2010 | Kenchington, 2014 | Lewis *et al.*, 2016**). Either way, fish-habitat associations are never considered, and are therefore not assessed or monitored.

There is a strong argument for the need to integrate the ecological relationship between protected benthic habitats and fish in conservation areas. In the spirit of assessing conservation area effectiveness, and comparing patterns inside *vs*. outside of the areas' boundaries, a similar approach should be taken comparing patterns inside *vs*. outside benthic habitats provided by CWCs and sponges. This will enable a better understanding of the ecological role CWCs and sponges provide in Canadian waters and thereby help to measure the effectiveness of conservation areas. Following the approach taken for the management of MPAs, a similar monitoring strategy integrating specific conservation objectives and clear indicators should be applied for Marine Refuges that should include species biology and ecology.

6-5 | Recommendations and future considerations

Throughout this dissertation I proposed several recommendations to help understand fish ecology, to improve fish assessment during video-based surveys, and to help conservation areas meet their objectives and assess their effectiveness. These recommendations are presented in Appendix 6-2.

Additionally, I propose further recommendations based on the general discussion of this dissertation:

- Sea pens should be considered as benthic habitat providers and protected as such. This implies that monitoring indicators should be developed accordingly and should account for the ecological role of sea pens. Yet, the nature of the relationship between sea pen habitats and associated fauna, especially fish, is not known in the Laurentian Channel MPA nor in the Canadian Atlantic and Arctic. I suggest that fish-related metrics and fish assemblage characteristics should be used as indicators related to sea pens and protected fish taxa. These indicators could include, fish diversity, density, size structure and trophic interactions, and should be assessed within and between sea pen habitats and other benthic habitats, as well as inside and outside the MPA.

- I suggest that similar studies on fish-habitat associations and the nature of ecological relationships should be conducted outside of the MPA in other marine protected and conserved areas, and in areas where fish and/or sea pens are distributed, as well as in other CWC and habitat-forming sponge areas (*i.e.*, SiBAs). Notably, I suggest that the Hermitage Channel and the southeast edge of the shelf of the Grand Banks are good first candidates as they might provide similar ecosystems to the Laurentian Channel (***Warren* et al.*, in prep.***).

- By extending the study area beyond the boundaries of the MPA, further data collection efforts could consider increasing the range of values of fish distribution drivers in the MPA, such as depth or benthic habitats, or of potential drivers whose influence has been reported in previous studies but were not significant in my study because of their narrow range. For instance, this includes bottom temperature (range in the MPA 3.6-8.9°C), slope (range in the MPA 0-8°) or other terrain attributes (*e.g.*, slope, aspect, rugosity) (**Parra *et al*., 2016 | Lecours *et al*., 2017 | Freitas *et al*., 2021**).

- Marine Refuges in eastern Canada generally lack comprehensive management, conservation objectives and monitoring indicators. I suggest that authorities responsible for managing MPAs and Marine Refuges adopt monitoring strategies that integrate benthic habitats, associated fauna and ecological processes as indicators.

- UVSs are efficient tools at collecting data on fish assemblages, but they might not be the most appropriate for the fish species targeted by conservation objectives in the MPA. I suggest that baited camera, acoustic tagging or eDNA might be the primary monitoring tool for Black Dogfish, Smooth Skate and Northern Wolffish.

- UVS surveys in this study were conducted during a narrow time window, during different months of the year, and during different months than DFO multispecies trawl surveys. Future dedicated studies need to find a trade-off between:

  - Conducting surveys the same month of the year – especially if different monitoring tools will be used – to reduce seasonality variability and assess annual patterns, and
  - Conducting surveys during different months of the year – when using the same monitoring tool – to assess temporal patterns of fish distribution.

- Similarly, while there is a need for regular monitoring of known habitats in the Laurentian Channel MPA, new areas should be surveyed to further delineate the extent of sea pen distribution, to monitor fish species targeted by conservation objectives in their preferred habitats, and to assess the diversity of benthic habitats in the MPA.

This study opened the doors to new considerations for future dedicated research in the area:

- As I could not record invertebrate abundance during the C2018 survey, I used presence/absence as a proxy to define small-scale benthic habitats. I suggest data be collected from the CAMPOD video footage on habitat-forming epibenthic invertebrate diversity and abundance, following the approach taken in Chapter 2. Thus, new information on invertebrate small-scale density will redefine the benthic habitat type characterization presented in Chapter 3 and used in the following chapters.

- Consequently, I suggest this new information be used in complement of the data collected during the R2017 survey to assess the influence of benthic habitat type and invertebrate taxon-specific density on fish density and on fish size following the approach taken in Chapter 2.

- Following the approach taken in Chapter 3, I suggest that the influence of time of day on fish density be assessed. Some groundfish undergo vertical dial migration for feeding purposes (**Auster *et al.*, 1995 | Bergstad, 2009**). Collecting additional data on near-the-seafloor fish density will improve our understanding of fish habitat use in a CWC ecosystem, and also improve fish survey design.

- Based on previous studies (**Diaz *et al*., 2003 | Buhl-Mortensen *et al*., 2005 | Du Preez & Tunnicliffe, 2011 | Henderson *et al*., 2020**), I suggest that additional metrics of fish-habitat associations to be assessed include the relation between fish size and habitat feature size, as well as fish distance to habitat feature. These data would be valuable to strengthen our understanding of the relationship between fish and CWCs.

- I assessed the patterns of distribution of groundfish taxa within the boundaries of the Laurentian Channel MPA during two summer months. Yet, my results suggest that the majority of fish in the MPA are juveniles and use the channel as a nursery before migrating outside the MPA when they reach sexual maturity. Connectivity should be assessed for groundfish distributed in the MPA through genetic studies, tagging or predictive modelling. These data will be valuable to help understand the role that the Laurentian Channel plays for fish populations in the Canadian Northwest Atlantic.

Finally, I collected additional data from the video footage that did not fall within the scope of this study but have the potential to lead to dedicated studies on the ecology and biology of marine organisms of the Laurentian Channel:

- I recorded data on the diversity, abundance and distribution of cephalopods in the Laurentian Channel MPA. A total of 1,391 cephalopods were observed in the channel representing four species. Northern Shortfin Squid (*Illex illecebrosus*) was the most dominant species (97%), while Butterfly Bobtail Squid (*Stoloteuthis leucoptera*), Baird's Octopus (*Bathypolypus bairdii*) and Warty Bobtail Squid (*Rossia palpebrosa*) each represented 1% or less of the assemblage. Most cephalopods (79%) were observed associated with *Pennatula* sea pens. Northern Shortfin Squid was often observed in shoals of up to 45 individuals. I suggest that a similar study be done on the distribution and habitat association of cephalopods in the Laurentian Channel, especially for Northern Shortfin Squid. This species was observed preying on Teleostei sp1 during the video surveys, and has been identified as a predator of

Atlantic Cod, Sandlance, Redfish and Hakes in Newfoundland waters (**Dawe *et al.*, 1997**). Integrating data on Northern Shortfin Squid to future studies on the ecology of groundfish in the channel would help understand fish-habitat relationships.

- I recorded data on ectoparasitism of Marlin-Spike Grenadier. A total of 469 fishes were observed with a parasite on their back, which represented 27% of all Marlin-Spike Grenadier observed. Most were observed in three benthic habitats: one *Pennatula* assemblage (32%), one CWC-and-sea pen habitat (24%) and one barren habitat (22%). I was able to measure 269 individuals (59% of all individuals observed with parasites) with total lengths between 5 and 37 cm. Ectoparasitism of Marlin-Spike Grenadier by either isopods or copepods has been previously reported in the Northwest Atlantic in comparable proportions (~25% of fish observed during *in-situ* video surveys) (**Ross *et al.*, 2001 | Quattrini & Demopoulos, 2016**). I suggest future dedicated studies should assess the variability of ectoparasitism of Marlin-Spike Grenadier with parasite diversity, depth and benthic habitat in the channel. This could provide valuable information on the assessment of fish assemblages, as ectoparasitism can influence fish behavior and ecosystem health (**Quattrini & Demopoulos, 2016**).

6-6 | Conclusion

Overall, this research contributed new knowledge of benthic habitats and fish assemblage characteristics in the Laurentian Channel MPA, the distribution of fish and benthic habitats at small and large spatial scales, and fish ecology in a deep-sea low-relief soft-bottom environment. My results highlighted the ecological importance of sea pens and other CWCs/invertebrates in the Laurentian Channel MPA as providers of resting and feeding habitats for many groundfish taxa, especially early-life stages. The results also suggest that UVSs are efficient tools for capturing the fine-scale relationships that exist between fish and habitat-forming invertebrates, which would not have been possible had I only collected data during scientific bottom-trawl surveys.

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Appendices

Appendix 1-1 | Characteristics of benthoscape classes derived in the Laurentian Channel MPA. For each characteristic, distinct groupings reflect average values in each class (retrieved from Lacharité *et al.*, 2020). Benthoscapes were named for the purpose of this study based on the characteristics provided in Lacharité *et al.* (2020).

Benthoscape name	Class	Surface area[1]	Depth[2]	Slope[3]	Iceberg scours[4]	Pockmarks/pits[5]	Surficial sediment
Shallow gravel-mud	B1	66 (0.5%)	Shallow	Very steep	Absent	Sparse	Gravel/sandy gravel
Shallow mud-gravel	B2	745 (5%)	Shallow	Steep	Absent	Sparse	Muddy/gravelly sand
Slope pockmarks	TZ1	1595 (12%)	Mid-depth	Low relief	Sparse	Intermediate	Mixed sediment (presence of gravel)
Slope dense pockmarks	A2	1564 (11%)	Mid-depth	Low relief	Sparse	Very abundant	Mixed sediment (presence of gravel)
Deep iceberg scours	C2	4654 (34%)	Deep	Low relief	Abundant	Sparse	Sandy mud (gravel traces)
Deep dense iceberg scours	C1	1274 (9%)	Deep	Low relief	Very abundant	Sparse	Bioturbated mud
Deep pockmarks	TZ2	589 (4%)	Deep	Flat	Sparse	Intermediate	Fine sediment (predominantly mud)
Deep dense pockmarks	A1	3178 (23%)	Deep	Flat	Sparse	Very abundant	Fine sediment (predominantly mud)

[1] km^2 (% of study area)

[2] Shallow (< 200 m) | Mid-depth (200-400 m) | Deep (> 400 m)

[3] Flat (< 0.5°) | Low relief (0.1°) | Steep (> 1°) | Very steep (> 3°)

[4] Absent (~0/km^2) | Sparse (< 1/km^2) | Abundant/Very abundant (> 2/km^2)

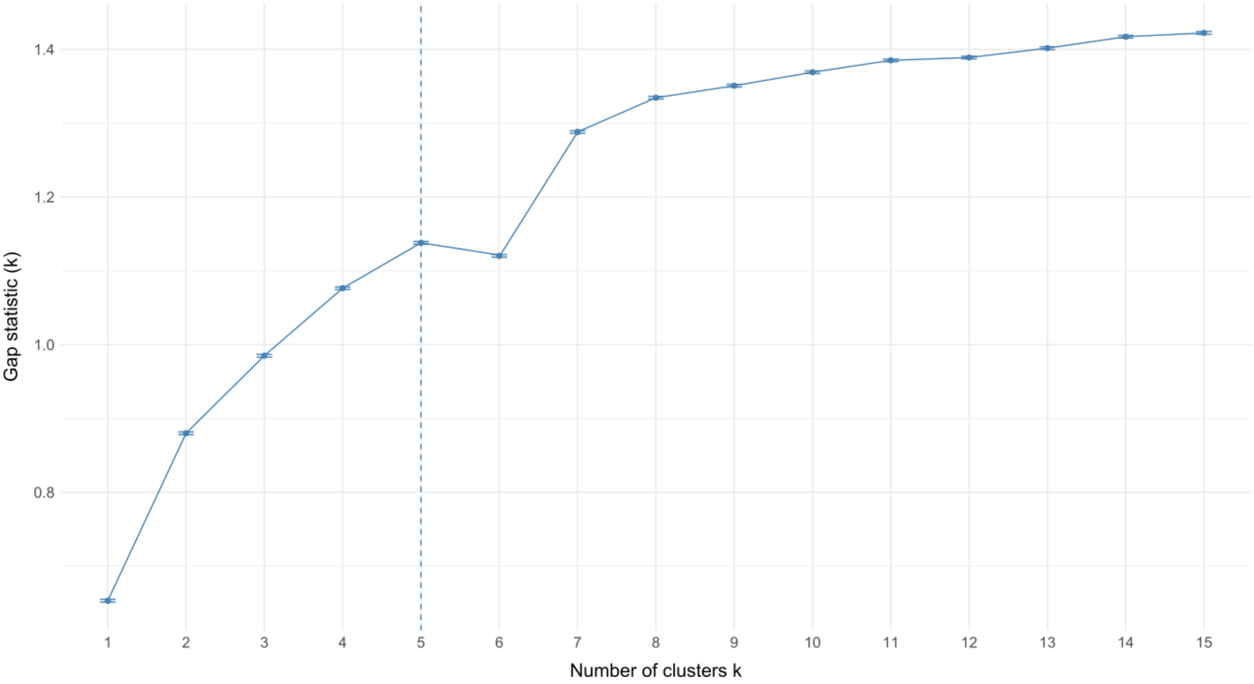
[5] Sparse (< 1/km^2) | Intermediate (1-2/km^2) | Very abundant (> 5/km^2)

Chapter 2

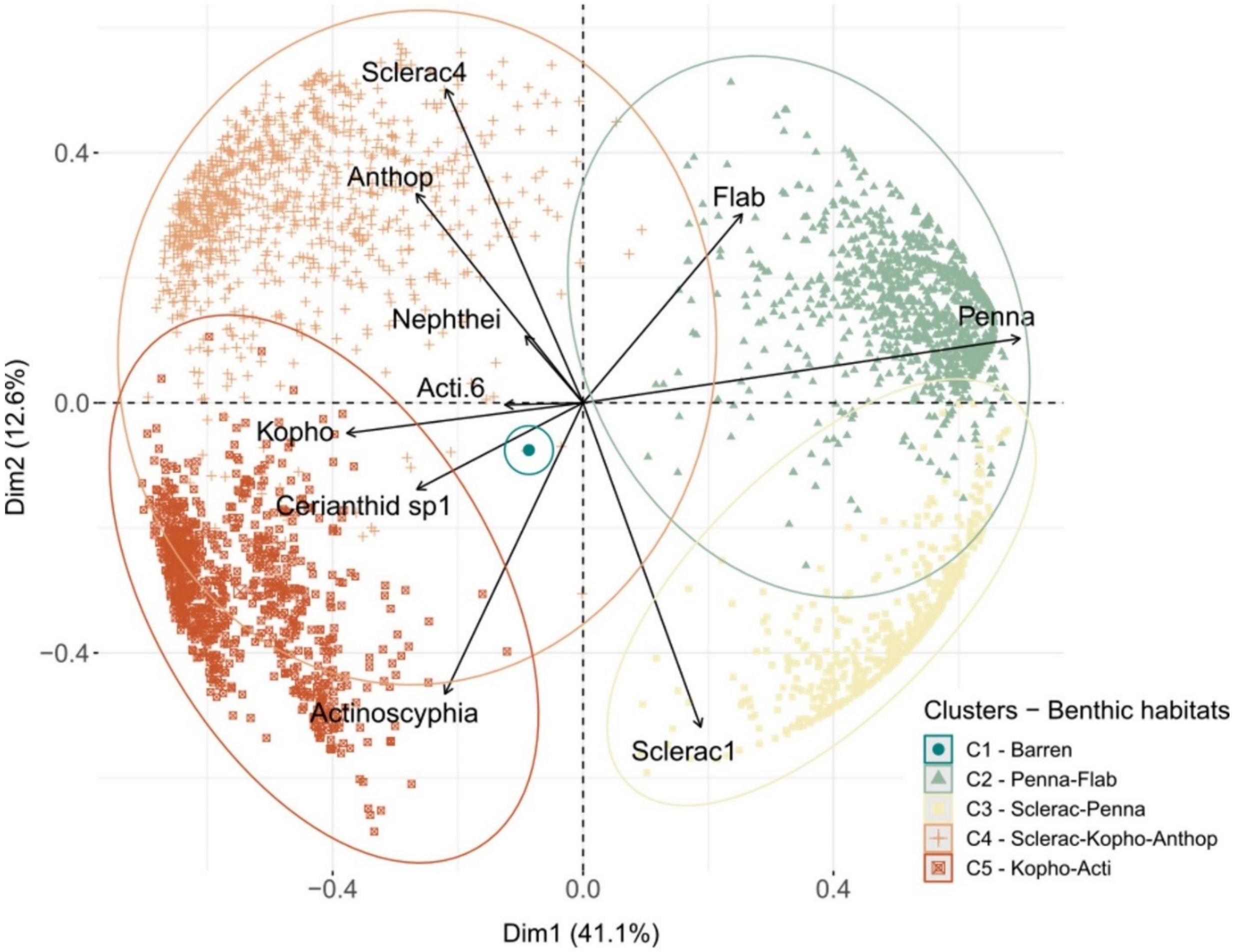
Appendix 2-1 | Classification of the most dominant invertebrate taxa within size classes, and size class characteristics. Size range based on height and diameter. Values were retrieved from Beazley & Kenchington, 2015 and Kenchington *et al*., 2015. We classified *Pennatula* sp. in the medium rather than in the tall size class, based on average size observed on the videos. *Pennatula* spp. specimens were globally smaller than *Anthoptilum* spp.

Size class	Invertebrate	Size range (cm)	
		Height	Diameter
Small	*Flabellum* spp, Scleractinia sp1, Scleractinia sp4	2-5	2-10
	Cerianthid sp1	-	10-45
Medium	*Actinoscyphia* sp, Actiniaria sp6	5-10	2.5-5
	Kophobelemnon sp, Nephtheidae sp.	5-10	3
	Pennatula spp.	3-20	3
Tall	*Anthoptilum* spp.	25	5-10

Appendix 2-2 | Optimal number of clusters representative of benthic habitat types, based on Hellinger-transformed invertebrate densities (ind./m^2), identified by the Gap statistic analysis.



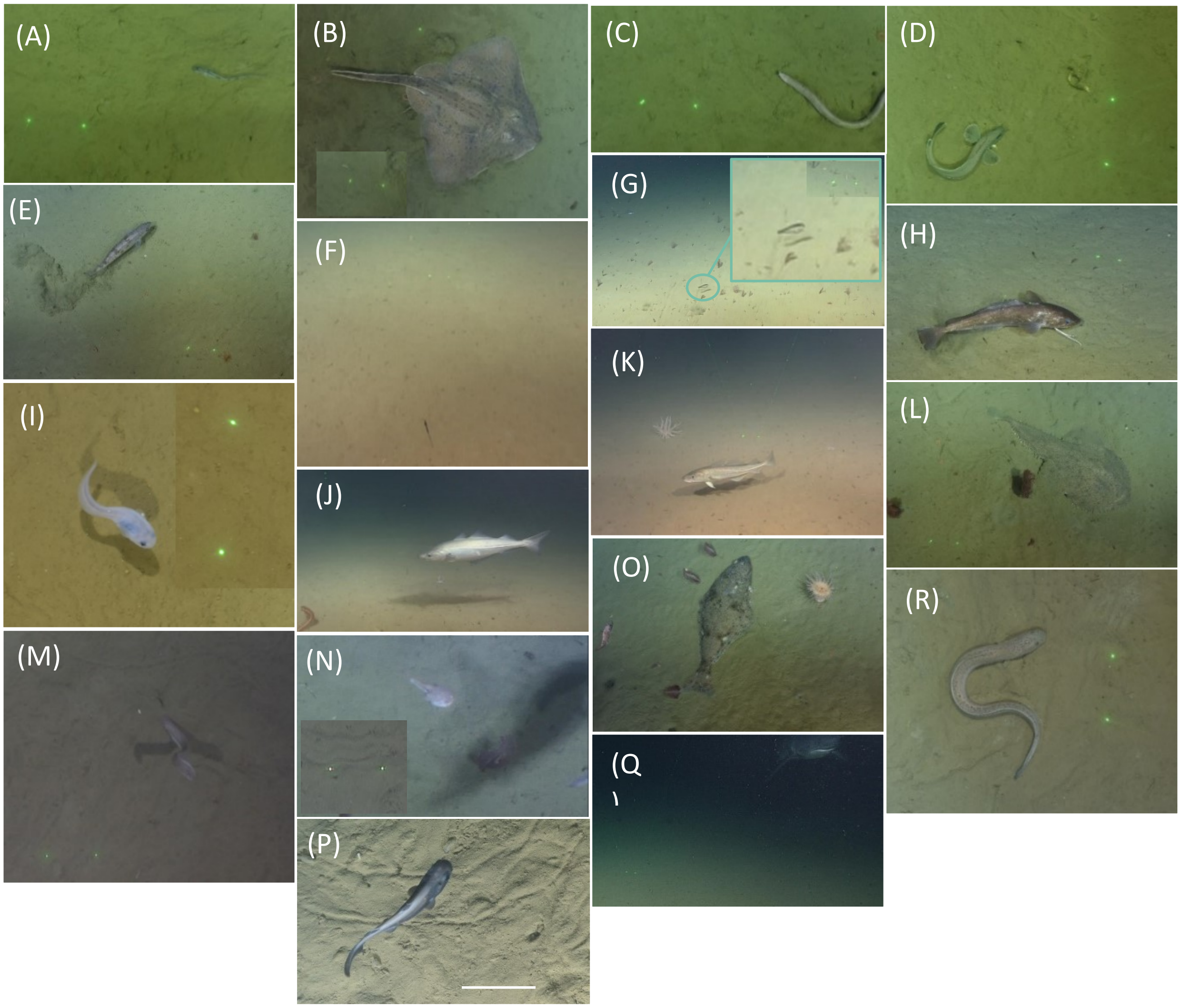
Appendix 2-3 | Results of the PCA on the five benthic clusters identified by the Gap statistic analysis. First two dimensions explain 53,7% of variance. 10 invertebrate taxa dominate four assemblages. Acti6: Actiniaria sp6., Anthop: *Anthoptilum* spp., Flab: *Flabellum* spp., Kopho: *Kophobelemnon* sp., Nephthei: Nephtheidae sp., Penna: *Pennatula* spp., Sclerac1: Scleractinia sp1., Sclerac4: Scleractinia sp4.



Appendix 2-4 | Summary characteristics of benthic habitat types identified by the cluster analysis, including mean depth (m), average invertebrate total density (ind./m^2), average invertebrate specific density (ind./m^2) for the ten taxa contributing to the habitats (± standard error), relative abundance (%) of invertebrates categorized by size class, and distribution of bottom types (%).

Characteristics	**Benthic habitat type**				
	Barren	Penna-Flab	Sclerac-Penna	Sclerac-Kopho-Anthop	Kopho-Acti
Average depth (m)	418 (± 2.5)	346 (± 0.2)	338 (± 0.2)	442 (± 0.2)	441 (± 0.8)
Invertebrate total density (ind./m^2)	0	1.6558 (± 0.0423)	1.0817 (± 0.0238)	0.3595 (± 0.0096)	0.577 (± 0.0109)
Invertebrate density by taxon (ind./m^2)					
Pennatula spp.	0	1.2329 (± 0.0396)	0.377 (± 0.0109)	0.0053 (± < 0.001)	0.0012 (± < 0.001)
Flabellum spp.	0	0.2894 (± 0.0103)	0.0271 (± 0.0021)	0.0067 (± 0.0005)	0.0016 (± < 0.001)
Scleractinia sp1	0	0.0048 (± < 0.001)	0.6587 (± 0.0203)	< 0.001 (± < 0.001)	0.0027 (± 0.0004)
Kophobelemnon sp.	0	< 0.001 (± < 0.001)	< 0.001 (± < 0.001)	0.074 (± 0.0039)	0.2077 (± 0.0076)
Actinoscyphia sp.	0	0.0116 (± < 0.001)	0	0.0017 (± < 0.001)	0.1691 (± 0.0041)
Scleractinia sp4	0	0.0151 (± 0.0014)	0.0037 (± < 0.001)	0.0941 (± 0.0025)	0.0095 (± < 0.001)
Anthoptilum spp.	0	0.0071 (± < 0.001)	0.002 (± < 0.001)	0.0721 (± 0.0021)	0.0339 (± 0.0013)
Cerianthid sp1	0	0.0013 (± < 0.001)	< 0.001 (± < 0.001)	0.0297 (± 0.0012)	0.082 (± 0.0019)
Actiniaria sp6	0	< 0.001 (± 0)	< 0.001 (± < 0.001)	0.0147 (± < 0.001)	0.0272 (± 0.0015)
Nephtheidae sp.	0	0.0012 (± < 0.001)	0.0014 (± < 0.001)	0.0238 (± 0.0013)	0.0096 (± < 0.001)
Relative abundance of invertebrate per size class (%)					
Small (< 5 cm tall)	0	23	61	41	20
Medium (5-25 cm tall)	0	76	38	34	73
Tall (25-100 cm tall)	0	1	1	25	7
Distribution of bottom types (% of total 10-m segments)					
Flat	59	60	23	74	45
Soft negative	39	36	69	24	53
Soft positive	2	0	1	0	0
Soft mixed	1	4	7	1	2
Hard	0	0	1	0	1

Appendix 2-5 | Frame captures from underwater video of the 18 other fish taxa observed during the survey sorted in descending order of abundance. (A) Wolf Eelpout (*Lycenchelys vyerrillii*), (B) Skate sp1 (Thorny Skate (*Amblyraja radiata*) or Smooth Skate (*Malacoraja senta*)), (C) Hagfish (*Myxine glutinosa*), (D) Fourbeard Rockling (*Enchelyopus cimbrius*), (E) Silver Hake (*Merluccius bilinearis),* (F) Actino sp1, (G) Greater Argentine (*Argentina silus*), (H) White Hake (*Urophycis tenuis*), (I) Snailfish sp1 (Liparidae sp. indet.), (J) Pollock (*Pollachius virens*), (K) Atlantic Cod (*Gadus morhua*), (L) Monkfish (*Lophius americanus*), (M) Zoarcidae sp1, (N) Batfish sp1 (*Dibranchus* sp. indet.), (O) Atlantic Halibut (*Hippoglossus hippoglossus*), (P) Black Dogfish (*Centroscyllium fabricii*), (Q) Porbeagle (*Lamna nasus*), (R) Wrymouth (*Cryptacanthodes maculata*). Distance between lasers: 10 cm.

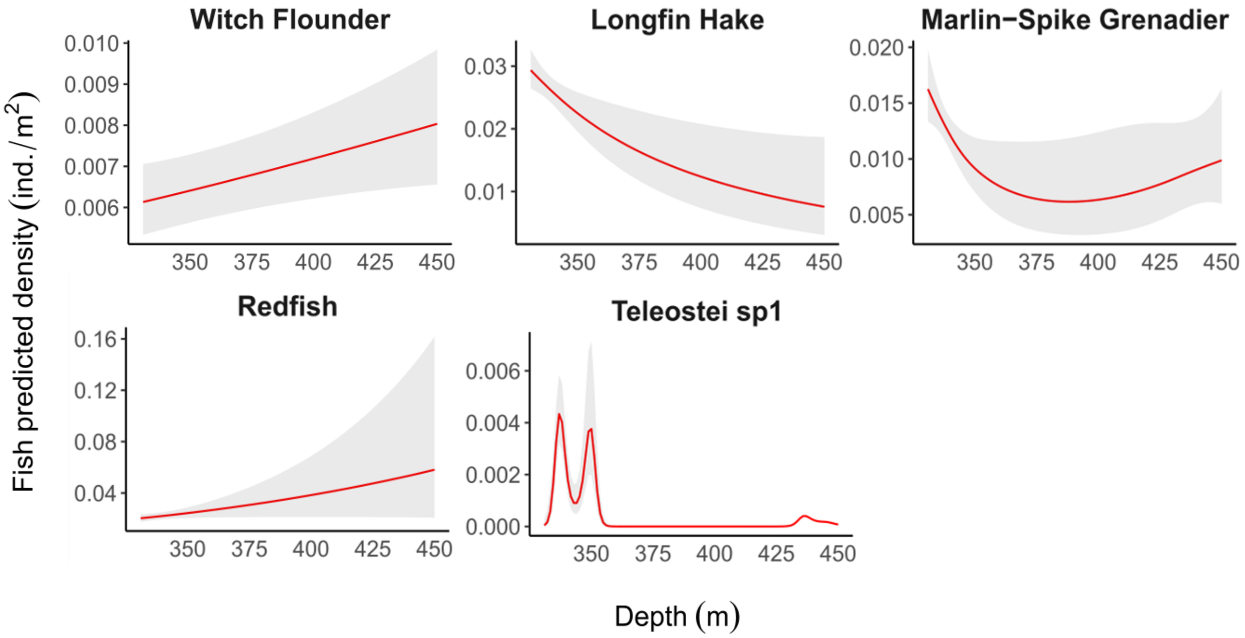


Appendix 2-6 | Results of ANOVA performed on square-root transformed fish total and specific densities between benthic habitat types and results of *post-hoc* Tukey's HSD pairwise comparisons when significant differences were found.

Variable of interest	Predictor	Df	Sum Sq	Mean Sq	F	Pr(>F)
Fish total density	Habitat	4	1.79	0.45	25	< 0.001
	Residuals	3555	63.59	0.02		
Fish taxon density	Habitat	4	0.29	0.07	36.1	< 0.001
	Taxa	23	66.96	2.91	1469	< 0.001
	Habitat:Taxa	92	15.97	0.17	87.6	< 0.001
	Residuals	85320	169.13	< 0.001		

Fish taxon	Tukey HSD test						
All			Barren Penna-Flab	<	Kopho-Acti	<	Sclerac-Penna Sclerac-Kopho-Anthop
Redfish	Penna-Flab	<	Barren Sclerac-Penna	<	Kopho-Acti	<	Sclerac-Kopho-Anthop
Longfin Hake	Barren Kopho-Acti	<	Sclerac-Kopho-Anthop	<	Penna-Flab	<	Sclerac-Penna
Witch Flounder	Sclerac-Penna	<	All				
Marlin-Spike Grenadier	Barren Kopho-Acti	<	Penna-Flab Sclerac-Kopho-Anthop	<	Sclerac-Penna		
Teleostei sp1	Penna-Flab	>	All				
Wolf Eelpout	Barren Penna-Flab	>	All				
Silver Hake	Barren Sclerac-Penna	>	All				

Appendix 2-7 | Model 1 (Eq. 1) partial dependence plots of fish predicted densities in relation to depth. Grey areas correspond to the 95% confidence interval. As no sampling was done between 356 and 429 m, values in this range are interpolated between end-members that have a variety of other co-variates.



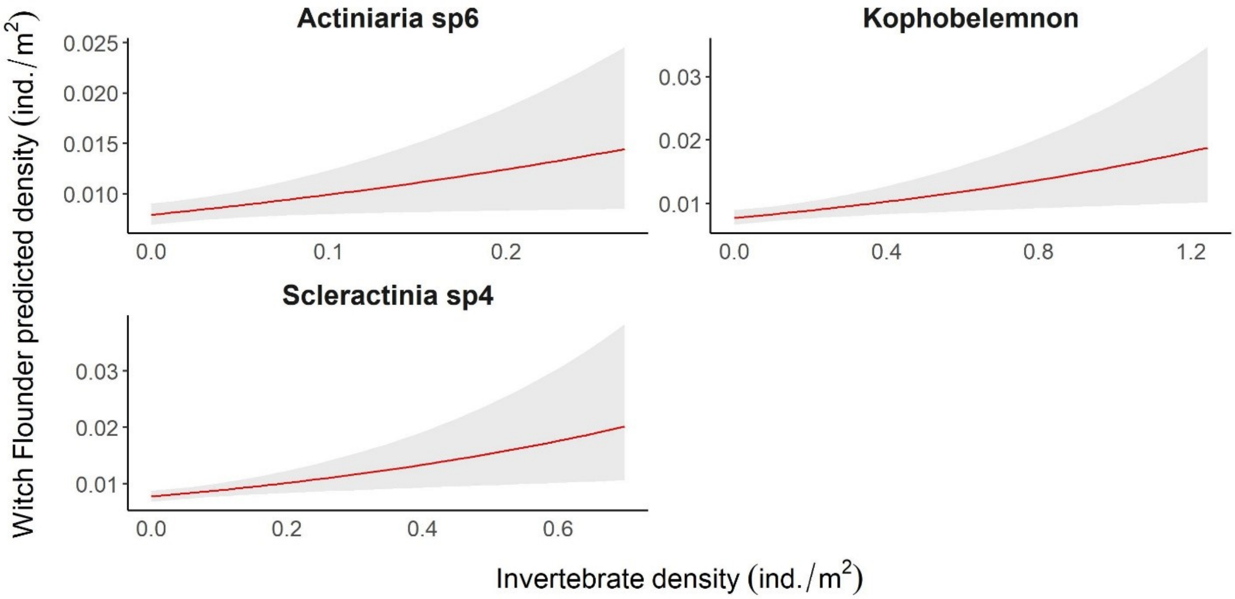
Appendix 2-8 | Witch Flounder Model 1 (Eq. 1) statistics summary.

Predictor		**Parametric coefficients**			
		Estimate	SE	t-value	Pr(>|t|)
Benthic habitat type	(Intercept)	-4.95	0.27	-18.04	< 0.001***
	Penna-Flab	-0.33	0.29	0.39	< 0.001***
	Sclerac-Penna	-0.41	0.31	1.77	< 0.001***
	Sclerac-Kopho-Anthop	-0.98	0.23	0.41	0.001**
	Kopho-Acti	-0.59	0.15	-0.96	< 0.001***
Bottom type	Soft negative	0.01	0.07	0.16	0.313
	Soft positive	-0.73	0.66	-1.11	0.263
	Soft mixed	-0.02	0.19	-0.1	0.448
	Hard	0.53	0.33	1.6	0.099
		Approximate significance of smooth terms			
		edf	Ref.df	F	p-value
	Depth	0.07	9	0.008	0.038*
	Invertebrate density	0.99	9	4.4	< 0.001***
	Stations (re)	3.14	6	1.34	0.028*
	R-sq.(adj) = 0.0161	Deviance explained = 2.69%			

Appendix 2-9 | Witch Flounder Model 2 (Eq. 2) statistics summary.

Predictor	**Parametric coefficients**			
	Estimate	SE	t-value	Pr(>|t|)
(Intercept)	-4.81	0.07	-69.52	< 0.001***
	Approximate significance of smooth terms			
	edf	Ref.df	F	p-value
Actinoscyphia sp.	< 0.001	9	0	0.61
Actiniria sp6	0.68	9	0.28	0.007**
Anthoptilum spp.	< 0.001	9	0	0.902
Cerianthid sp1	< 0.001	9	0	0.505
Flabellum spp.	< 0.001	9	0	0.365
Kophoelemnon sp.	0.9	9	2.57	0.006*
Nephtheidae sp.	< 0.001	9	0	0.852
Pennatula spp.	< 0.001	9	0	0.873
Scleractinia sp1	0.37	9	0.15	0.204
Scleractinia sp4	0.88	9	2.32	0.004*
Station (re)	4.26	6	2.65	0.001***
R-sq.(adj) = 0.014	Deviance explained = 1.89%			

Appendix 2-10 | Model 2 (Eq. 2) partial dependence plots of Witch Flounder **predicted densities in relation to significant invertebrate taxa densities. Grey areas correspond to the 95% confidence interval.**



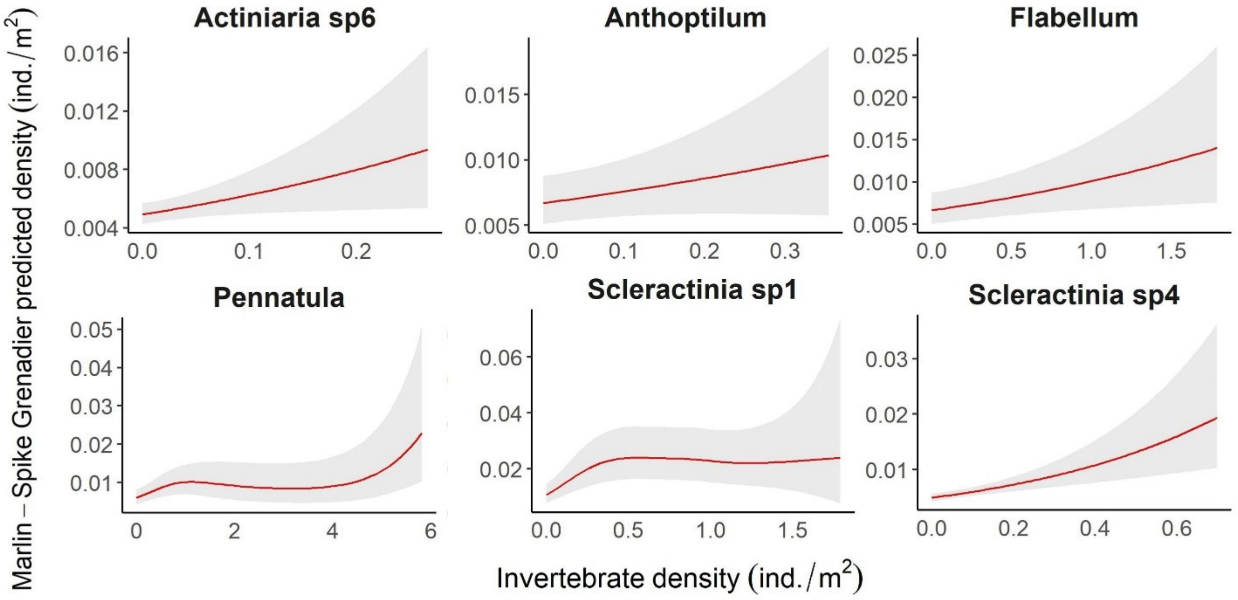
Appendix 2-11 | Marlin-Spike Grenadier Model 1 (Eq. 1) statistics summary.

Predictor		**Parametric coefficients**			
		Estimate	SE	t-value	Pr(>|t|)
	(Intercept)	-5.87	0.31	-18.87	< 0.001***
Benthic habitat type	Penna-Flab	0.79	0.28	2.8	0.51
	Sclerac-Penna	1.06	0.34	3.15	0.032*
	Sclerac-Kopho-Anthop	0.61	0.29	2.11	0.736
	Kopho-Acti	0.38	0.22	2.93	0.545
Bottom type	Soft negative	0.21	0.07	2.93	0.003**
	Soft positive	0.68	0.38	1.78	0.076
	Soft mixed	0.15	0.17	0.9	0.368
	Hard	0.18	0.36	0.5	0.62
		Approximate significance of smooth terms			
		edf	Ref.df	F	p-value
	Depth	3.26	9	3.72	0.038*
	Invertebrate density	3.28	9	8.8	< 0.001***
	Stations (re)	2.51	6	1.17	0.0167*
	R-sq.(adj) = 0.073	Deviance explained = 7.98%			

Appendix 2-12 | Marlin-Spike Grenadier Model 2 (Eq. 2) statistics summary.

Predictor	**Parametric coefficients**			
	Estimate	SE	t-value	Pr(>|t|)
(Intercept)	-4.98	0.15	-33.1	< 0.001***
	Approximate significance of smooth terms			
	edf	Ref.df	F	p-value
Actinoscyphia sp.	0.62	9	0.34	0.098
Actiniria sp6	0.8	9	0.57	0.024*
Anthoptilum spp.	0.7	9	0.95	0.006**
Cerianthid sp1	0.002	9	0	0.425
Flabellum spp.	0.8	9	1.43	0.016*
Kophoelemnon sp.	0.5	9	0.4	0.130
Nephtheidae sp.	< 0.001	9	0	0.971
Pennatula spp.	3.57	9	14.25	0.015*
Scleractinia sp1	0.87	9	1.24	0.007*
Scleractinia sp4	0.91	9	2.38	0.001**
Station (re)	5.18	6	9	< 0.001***
R-sq.(adj) = 0.07	Deviance explained = 7.38%			

Appendix 2-13 | Model 2 (Eq. 2) partial dependence plots of Marlin-Spike Grenadier predicted densities in relation to significant invertebrate taxa densities. Grey areas correspond to the 95% confidence interval.



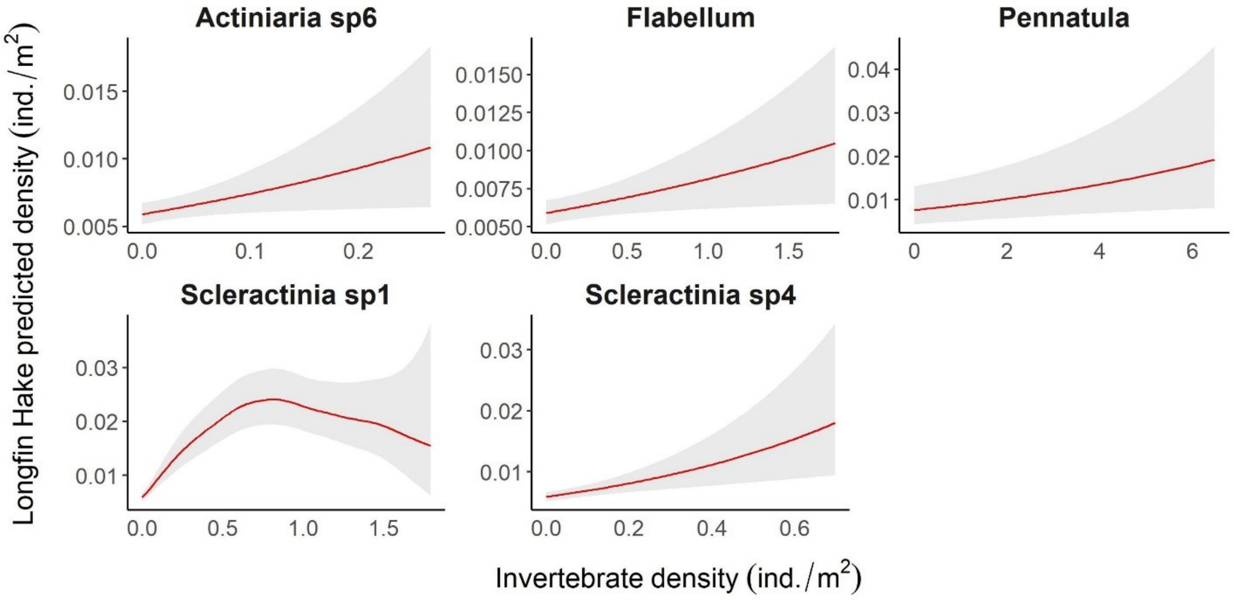
Appendix 2-14 | Longfin Hake Model 1 (Eq. 1) statistics summary.

Predictor		Parametric coefficients			
		Estimate	SE	t-value	Pr(>|t|)
	(Intercept)	-5.65	0.29	-19.5	< 0.001***
Benthic habitat type	Penna-Flab	1.22	0.29	3.32	0.018*
	Sclerac-Penna	2.32	0.29	5.4	< 0.001***
	Sclerac-Kopho-Anthop	0.85	0.26	1.82	0.067
	Kopho-Acti	0.07	0.22	0.31	0.693
Bottom type	Soft negative	0.35	0.06	5.82	< 0.001***
	Soft positive	0.03	0.42	0.06	0.99
	Soft mixed	0.46	0.12	3.89	< 0.001***
	Hard	-0.6	0.41	-1.47	0.32
		Approximate significance of smooth terms			
		edf	Ref.df	F	p-value
	Depth	2.48	9	5.86	0.019*
	Invertebrate density	5.67	9	32.1	< 0.001***
	Stations (re)	4.9	6	10.43	< 0.001***
	R-sq.(adj) = 0.0484	Deviance explained = 21.5%			

Appendix 2-15 | Longfin Hake Model 2 (Eq. 2) statistics summary.

Predictor	Parametric coefficients			
	Estimate	SE	t-value	Pr(>|t|)
(Intercept)	-4.79	0.23	-20.93	< 0.001***
	Approximate significance of smooth terms			
	edf	Ref.df	F	p-value
Actinoscyphia sp.	< 0.001	9	0	0.932
Actiniria sp6	0.82	9	2.2	0.02*
Anthoptilum spp.	0.29	9	0.14	0.700
Cerianthid sp1	< 0.001	9	0	0.329
Flabellum spp.	0.39	9	0.34	0.005**
Kophoelemnon sp.	< 0.001	9	0	0.458
Nephtheidae sp.	0.20	9	0	0.065
Pennatula spp.	0.91	9	29.9	0.002**
Scleractinia sp1	2.99	9	99	< 0.001***
Scleractinia sp4	0.93	9	6.22	< 0.001***
Station (re)	5.76	6	28.49	< 0.001***
R-sq.(adj) = 0.28	Deviance explained = 26.1%			

Appendix 2-16 | Model 2 (Eq. 2) partial dependence plots of Longfin Hake predicted densities in relation to significant invertebrate taxa densities. Grey areas correspond to the 95% confidence interval.



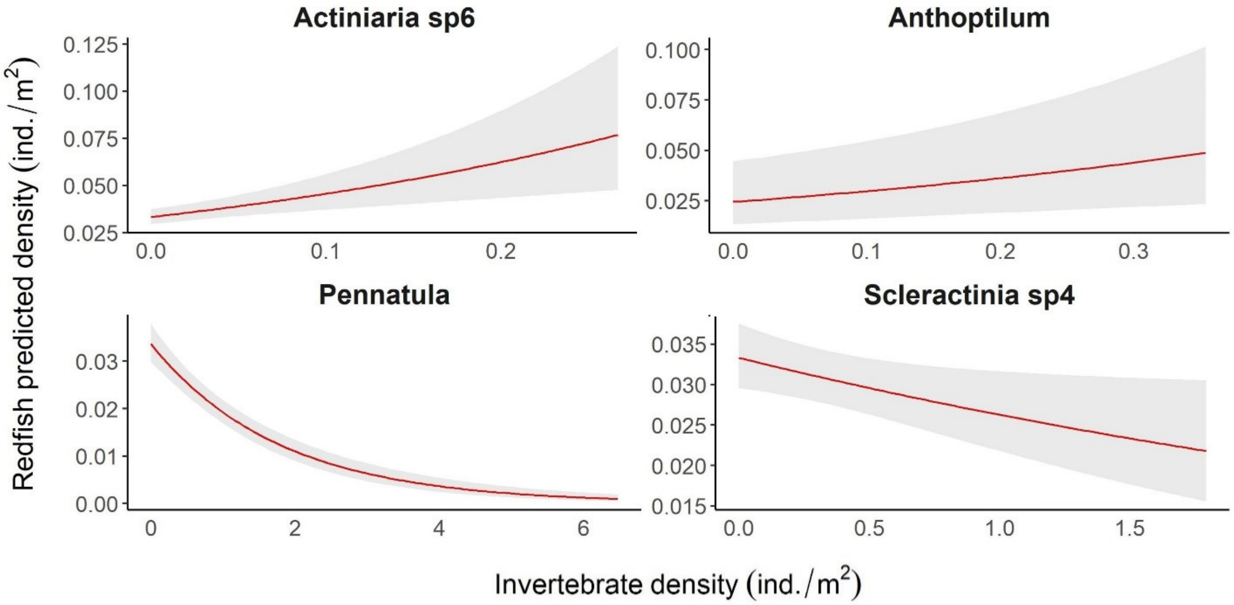
Appendix 2-17 | Redfish Model 1 (Eq. 1) statistics summary.

Predictor		**Parametric coefficients**			
		Estimate	SE	t-value	Pr(>|t|)
	(Intercept)	-4	0.62	-6.41	< 0.001***
Benthic habitat type	Penna-Flab	0.05	0.28	2.8	0.005**
	Sclerac-Penna	0.47	0.22	2.13	0.004**
	Sclerac-Kopho-Anthop	1.08	0.2	5.36	< 0.001***
	Kopho-Acti	0.64	0.2	3.15	0.002**
Bottom type	Soft negative	-0.259	0.06	-4.63	0.471
	Soft positive	-0.29	0.45	-0.64	0.059
	Soft mixed	-0.472	0.17	-2.75	0.191
	Hard	0.717	0.26	2.77	< 0.001***
		Approximate significance of smooth terms			
		edf	Ref.df	F	p-value
	Depth	0.85	9	0.4	0.034*
	Invertebrate density	5.86	9	67.9	< 0.001***
	Stations (re)	4.9	6	60	< 0.001***
	R-sq.(adj) = 0.0484	Deviance explained = 21.5%			

Appendix 2-18 | Redfish Model 2 (Eq. 2) statistics summary.

Predictor	**Parametric coefficients**			
	Estimate	SE	t-value	Pr(>|t|)
(Intercept)	-3.64	0.30	-12.18	< 0.001***
	Approximate significance of smooth terms			
	edf	Ref.df	F	p-value
Actinoscyphia sp.	0	9	0	0.711
Actiniria sp6	0.82	9	0.63	0.019*
Anthoptilum spp.	0.92	9	6.17	< 0.001***
Cerianthid sp1	0.68	9	2.17	0.594
Flabellum spp.	0.79	9	15.55	0.394
Kophobelemnon sp.	0.47	9	0.37	0.175
Nephtheidae sp.	0.81	9	1	0.626
Pennatula spp.	0.48	9	2.57	< 0.001***
Scleractinia sp1	0	9	0	0.937
Scleractinia sp4	0.67	9	0.43	0.02*
Station (re)	5.89	6	75.23	< 0.001***
R-sq.(adj) = 0.14	Deviance explained = 19.9%			

Appendix 2-19 | Model 2 (Eq. 2) partial dependence plots of Redfish predicted densities in relation to significant invertebrate taxa densities. Grey areas correspond to the 95% confidence interval.



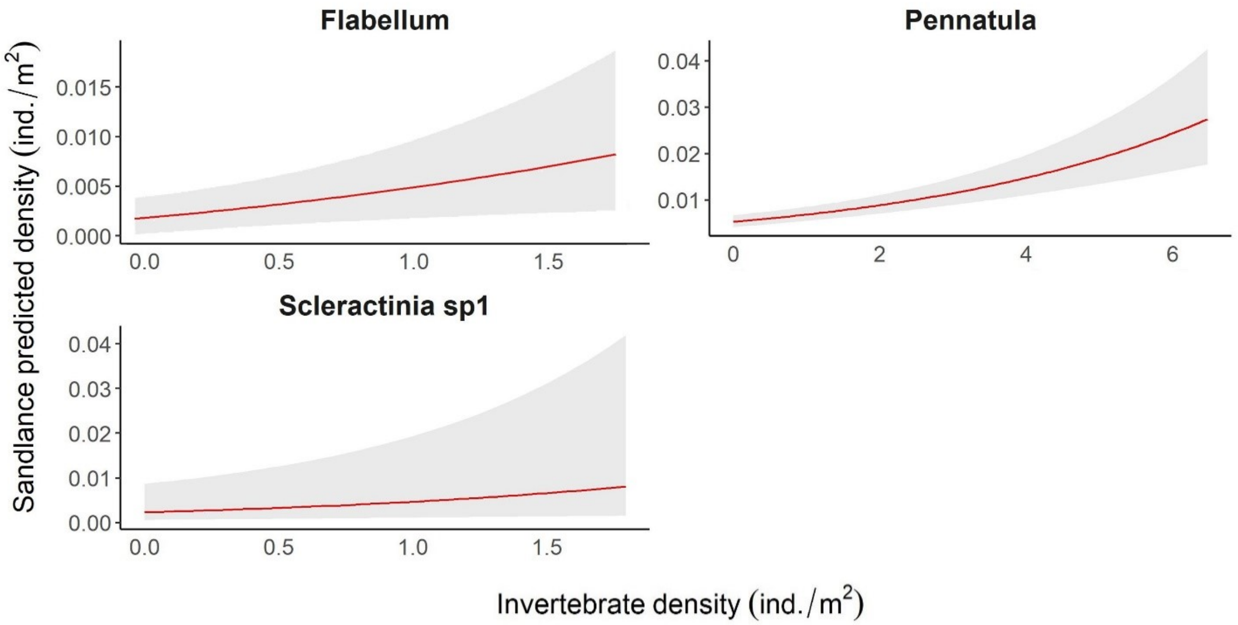
Appendix 2-20 | Teleostei sp1 Model 1 (Eq. 1) statistics summary.

Predictor		**Parametric coefficients**			
		Estimate	SE	t-value	Pr(>|t|)
	(Intercept)	-6.02	0.45	-13.4	< 0.001***
Benthic habitat type	Penna-Flab	3.14	0.34	-0.6	< 0.001***
	Sclerac-Penna	1.75	0.4	-0.28	0.02*
	Sclerac-Kopho-Anthop	0.06	0.57	-0.21	0.005**
	Kopho-Acti	0.98	1.34	1.84	0.002**
Bottom type	Soft negative	-0.183	0.12	-1.57	0.313
	Soft positive	-0.26	0.68	-0.39	0.263
	Soft mixed	-0.21	0.26	-0.82	0.448
	Hard	0.47	0.52	0.9	0.099
		Approximate significance of smooth terms			
		edf	Ref.df	F	p-value
	Depth	7.76	9	11.93	0.002*
	Invertebrate density	4.50	9	3.6	< 0.001***
	Stations (re)	4.35	6	17.98	< 0.001***
	R-sq.(adj) = 0.23	Deviance explained = 42.5%			

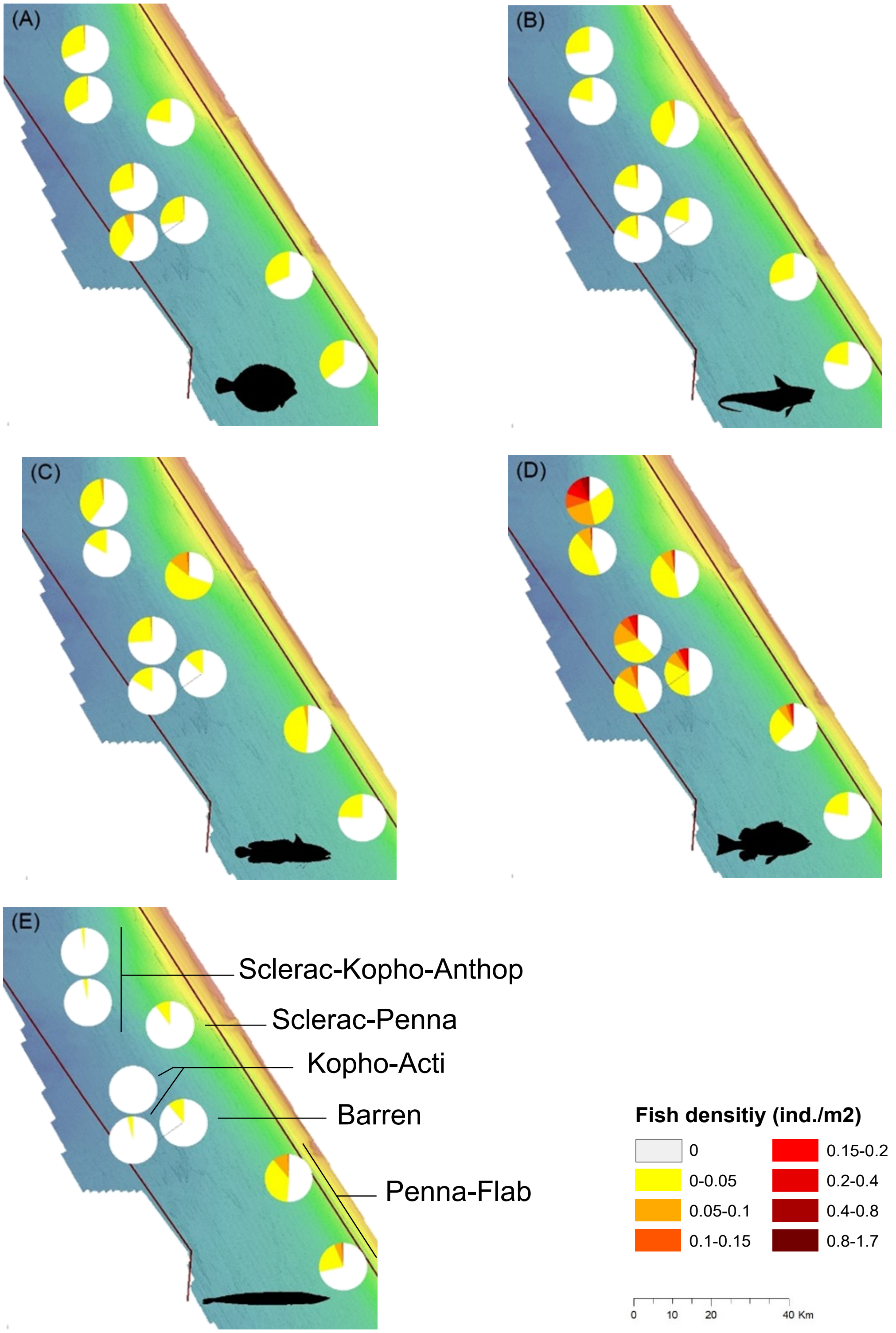
Appendix 2-21 | Teleostei sp1 Model 2 (Eq. 2) statistics summary.

Predictor	**Parametric coefficients**			
	Estimate	SE	t-value	Pr(>|t|)
(Intercept)	-6.09	0.75	-8.172	< 0.001***
	Approximate significance of smooth terms			
	edf	Ref.df	F	p-value
Actinoscyphia sp.	1	9	8.66	0.186
Actiniria sp6	0.48	9	0.12	0.194
Anthoptilum spp.	< 0.001	9	0	0.812
Cerianthid sp1	0.29	9	0.062	0.241
Flabellum spp.	3.64	9	13.29	< 0.001***
Kophobelemnon sp.	0.2	9	0.12	0.249
Nephtheidae sp.	< 0.001	9	0	0.854
Pennatula spp.	3.74	9	59.9	< 0.001***
Scleractinia sp1	0.75	9	3.33	0.046
Scleractinia sp4	0.41	9	0.10	< 0.001***
Station (re)	5.86	6	57.86	< 0.001
R-sq.(adj) = 0.2	Deviance explained = 40.6%			

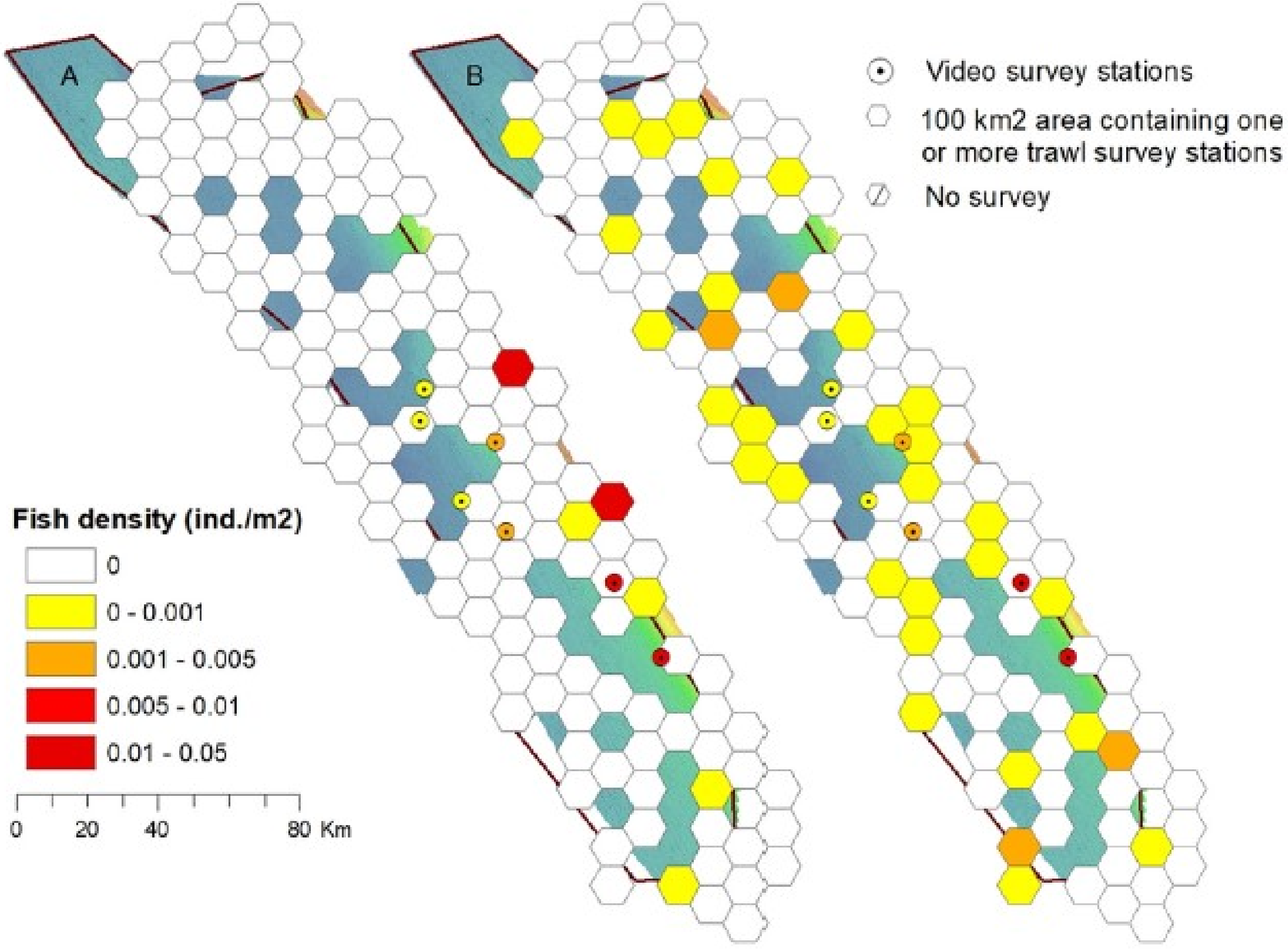
Appendix 2-22 | Model 2 (Eq. 2) partial dependence plots of Teleostei sp1 predicted densities in relation to significant invertebrate taxa densities. Grey areas correspond to the 95% confidence interval.



Appendix 2-23 | Fish density frequency distribution per station in the Laurentian Channel MPA of (A) Witch Flounder, (B) Marlin-Spike Grenadier, (C) Longfin Hake, (D) Redfish, (E) Teleostei sp1. While most of the stations are dominated by one benthic habitat type, we differentiated the Barren habitat from Kopho-Acti at station LC13 (see Fig. 2-1 for station locations).



Appendix 2-24 | (A) Sandlance (*Ammodytes* spp.), (B) Barracudina (*Arctozenus* sp. and *Paralepis* spp.) average density (ind./m^2) assessed by DFO trawls within hexagonal cells (⬡). Each cell contains one or more stations surveyed by bottom-trawl between 2015 and 2019. For each map we also reported Teleostei sp1 average density (ind./m^2) per station surveyed by ROPOS during the 2017 video survey (⊙).

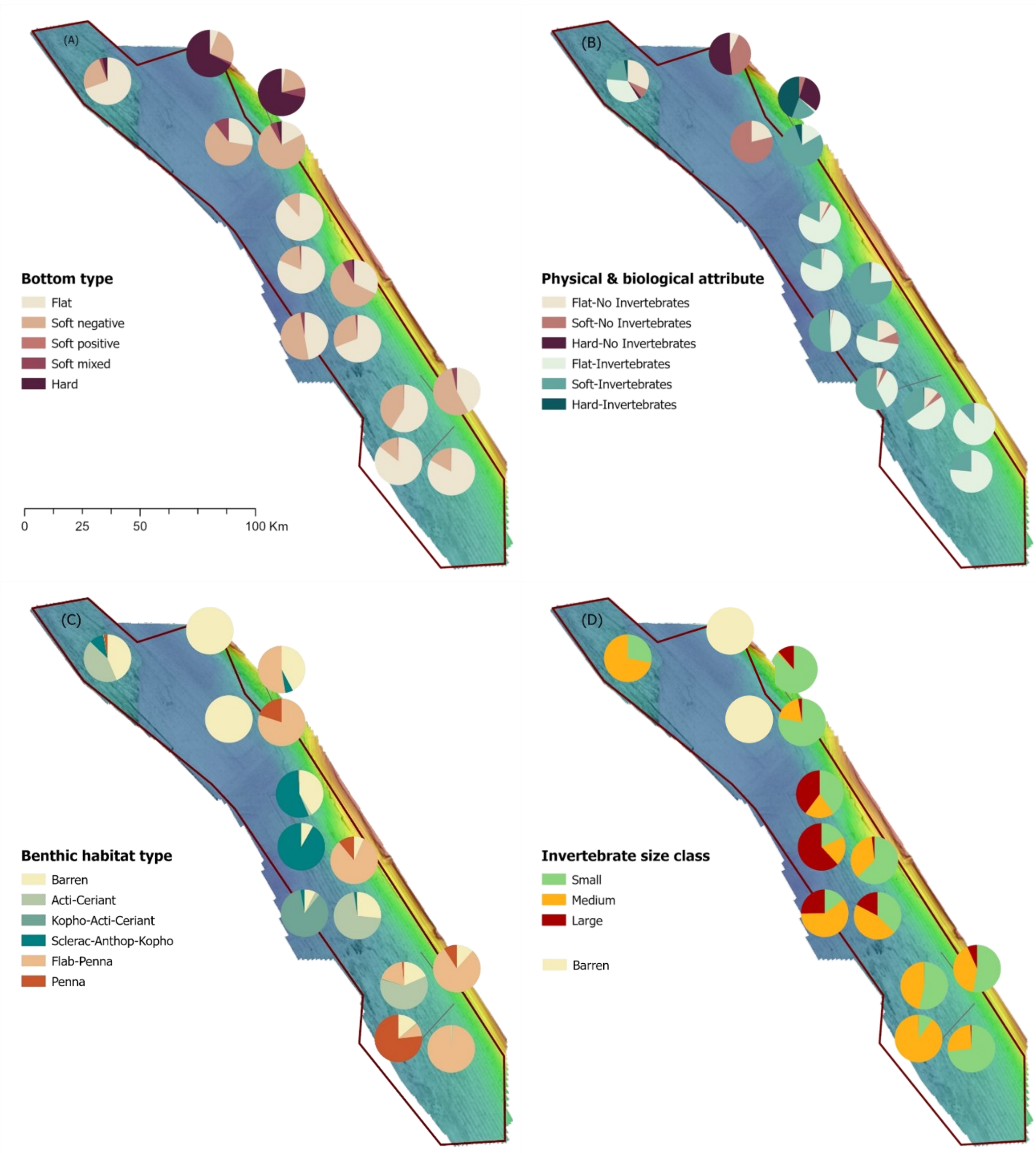


Chapter 3

Appendix 3-1 | Distribution of sampling effort by year, time of day and depth range.

Parameter	Number of 10-m segments	Area (ha)	Number of fish observed	Number of fish measured
Year				
2017	5649	26.3	14598	5887
2018	3763	17.3	4645	1624
Time of day				
Day	6738	31.5	10048	3743
Night	2674	12.1	9195	3768
Depth (m)				
179-250	133	0.6	121	42
250-300	152	0.7	356	88
300-350	3034	15.1	5772	2162
350-400	1616	7	1594	655
400-455	4477	20.3	11400	4564
Total	9412	43.6	19243	7511

Appendix 3-2 | Characterization of habitat heterogeneity according to (A) bottom types, (B) physical and biological attributes, (C) benthic habitat types, (D) invertebrate size classes defined by the cluster analysis across stations. Pie charts show the proportion of each category found at each station.



Appendix 3-3 | Summary characteristics of benthic habitat types identified by the cluster analysis, depth range (m), relative presence (% of 10-m segments) of the nine invertebrate taxa contributing to the habitats, relative presence (% of 10-m segments) of invertebrates categorized by size class (Chapter 2), and distribution of bottom types (% of 10-m segments).

Characteristics	Benthic habitat type					
	Barren	Acti-Ceriant	Kopho-Acti-Ceriant	Sclerac-Anthop-Kopho	Flab-Penna	Penna
Depth range (m)	179-455	341-450	433-450	317-449	305-441	265-439
Relative presence of invertebrate per taxon (%)						
Pennatula aculeata	0	12	1	2	36	96
Flabellum (Ulocyathus) alabastrum	0	15	< 1	2	63	3
Kophobelemnon sp.	0	< 1	49	22	< 1	< 1
Actinauge cristata	0	36	25	< 1	< 1	< 1
Cerianthid sp1	0	26	12	9	< 1	< 1
Anthoptilum spp.	0	6	7	24	< 1	< 1
Flabellum (Ulocyathus) angulare	0	1	1	28	< 1	1
Actiniaria sp6	0	1	6	4	1	< 1
Nephtheidae sp.	0	2	1	9	< 1	< 1
Relative presence of invertebrate per size class (%)						
Small (< 5 cm tall)	0	42	13	39	62	4
Medium (5-25 cm tall)	0	51	82	37	38	96
Tall (25-100 cm tall)	0	6	7	24	< 1	< 1
Distribution of bottom types (%)						
Flat	63	69	38	77	33	78
Soft negative	24	30	59	20	58	20
Soft positive	0	0	0	0	0	0
Soft mixed	2	1	3	1	5	1
Hard	10	1	0	2	4	1

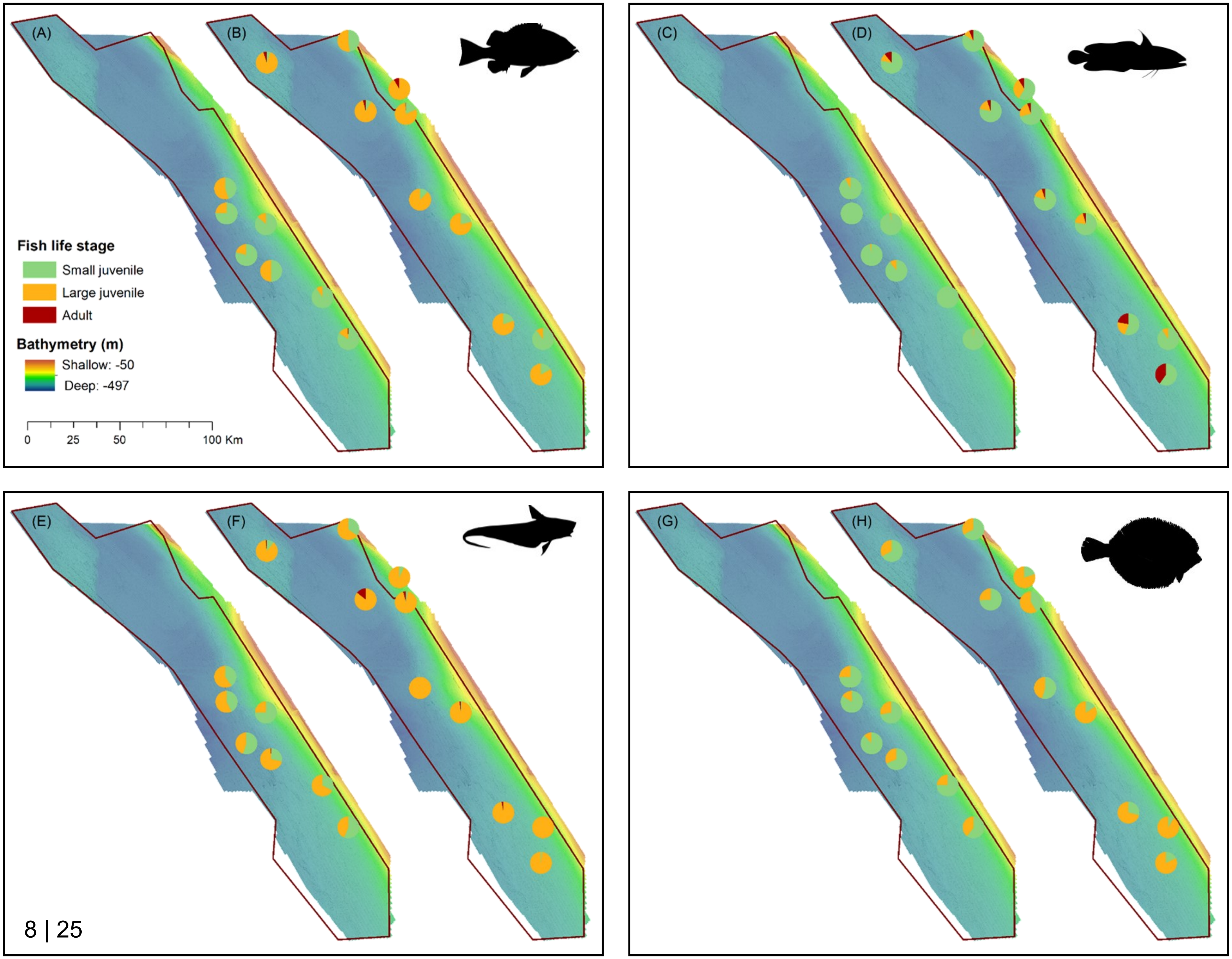
Appendix 3-4 | Number of fish measured (and observed) per taxon, benthic habitat type (per year and time of day) and bottom type.

Year	Benthic habitat type	Fish taxon			
		Longfin Hake	Marlin-Spike Grenadier	Redfish	Witch Flounder
2017	Barren	15 (64)	21 (34)	327 (1497)	47 (94)
	Acti-Ceriant	18 (61)	37 (96)	281 (849)	58 (124)
	Kopho-Acti-Ceriant	62 (149)	65 (127)	406 (1221)	97 (172)
	Sclerac-Anthop-Kopho	169 (354)	132 (289)	1978 (4416)	205 (389)
	Flab-Penna	480 (1155)	249 (604)	544 (1505)	214 (399)
	Penna	104 (201)	73 (142)	156 (421)	149 (235)
2018	Barren	132 (411)	128 (236)	164 (585)	93 (224)
	Acti-Ceriant	21 (44)	28 (46)	45 (142)	54 (121)
	Kopho-Acti-Ceriant	0 (11)	0 (23)	0 (42)	0 (35)
	Sclerac-Anthop-Kopho	61 (117)	61 (70)	110 (260)	69 (97)
	Flab-Penna	362 (70)	132 (30)	845 (100)	259 (104)
	Penna	230 (1199)	62 (856)	353 (4303)	272 (1153)

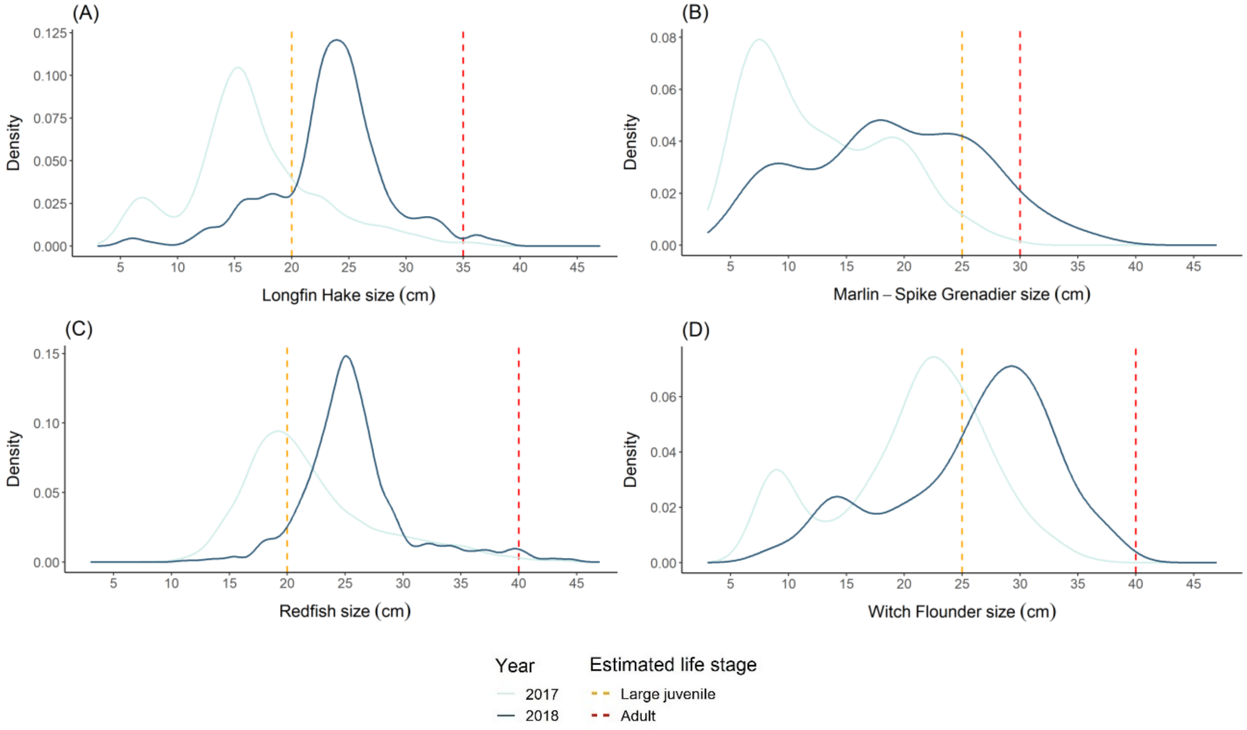
Time of day	Benthic habitat type	Fish taxon			
		Longfin Hake	Marlin-Spike Grenadier	Redfish	Witch Flounder
Day	Barren	141 (455)	147 (266)	249 (856)	130 (300)
	Acti-Ceriant	39 (99)	59 (130)	249 (752)	108 (236)
	Kopho-Acti-Ceriant	0 (2)	0 (4)	0 (15)	0 (5)
	Sclerac-Anthop-Kopho	45 (151)	80 (187)	236 (675)	128 (250)
	Flab-Penna	429 (1130)	222 (499)	597 (1895)	258 (552)
	Penna	141 (363)	75 (148)	195 (639)	215 (439)
Night	Barren	6 (20)	2 (4)	242 (1226)	10 (18)
	Acti-Ceriant	0 (6)	6 (12)	77 (239)	4 (9)
	Kopho-Acti-Ceriant	62 (149)	65 (126)	406 (1217)	97 (171)
	Sclerac-Anthop-Kopho	135 (264)	75 (163)	1784 (3851)	112 (208)
	Flab-Penna	168 (387)	97 (237)	207 (455)	53 (106)
	Penna	33 (68)	28 (56)	61 (135)	38 (68)

	Bottom type	Fish taxon			
		Longfin Hake	Marlin-Spike Grenadier	Redfish	Witch Flounder
	Flat	432 (1106)	381 (783)	2948 (7775)	678 (1346)
	Soft negative	668 (1691)	395 (862)	1197 (3605)	437 (906)
	Soft positive	4 (12)	2 (8)	2 (17)	0 (4)
	Soft mixed	54 (145)	32 (74)	52 (150)	25 (47)
	Hard	41 (140)	46 (105)	104 (408)	13 (59)
	Total	**1199 (3094)**	**856 (1832)**	**4303 (11955)**	**1153 (2362)**

Appendix 3-5 | Size structure per station of (A & B) Redfish, (C & D) Longfin Hake, (E & F) Marlin-Spike Grenadier, (G & H) Witch Flounder according to life stage contribution in 2017 (left) and 2018 (right). Pie charts show the proportion of life stages found at each station. Corresponding size classes (cm) to each life stage for each fish taxon can be found in Table 3-1.



Appendix 3-6 | Frequency distribution of size (total length (TL) in cm) for (A) Longfin Hake, (B) Marlin-Spike Grenadier, (C) Redfish, (D) Witch Flounder in 2017 (light blue) and 2018 (dark blue). The vertical dashed lines represent the estimated transition threshold to the 'Large juvenile' (orange) and 'Adult' (red) life stages of each taxon.



Appendix 3-7 | Results of ANCOVA performed on fish size (TL) between benthic habitat types, years and times of day (ToD), and results of *post-hoc* Tukey's HSD pairwise comparisons when significant differences were found.

Fish taxon	Predictor	Df	Sum Sq	Mean Sq	F	Pr(>F)	Tukey test			
Longfin Hake	Year	1	7540	7540	277.39	< 0.001***	Year	2017	<	2018
	ToD	1	146	146	5.38	0.020552*	ToD	Day	>	Night
	Habitat	5	8128	1626	59.81	< 0.001***				
	Hab:Year	4	1103	276	10.14	< 0.001***				
	Hab:ToD	3	500	167	6.13	< 0.001***				
	Residuals	1180	32075	2.7						
Marlin- Spike Grenadier	Year	1	5726	5726	144.771	< 0.001***	Year	2017	<	2018
	ToD	1	376	376	9.51	0.0611				
	Habitat	5	3103	621	15.69	< 0.001***				
	Hab:Year	4	1234	308	7.8	< 0.001***				
	Hab:ToD	4	373	93	2.36	0.052				
	Residuals	838	33143	40						
Redfish	Year	1	7994	7994	251.83	< 0.001***	Year	2017	<	2018
	ToD	1	98	98	3.08	< 0.001***	ToD	Day	>	Night
	Habitat	5	2727	545	17.18	< 0.001***				
	Hab:Year	4	1234	308	9.72	< 0.001***				
	Hab:ToD	4	843	211	6.64	< 0.001***				
	Residuals	4285	136014	32						
Witch Flounder	Year	1	5902	5902	141.71	< 0.001***	Year	2017	<	2018
	ToD	1	229	229	5.5	0.0792				
	Habitat	5	5209	1042	25.02	< 0.001***				
	Hab:Year	4	1007	252	6.05	< 0.001***				
	Hab:ToD	4	283	71	1.7	0.1476				
	Residuals	1137	47353	42						

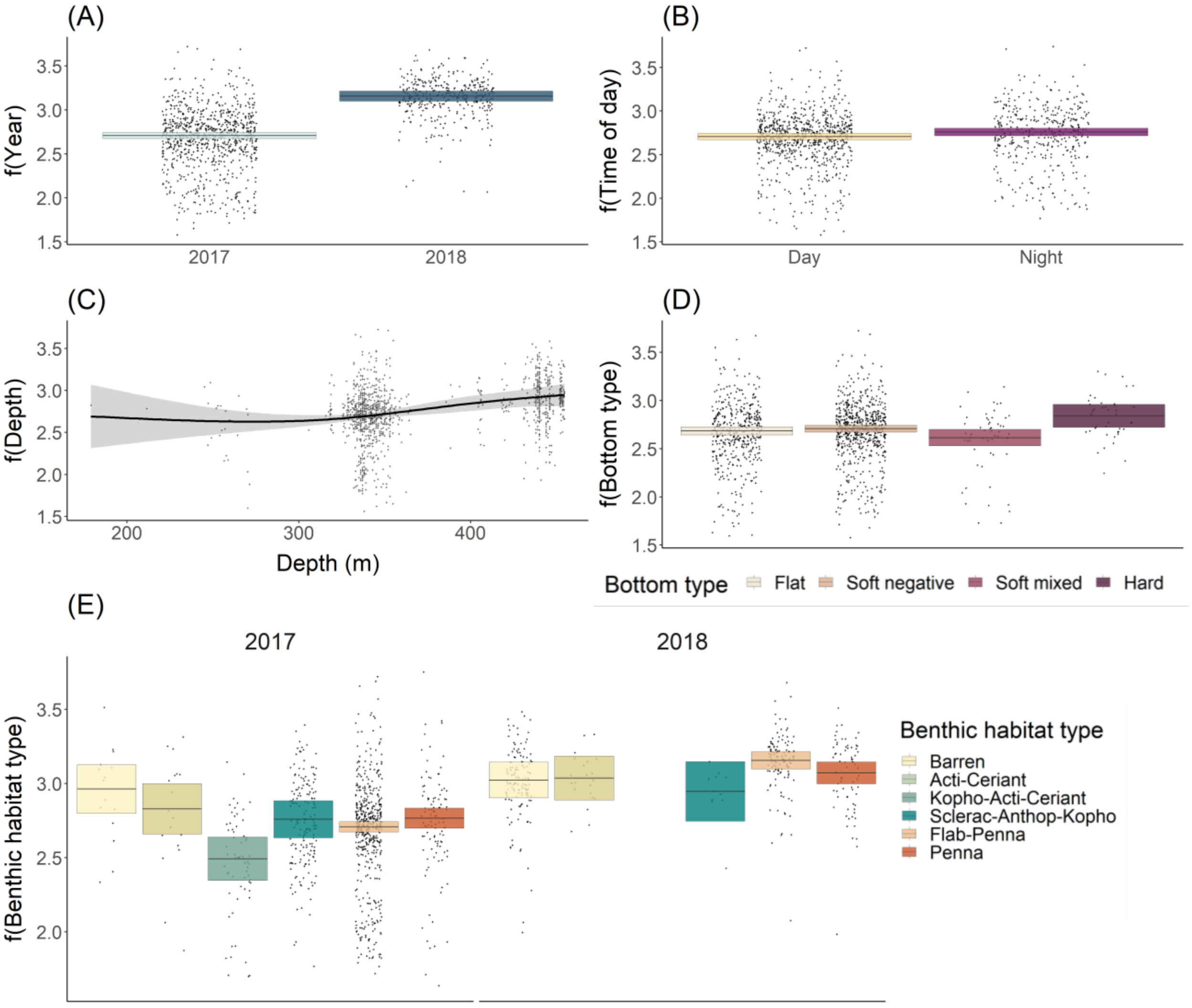
Appendix 3-8 | Longfin Hake Model 1 (Eq. 1) statistics summary. *Flat* and *Barren* were used as reference factors for benthic habitat type and bottom type respectively.

Final formula = Size ~ s(Depth, k = 4) + Year + Time of day + Benthic habitat type * Year + Bottom type

Predictor		**Parametric coefficients**			
		Estimate	SE	t-value	Pr(>|t|)
	(Intercept)	3.00	0.08	37.89	< 0.001***
Year	2018	0.06	0.09	0.69	< 0.001***
Time of day	Night	0.05	0.02	2.21	0.0102*
Bottom type	Soft negative	0.02	0.02	1.08	0.3533
	Soft mixed	-0.07	0.05	-1.53	0.12532
	Hard	0.16	0.06	2.61	0.0039**
Benthic habitat type 2017	Acti-Ceriant	-0.13	0.11	-1.26	0.20889
	Kopho-Acti-Ceriant	-0.47	0.09	-5.14	< 0.001***
	Sclerac-Anthop-Kopho	-0.20	0.08	-2.42	0.01583*
	Flab-Penna	-0.26	0.08	-3.04	< 0.001***
	Penna	-0.20	0.09	-2.27	< 0.001***
Benthic habitat type 2018	Acti-Ceriant	0.15	0.14	1.08	0.2799
	Kopho-Acti-Ceriant	-	-	-	-
	Sclerac-Anthop-Kopho	0.13	0.13	0.99	0.32071
	Flab-Penna	0.39	0.09	4.28	< 0.001***
	Penna	0.25	0.10	2.54	0.01131*

Predictor		**Approximate significance of smooth terms**			
		edf	Ref.df	F	p-value
	Depth	2.6	3	0.79	0.009**
		R-sq.(adj) = 0.36			
		Deviance explained = 30.4%			

Appendix 3-9 | Smooth and parametric effect plots of Longfin Hake size (TL) in relation to (A) year, (B) time of day, (C) depth, (D) bottom type, (E) benthic habitat type, extracted from Model 1 (Eq. 1). The grey area in Figure C corresponds to the 95% confidence interval. The dots represent the partial residuals. Default median values or most common categories held constant: depth: 345 m, year: 2017, time of day: day, benthic habitat type: Sclerac-Penna, bottom type: soft negative.

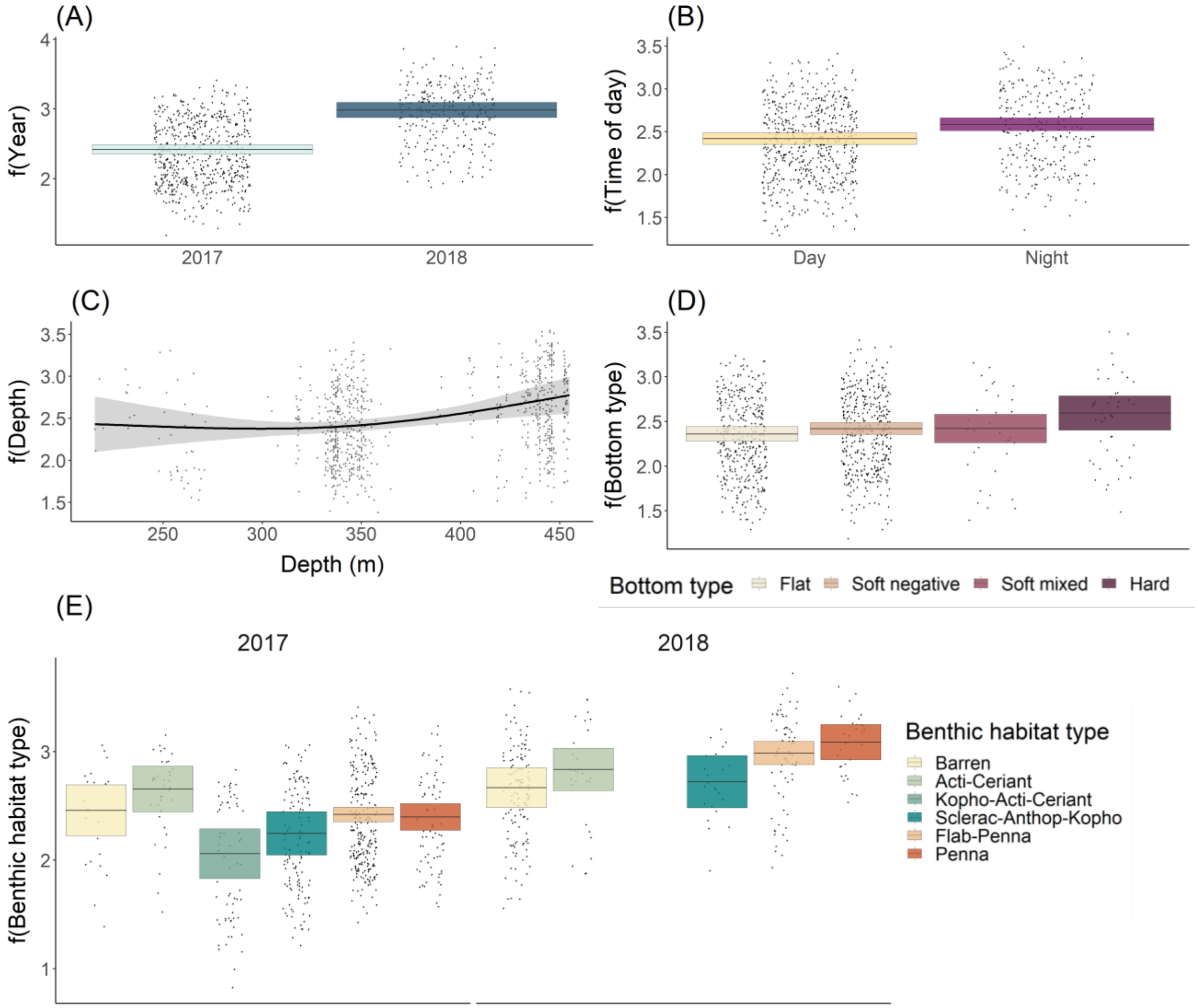


Appendix 3-10 | Marlin-Spike Grenadier Model 1 (Eq. 1) statistics summary. *Flat* and *Barren* were used as reference factors for benthic habitat type and bottom type respectively.

Final formula = Size ~ s(Depth, k = 3) + Year + Time of day + Benthic habitat type * Year + Bottom type

Predictor		**Parametric coefficients**			
		Estimate	SE	t-value	Pr(>|t|)
	(Intercept)	2.52	0.10	25.29	< 0.001***
Year	2018	0.21	0.11	1.92	< 0.001***
Time of day	Night	0.17	0.04	4.09	< 0.001***
Bottom type	Soft negative	0.06	0.04	1.67	0.042098*
	Soft mixed	0.06	0.08	0.73	0.640017
	Hard	0.23	0.09	2.49	0.019708*
Benthic habitat type 2017	Acti-Ceriant	0.20	0.12	1.65	0.099354
	Kopho-Acti-Ceriant	-0.40	0.12	-3.36	< 0.001***
	Sclerac-Anthop-Kopho	-0.21	0.11	-2.01	0.046564*
	Flab-Penna	-0.04	0.12	-0.31	0.028324*
	Penna	-0.06	0.13	-0.48	< 0.001***
Benthic habitat type 2018	Acti-Ceriant	-0.03	0.16	-0.17	0.84061
	Kopho-Acti-Ceriant	-	-	-	-
	Sclerac-Anthop-Kopho	0.27	0.15	1.81	0.074273
	Flab-Penna	0.36	0.12	2.89	0.003551**
	Penna	0.48	0.14	3.39	< 0.001***
Predictor		**Approximate significance of smooth terms**			
		edf	Ref.df	F	p-value
	Depth	1.8	2	1.46	0.0544
		R-sq.(adj) = 0.24 Deviance explained = 23%			

Appendix 3-11 | Smooth and parametric effect plots of Marlin-Spike Grenadier size (TL) in relation to (A) year, (B) time of day, (C) depth, (D) bottom type, (E) benthic habitat type, extracted from Model 1 (Eq. 1). The grey area in Figure C corresponds to the 95% confidence interval. The dots represent the partial residuals. Default median values or most common categories held constant: depth: 351 m, year: 2017, time of day: day, benthic habitat type: Flab-Penna, bottom type: soft negative.

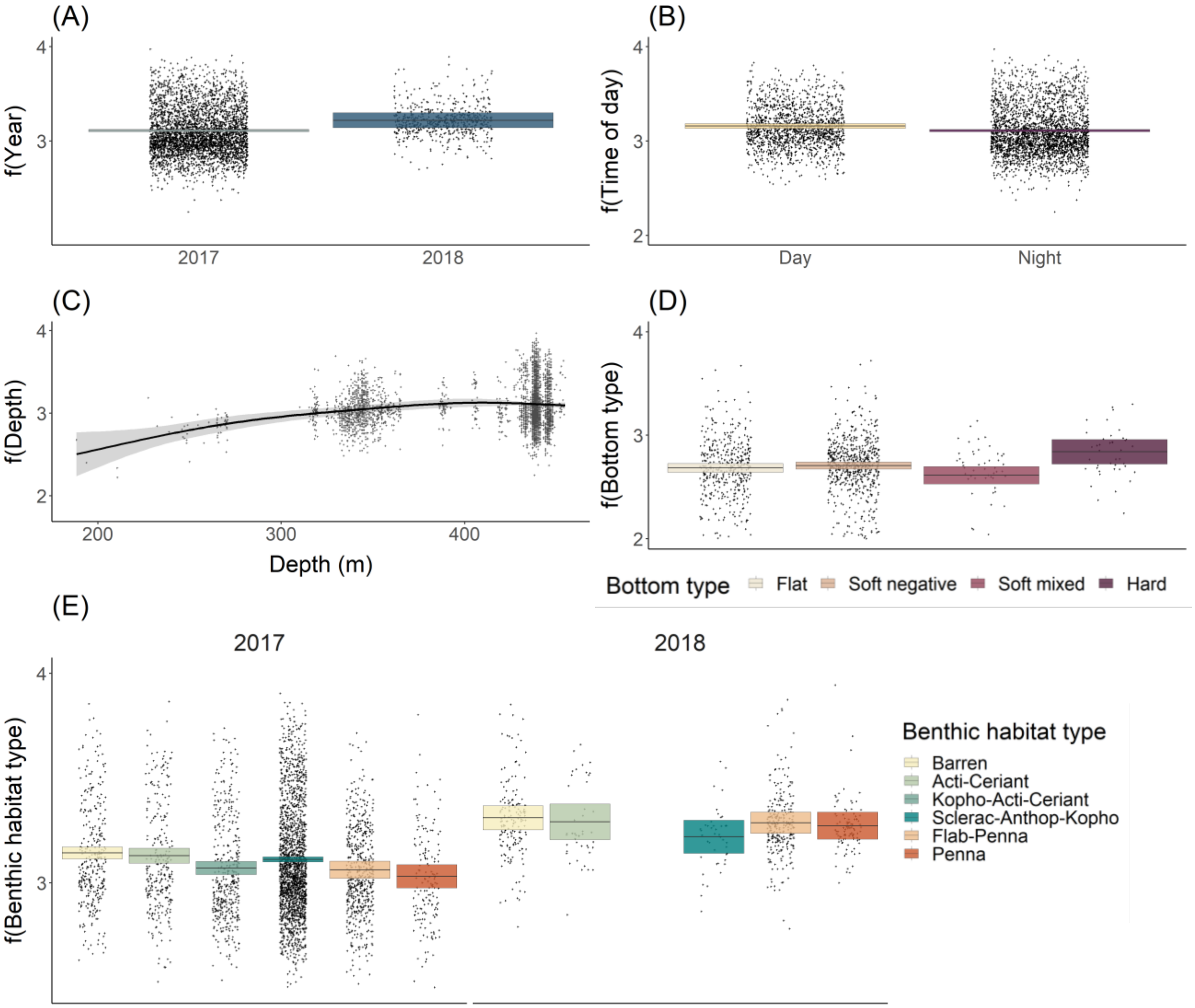


Appendix 3-12 | Redfish Model 1 (Eq. 1) statistics summary. *Flat* and *Barren* were used as reference factors for benthic habitat type and bottom type respectively.

Final formula = Size ~ s(Depth, k = 6) + Year + Time of day + Benthic habitat type * Year + Bottom type

Predictor		**Parametric coefficients**			
		Estimate	SE	t-value	Pr(>|t|)
	(Intercept)	3.17	0.02	190.39	< 0.001***
Year	2018	0.17	0.03	5.43	< 0.001***
Time of day	Night	-0.05	0.01	-3.82	< 0.001***
Bottom type	Soft negative	-0.04	0.01	-4.29	< 0.001***
	Soft mixed	-0.07	0.04	-1.83	0.0394**
	Hard	-0.03	0.03	-1.08	< 0.001***
Benthic habitat type 2017	Acti-Ceriant	-0.01	0.02	-0.62	0.593045
	Kopho-Acti-Ceriant	-0.07	0.02	-3.37	< 0.001***
	Sclerac-Anthop-Kopho	-0.03	0.02	-2.04	0.049954*
	Flab-Penna	-0.08	0.02	-3.35	< 0.001***
	Penna	-0.11	0.03	-3.63	< 0.001***
Benthic habitat type 2018	Acti-Ceriant	-0.01	0.05	-0.12	0.912467
	Kopho-Acti-Ceriant	-	-	-	-
	Sclerac-Anthop-Kopho	-0.06	0.05	-1.22	0.281385
	Flab-Penna	0.06	0.03	1.64	0.012413*
	Penna	0.07	0.04	1.70	0.006698**
Predictor		**Approximate significance of smooth terms**			
		edf	Ref.df	F	p-value
	Depth	4.4	5	16.14	< 0.001***
		R-sq.(adj) = 0.1 Deviance explained = 11.5%			

Appendix 3-13 | Smooth and parametric effect plots of Redfish size (TL) in relation to (A) year, (B) time of day, (C) depth, (D) bottom type, (E) benthic habitat type, extracted from Model 1 (Eq. 1). The grey area in Figure C corresponds to the 95% confidence interval. The dots represent the partial residuals. Default median values or most common categories held constant: depth: 438 m, year: 2017, time of day: night, benthic habitat type: Sclerac-Anthop-Kopho, bottom type: flat.

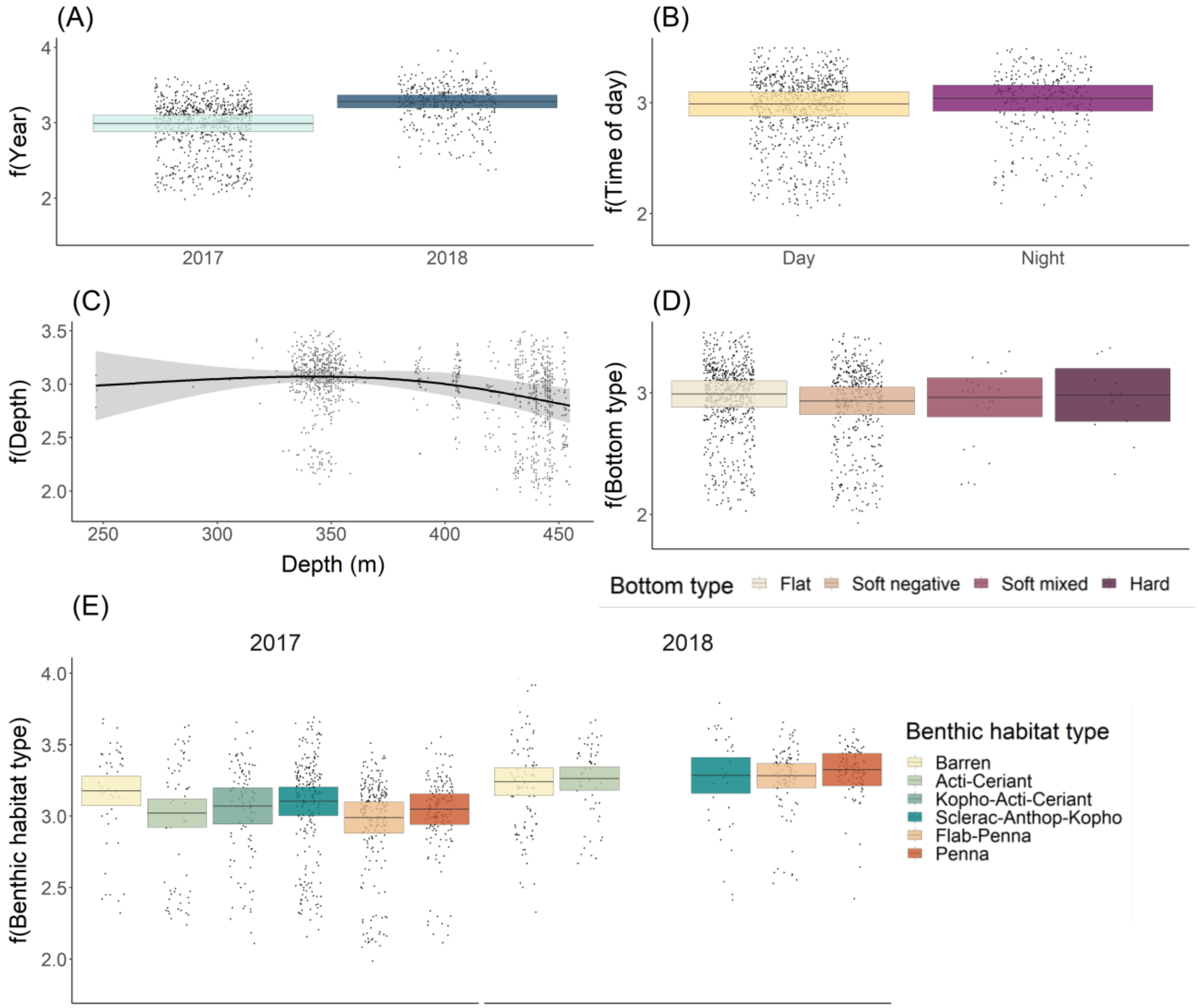


Appendix 3-14 | Witch Flounder Model 1 (Eq. 1) statistics summary. *Flat* and *Barren* were used as reference factors for benthic habitat type and bottom type respectively.

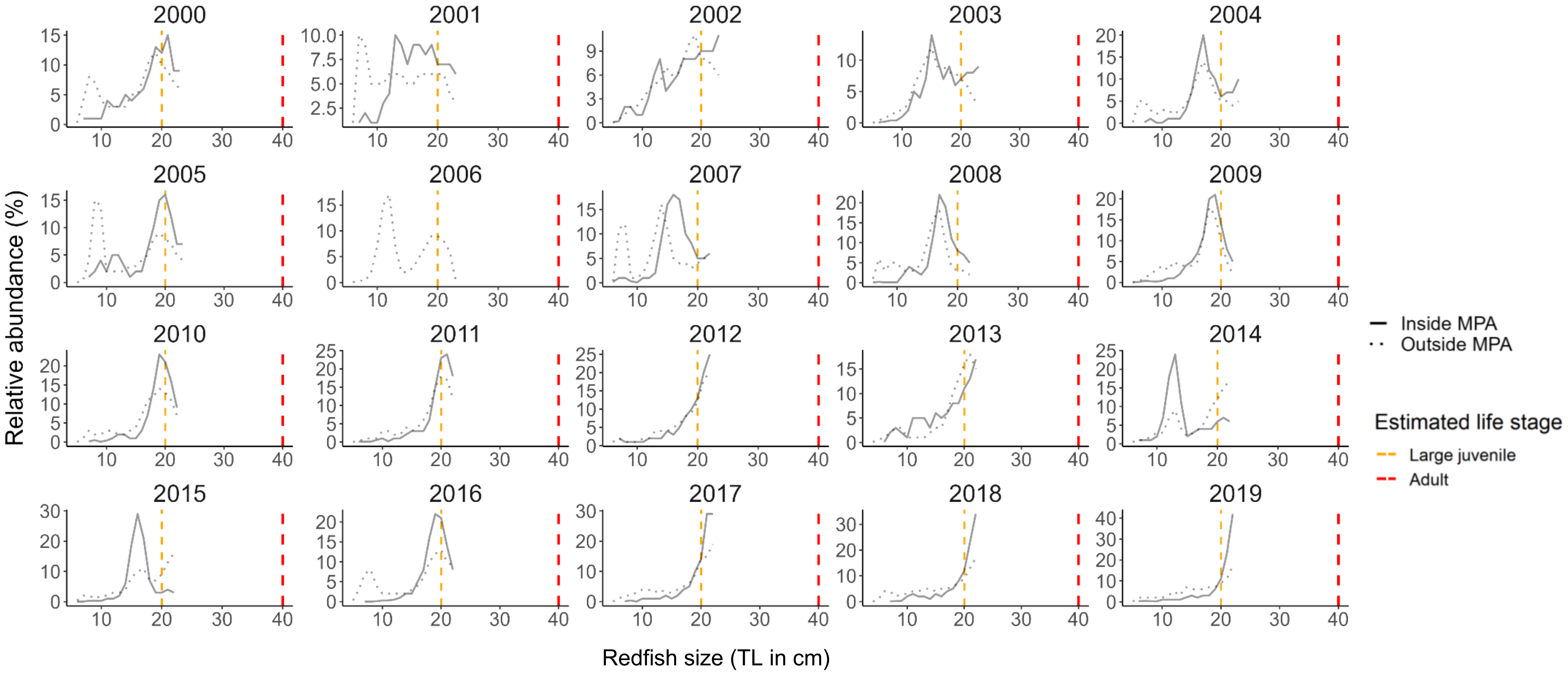
Final formula = Size ~ s(Depth, k = 4) + Year + Time of day + Benthic habitat type + Bottom type

Predictor		**Parametric coefficients**			
		Estimate	SE	t-value	Pr(>|t|)
	(Intercept)	3.15	0.05	62.29	< 0.001***
Year	2018	0.06	0.06	1.17	< 0.001***
Time of day	Night	0.05	0.03	2.03	0.0424*
Bottom type	Soft negative	-0.06	0.02	-2.73	0.00563**
	Soft mixed	-0.03	0.06	-0.43	0.59216
	Hard	-0.01	0.09	-0.08	0.92467
Benthic habitat type 2017	Acti-Ceriant	-0.16	0.06	-2.62	0.00867**
	Kopho-Acti-Ceriant	-0.11	0.06	-1.73	0.002551**
	Sclerac-Anthop-Kopho	-0.07	0.05	-1.42	0.012548*
	Flab-Penna	-0.19	0.08	-2.47	0.00979**
	Penna	-0.13	0.07	-1.71	0.04156*
Benthic habitat type 2018	Acti-Ceriant	0.18	0.09	2.05	0.04233*
	Kopho-Acti-Ceriant	-	-	-	-
	Sclerac-Anthop-Kopho	0.12	0.08	1.49	0.04848*
	Flab-Penna	0.23	0.07	3.22	0.0013**
	Penna	0.21	0.07	3.17	0.00156***
Predictor		**Approximate significance of smooth terms**			
		edf	Ref.df	F	p-value
	Depth	2.6	3	1.32	0.0853
		R-sq.(adj) = 0.21 Deviance explained = 20%			

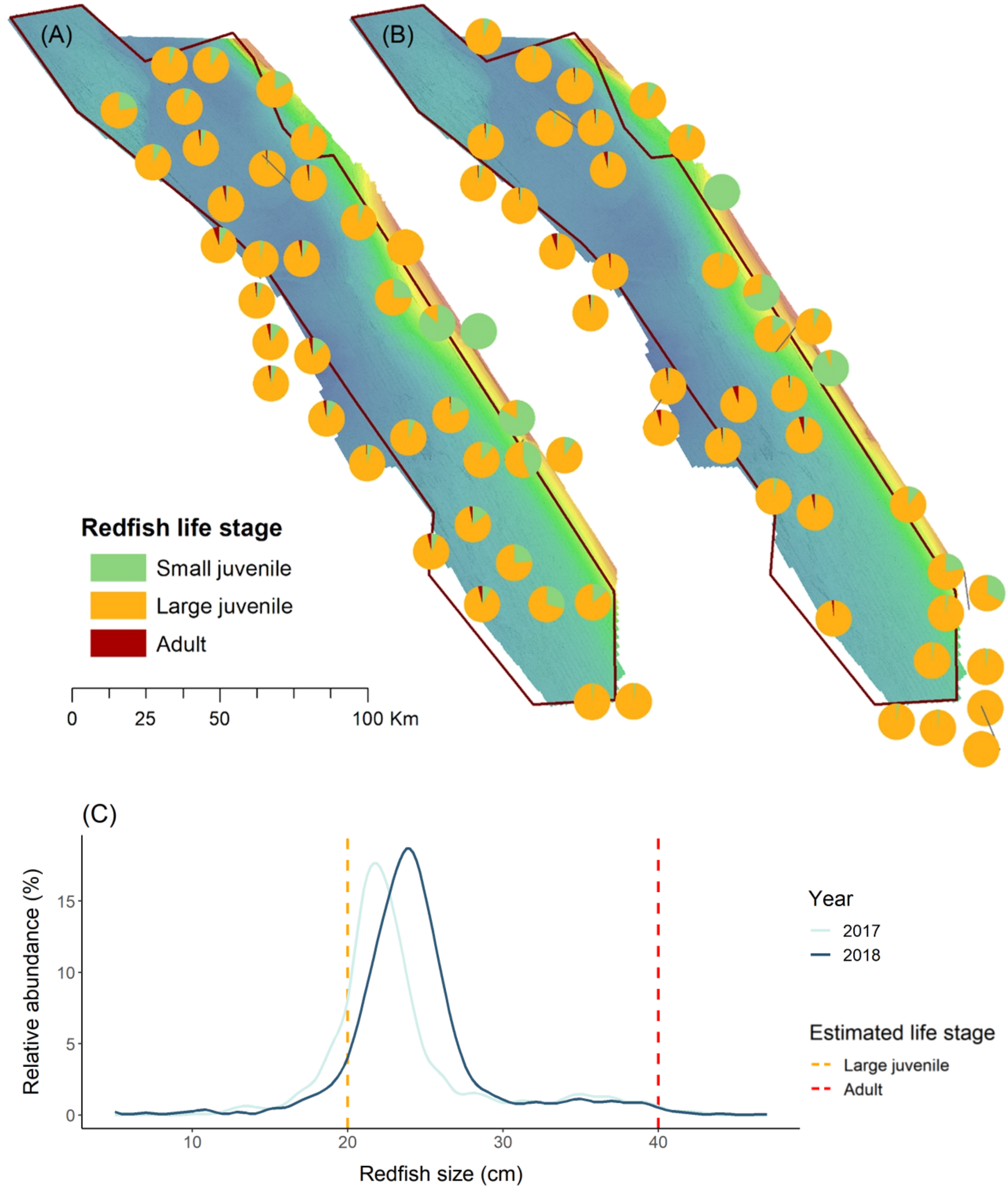
Appendix 3-15 | Smooth and parametric effect plots of Witch Flounder size (TL) in relation to (A) year, (B) time of day, (C) depth, (D) bottom type, (E) benthic habitat type, extracted from Model 1 (Eq. 1). The grey area in Figure C corresponds to the 95% confidence interval. The dots represent the partial residuals. Default median values or most common categories held constant: depth: 351 m, year: 2017, time of day: day, benthic habitat type: Flab-Penna, bottom type: soft negative.



Appendix 3-16 | Redfish size (TL) frequency distribution (percent of fish measured) assessed by DFO bottom-trawls between 2000 and 2019 inside and around the Laurentian Channel MPA (designated in 2019) on the shelf off the southern shore of Newfoundland, Canada. The vertical dashed lines represent the estimated transition threshold to the 'Large juvenile' (orange) and 'Adult' (red) life stages of the taxon.



Appendix 3-17 | Redfish size structure according to life stage contribution per station assessed by DFO trawls in April/May in (A) 2017 and (B) 2018. Pie charts show the proportion of life stages found at each station. (C) Redfish size (TL) frequency distribution (percent of fish measured) assessed by DFO trawls in 2017 (light blue) and 2018 (dark blue). The vertical dashed lines represent the estimated transition threshold to the 'Large juvenile' (orange) and 'Adult' (red) life stages of the taxon. Small juvenile: 5-20 cm in total length, Large juvenile: 20-40 cm, Adult: 40-54 cm.



Appendix 4-1 | Number of fish observed (and relative percentage) for the nine taxa selected for analysis per activity, altitude and locomotion category (fish *in-situ* behavior). The description of each category is presented in Table 4-1. BM: Body movement, Mvt: Movement, SF: Seafloor, UVS: Underwater video system.

		Fish taxon										
Attribute	**Category**	Redfish	Longfin Hake	Witch Flounder	Marlin-Spike Grenadier	Teleostei sp1	Skate sp1	Black Dogfish	Pollock	Atlantic Cod	**Total observed**	**Relative percentage**
Activity	No activity	4800	2692	2353	69	305	217	9	1	1	10447	63
	Resting	2375	16	0	0	0	0	0	0	0	2391	14
	Low BM	222	99	1	866	39	1	0	1	0	1229	7
	Medium BM	50	77	0	726	37	3	1	0	0	894	5
	High BM	441	187	3	165	814	7	35	23	12	1687	10
Altitude	Buried	7	14	0	1	2	1	0	0	0	25	<1
	On seafloor	7266	2760	2357	57	262	224	8	1	1	12936	78
	Above SF	332	291	0	1761	231	3	35	9	8	2670	16
	UVS level	165	6	0	5	467	0	1	6	3	653	4
	Above UVS	118	0	0	2	233	0	1	9	1	364	2
Locomotion	No mvt.	7201	2715	2354	75	307	219	9	1	1	12882	77
	Hovering	180	142	1	1609	105	1	0	1	0	2039	12
	Drifting	1	2	0	41	7	0	0	0	0	51	<1
	Swimming	506	212	2	101	776	8	36	23	12	1676	10

Appendix 4-2 | Number of fish observed (and relative percentage) for the nine taxa selected for analysis per depth range (m), time of day, benthic habitat type and bottom type (environmental factors). The description of each category is presented in Table 4-3.

Factor	**Category**	**Fish taxon**									**Total observed**	**Relative percentage**
		Redfish	Longfin Hake	Witch Flounder	Marlin-Spike Grenadier	Teleostei sp1	Skate sp1	Black Dogfish	Pollock	Atlantic Cod		
Depth	178-200	8	1	0	1	0	0	0	1	0	11	<1
	200-250	36	21	9	35	0	0	1	1	0	103	1
	250-300	140	92	8	59	1	0	0	0	0	300	2
	300-350	1970	1688	806	788	807	81	0	10	3	6153	37
	350-400	747	309	363	166	238	24	0	3	0	1850	11
	400-455	4977	960	1165	777	149	123	44	10	10	8215	49
Time of day	Day	4194	2188	1781	1233	1104	146	44	19	7	10716	64
	Night	3694	883	576	593	91	82	1	6	6	5932	36
Benthic habitat type	Barren	1066	480	322	287	125	23	40	9	1	2353	14
	Acti	926	106	246	141	95	18	4	2	3	1541	9
	Kopho	877	147	172	127	7	16	1	0	0	1347	8
	Sclerac	2483	401	455	334	33	70	0	4	7	3787	23
	Flab	1905	1509	657	733	586	81	0	8	2	5481	33
	Penna	631	428	505	204	349	20	0	2	0	2139	13
Bottom type	Flat	4507	1100	1343	780	730	127	18	13	6	8624	52
	Soft neg	2852	1675	904	859	423	91	22	7	6	6839	41
	Soft pos	13	12	4	8	4	1	0	0	0	42	<1
	Soft mixed	144	145	47	74	30	8	3	1	0	452	3
	Hard	372	139	59	105	8	1	2	4	1	691	4

Appendix 4-3 | Number of fish observed (and relative percentage) for the nine taxa selected for analysis per fish total density range, life stage, distance to UVS and reaction timing (fish-related factors). The description of each category is presented in Table 4-3.

Factor	Category	Fish taxon									Total observed	Relative percentage
		Redfish	Longfin Hake	Witch Flounder	Marlin-Spike Grenadier	Teleostei sp1	Skate sp1	Black Dogfish	Pollock	Atlantic Cod		
Fish total density	Very low	2684	1392	1360	846	456	92	39	11	4	5011	30
	Low	1699	898	579	538	357	79	6	5	7	4168	25
	Medium	1722	597	297	347	268	38	0	5	1	3275	20
	High	1162	149	96	82	94	16	0	0	1	1600	10
	Very high	621	35	25	13	20	3	0	4	0	721	4
Fish life stage	Small juv.	1643	726	772	696	-	-	-	-	-	3837	51
	Large juv.	2623	462	63	457	-	-	-	-	-	3605	48
	Adult	37	11	21	0	-	-	-	-	-	69	1
Distance to UVS	Close	4453	1785	1829	1198	772	138	14	10	7	10206	61
	Side	3224	1235	501	589	232	80	25	6	1	5893	35
	Far	211	51	27	39	191	10	6	9	5	462	3
Reaction timing	Before	74	11	2	11	138	9	1	1	2	249	4
	During	2363	1205	116	643	803	142	41	6	3	5322	92
	After	96	4	29	34	23	4	0	1	0	191	3
	Before-During	1	0	0	0	1	0	0	1	2	5	<1
	During-After	5	0	0	0	1	2	0	8	3	19	<1
	Before-After	0	0	0	0	0	0	1	3	2	6	<1

Appendix 4-4 | Number of fish observed (and relative percentage) for the nine taxa selected for analysis per reaction type and response behavior to UVS. The description of each category is presented in Table 4-2.

Reaction type	**Fish taxon**									**Total observed**	**Relative percentage**
Response behavior	Redfish	Longfin Hake	Witch Flounder	Marlin-Spike Grenadier	Teleostei sp1	Skate sp1	Black Dogfish	Pollock	Atlantic Cod		
Avoidance	**94**	**60**	**48**	**150**	**33**	**124**	**6**	**2**	**0**	**517**	**3**
Escaping	94	43	40	149	32	45	6	2	0	411	2
Hiding	0	17	8	1	1	79	0	0	0	106	1
Neutral	**7559**	**2996**	**2301**	**1658**	**1134**	**99**	**31**	**7**	**1**	**15786**	**95**
No reaction	5349	1851	2210	1138	229	71	2	5	1	10856	65
Minor reaction	2205	1145	91	520	30	26	29	2	0	4048	24
Major reaction	5	0	0	0	875	2	0	0	0	882	5
Attraction	**235**	**15**	**8**	**18**	**28**	**5**	**8**	**16**	**12**	**345**	**2**
Attraction	180	12	2	16	21	3	6	4	4	248	1
Minor follow	46	2	6	2	0	0	0	0	1	57	<1
Major follow	0	0	0	0	0	0	0	10	2	12	<1
Multi	**9**	**1**	**0**	**0**	**7**	**2**	**2**	**2**	**5**	**28**	**<1**

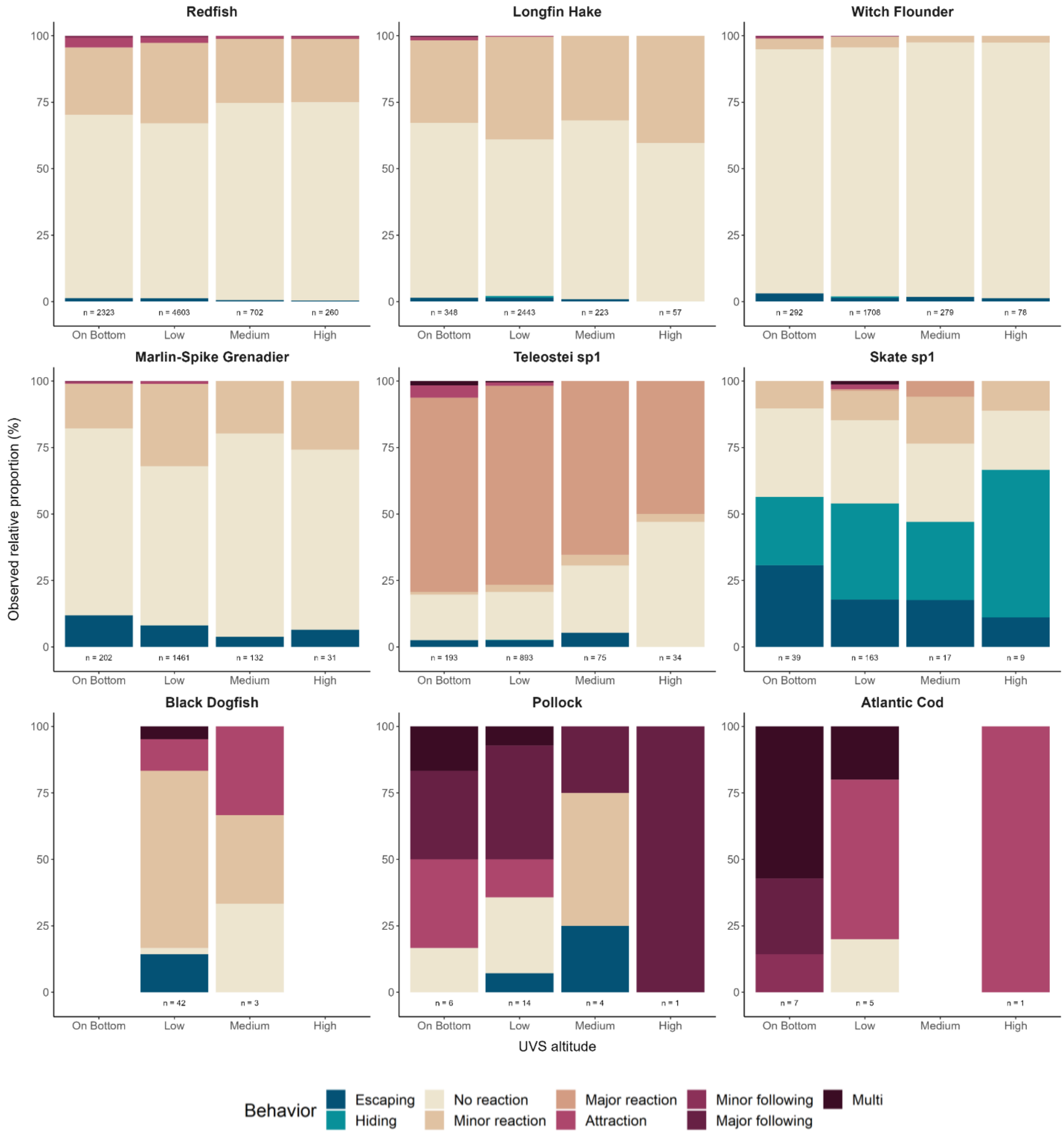
Appendix 4-5 | Number of fish observed (and relative percentage) for the nine taxa selected for analysis per UVS type, speed and altitude, and survey operation/UVS attitude (technical factors). The description of each category is presented in Table 4-3.

Factor	Category	Fish taxon									Total observed	Relative percentage
		Redfish	Longfin Hake	Witch Flounder	Marlin-Spike Grenadier	Teleostei sp1	Skate sp1	Black Dogfish	Pollock	Atlantic Cod		
UVS type	ROPOS	5908	1968	1409	1286	1174	181	1	21	13	11961	72
	CAMPOD	1980	1103	948	540	21	47	44	4	0	4687	28
UVS speed	No motion	284	126	110	53	65	6	5	2	1	652	4
	Low	5719	2148	1527	1370	998	190	18	20	12	12002	72
	Medium	1216	487	420	232	15	17	10	1	0	2398	14
	High	669	310	300	171	117	15	12	2	0	1596	10
UVS altitude	On bottom	2323	348	292	202	193	39	0	6	7	3410	20
	Low	4604	2447	1712	1463	893	163	42	14	5	11343	68
	Medium	704	223	279	132	75	17	3	4	0	1437	9
	High	257	53	74	29	34	9	0	1	1	458	3
Survey operation	On bottom	89	11	15	10	71	1	0	0	0	197	1
	Investigating	25	19	12	14	23	3	0	1	0	97	1
	Sampling	7	5	0	1	25	1	0	0	0	39	<1
	Maint.	118	24	31	9	83	2	0	0	2	269	2
	Transect	5362	2407	1873	1439	723	167	45	17	7	12040	72
	Transit	2000	558	374	329	229	49	0	3	4	3546	21
	Drifting	2	2	3	2	0	0	0	0	0	9	<1
	Off bottom	285	45	49	22	41	5	0	4	0	451	3

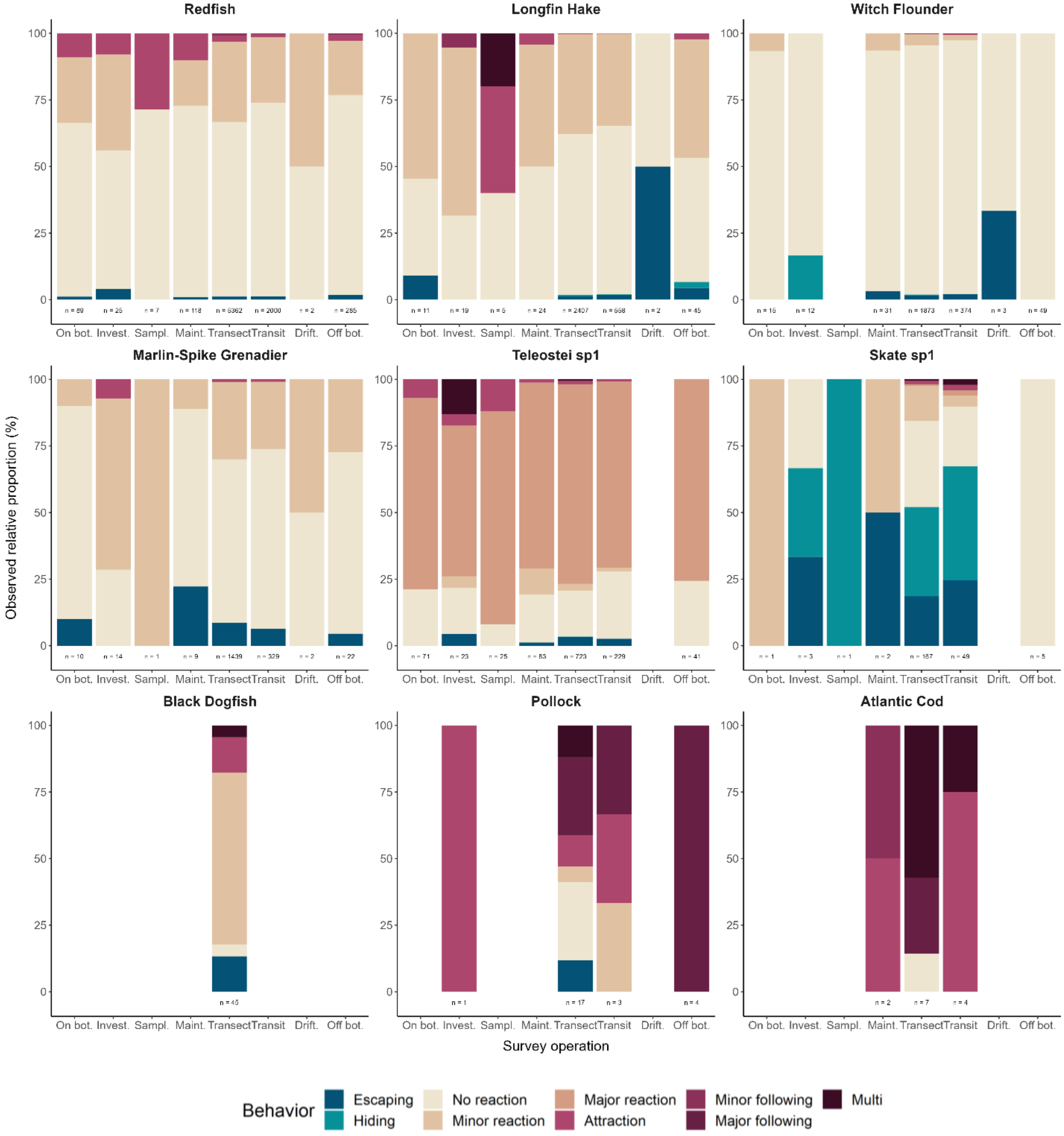
Appendix 4-6 | Patterns of observed response behaviors of fish in relation to UVS type per fish taxon. n = number of fish observed per category. See Table 4-2 for detail of fish reactions.

Appendix 4-7 | Patterns of observed response behaviors of fish in relation to UVS speed per fish taxon. n = number of fish observed per category. See Table 4-2 for detail of fish reactions and Table 4-3 for detail of UVS speed categories.

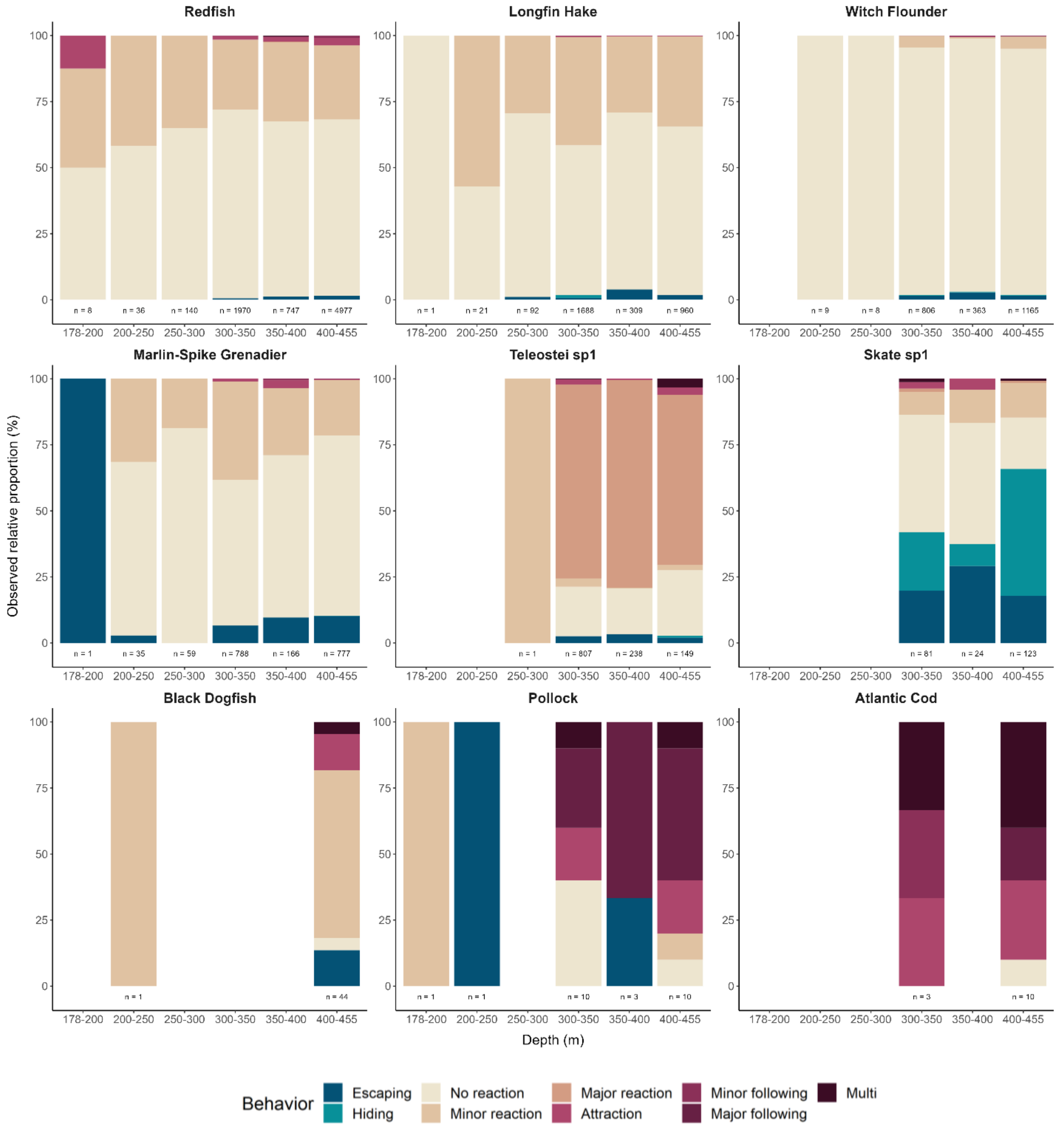
Appendix 4-8 | Patterns of observed response behaviors of fish in relation to UVS altitude per fish taxon. n = number of fish observed per category. See Table 4-2 for detail of fish reactions and Table 4-3 for detail of UVS altitude categories.



Appendix 4-9 | Patterns of observed response behaviors of fish in relation to survey operation per fish taxon. n = number of fish observed per category. See Table 4-2 for detail of fish reactions and Table 4-3 for detail of survey operation/UVS attitude categories.

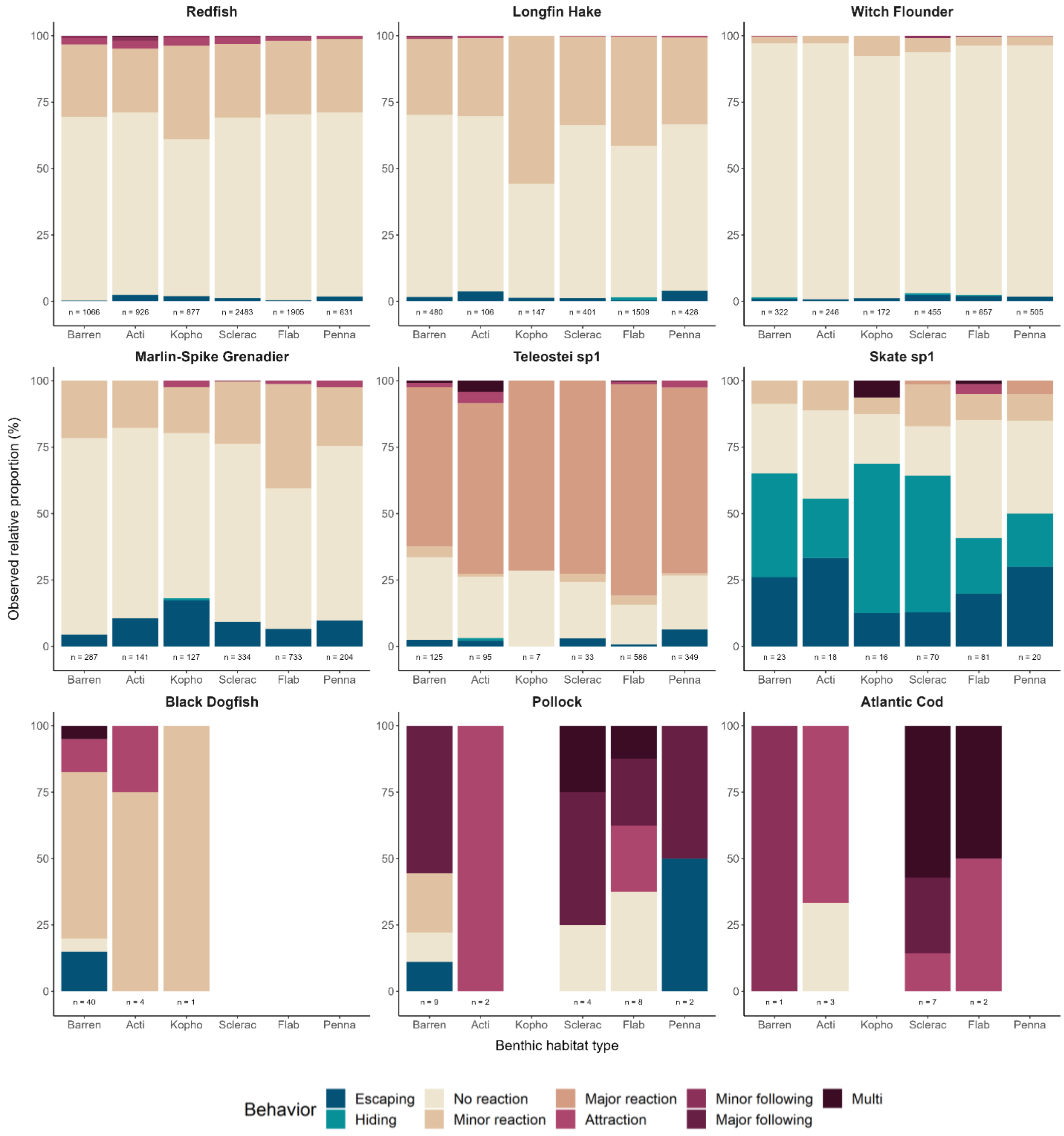


Appendix 4-10 | Patterns of observed response behaviors of fish in relation to depth per fish taxon. n = number of fish observed per category. See Table 4-2 for detail of fish reactions.

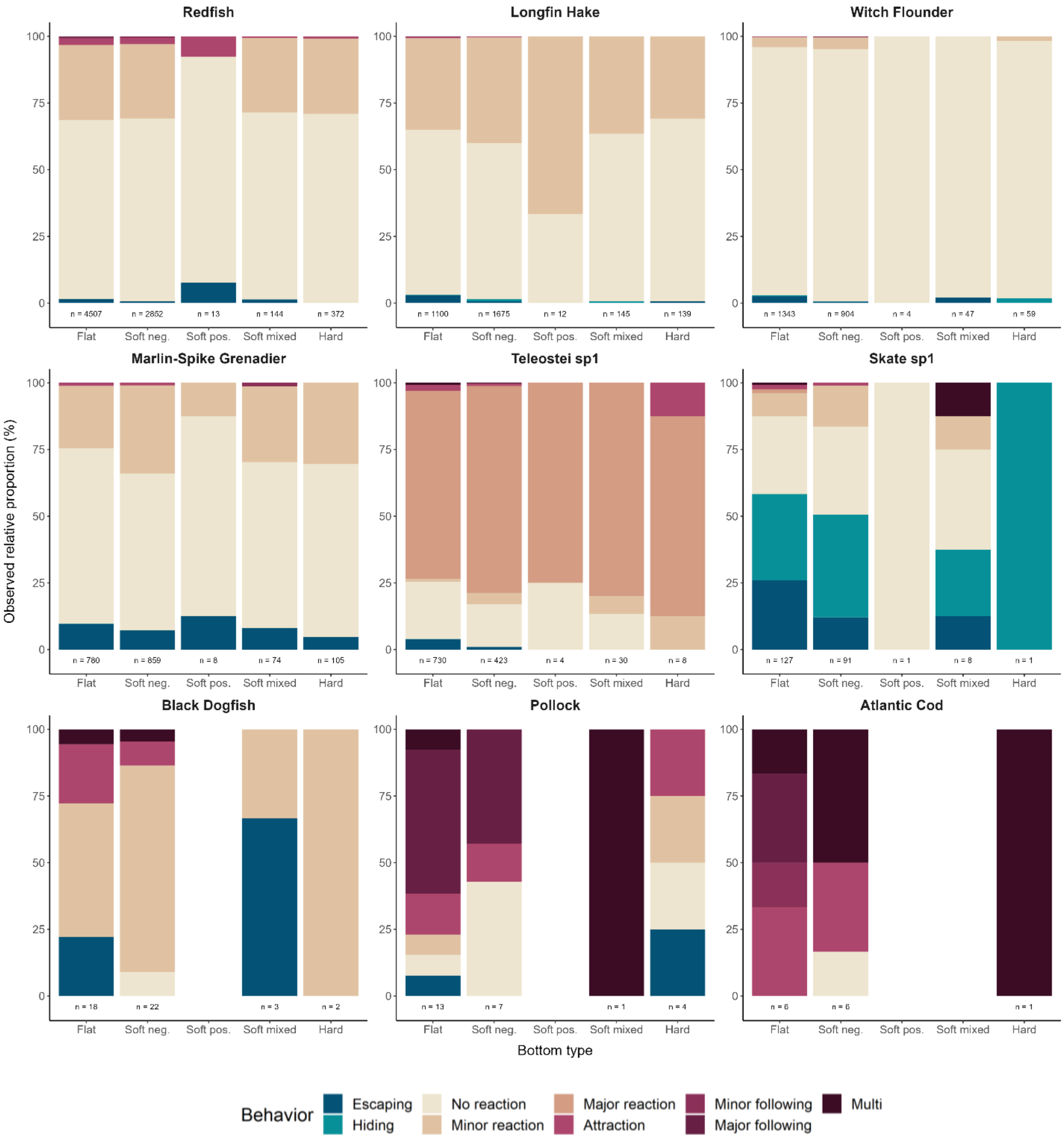


Appendix 4-11 | Patterns of observed response behaviors of fish in relation to time of day per fish taxon. n = number of fish observed per category. See Table 4-2 for detail of fish reactions and Table 4-3 for detail of time of day categories.

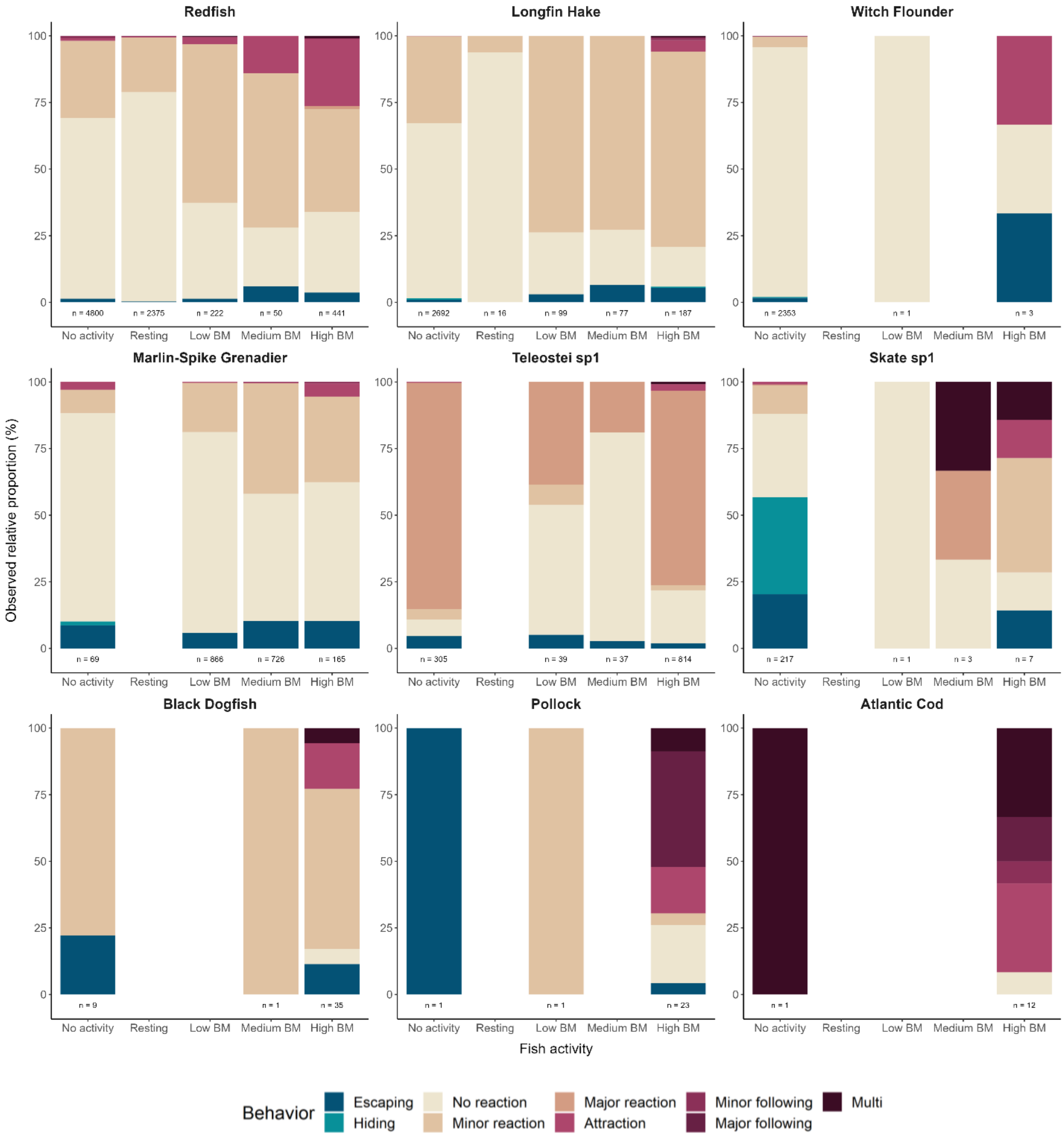
Appendix 4-12 | Patterns of observed response behaviors of fish in relation to benthic habitat type per fish taxon. See Table 4-2 for detail of fish reactions and Table 4-3 of benthic habitat types.



Appendix 4-13 | Patterns of observed response behaviors of fish in relation to bottom type per fish taxon. See Table 4-2 for detail of fish reactions and Table 4-3 of bottom types.

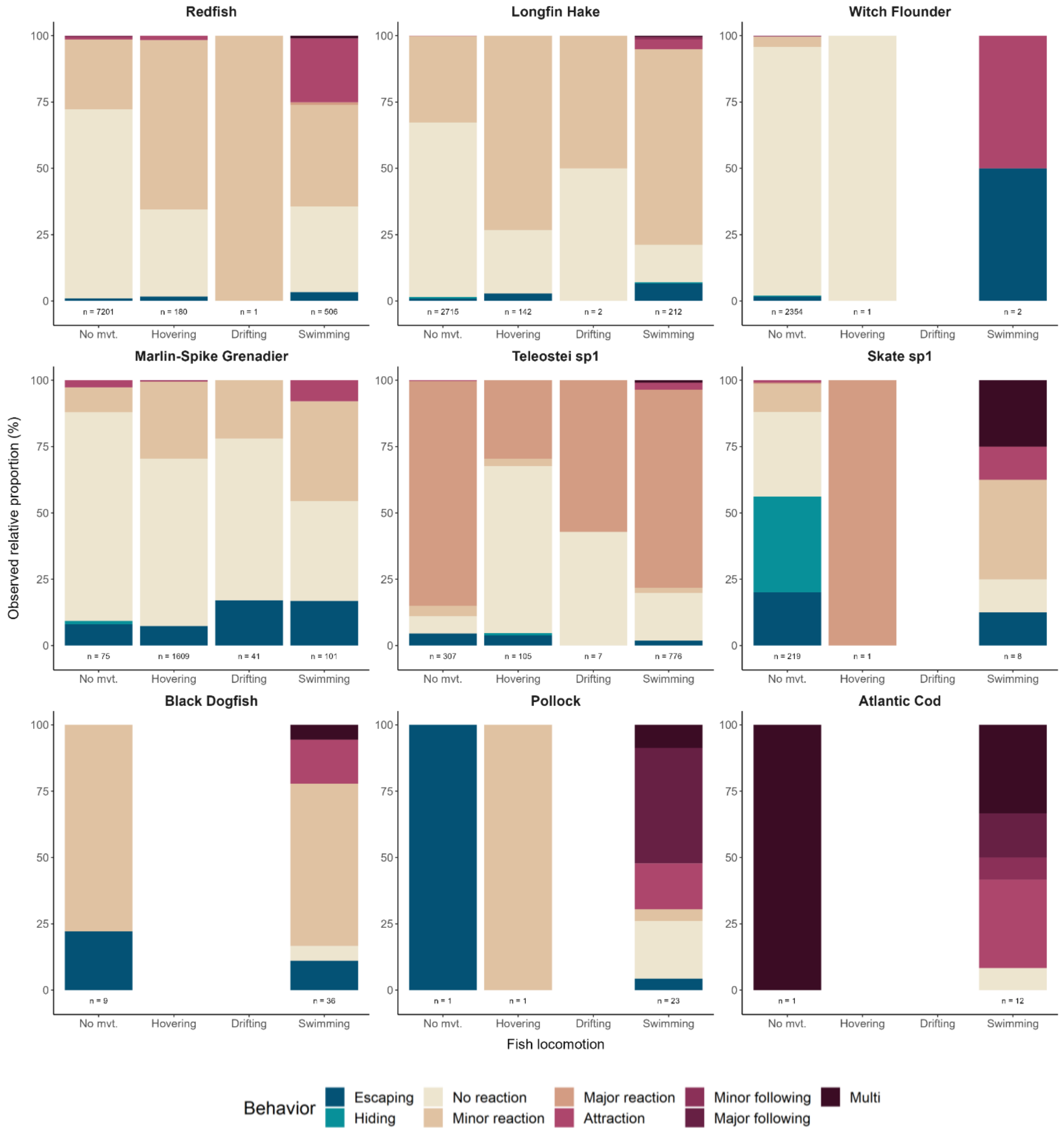


Appendix 4-14 | Patterns of observed response behaviors of fish in relation to fish activity per fish taxon. See Table 4-2 for detail of fish reactions and Table 4-3 of fish activity categories.

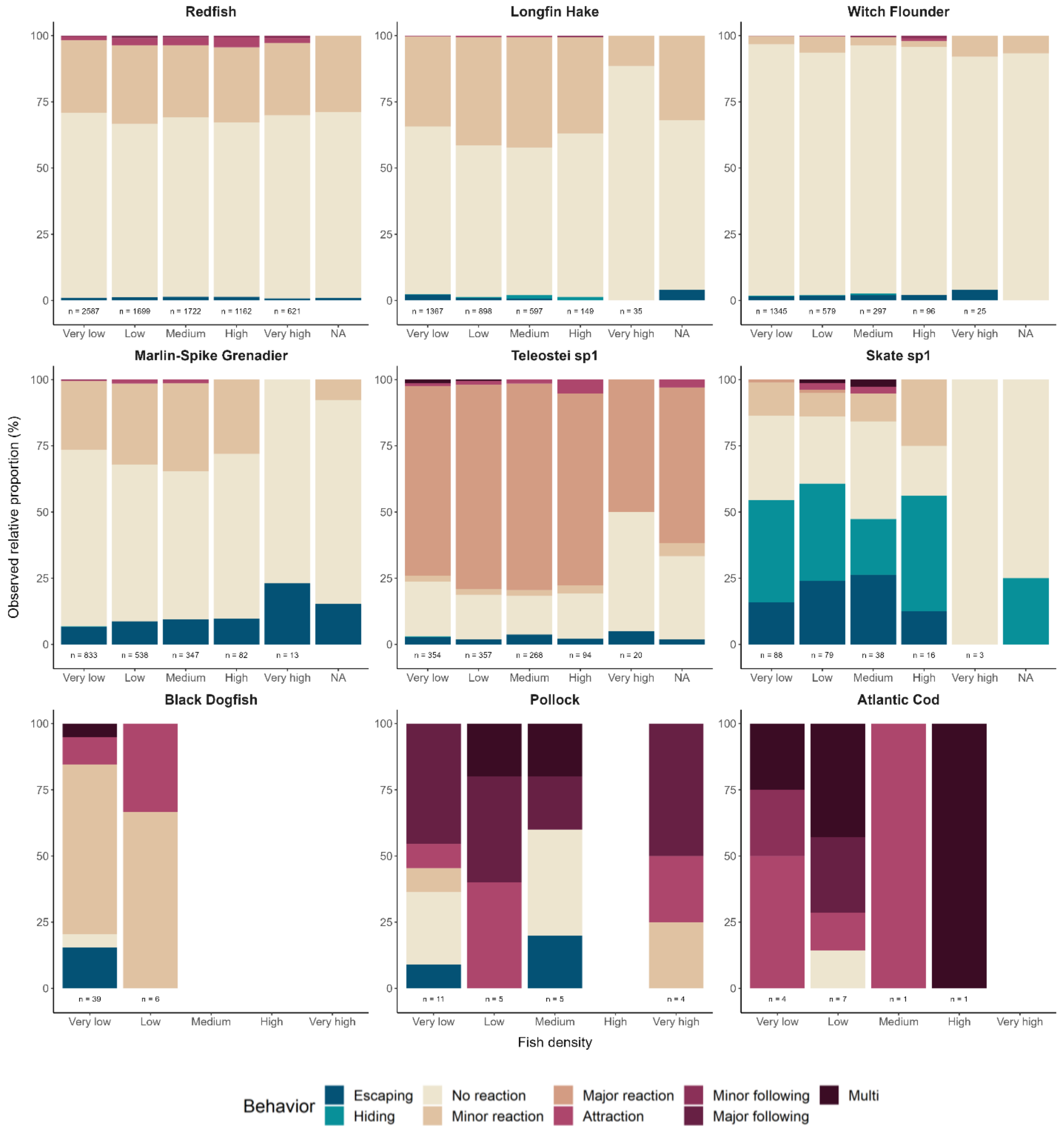


Appendix 4-15 | Patterns of observed response behaviors of fish in relation to fish altitude per fish taxon. See Table 4-2 for detail of fish reactions and Table 4-3 of fish altitude categories.

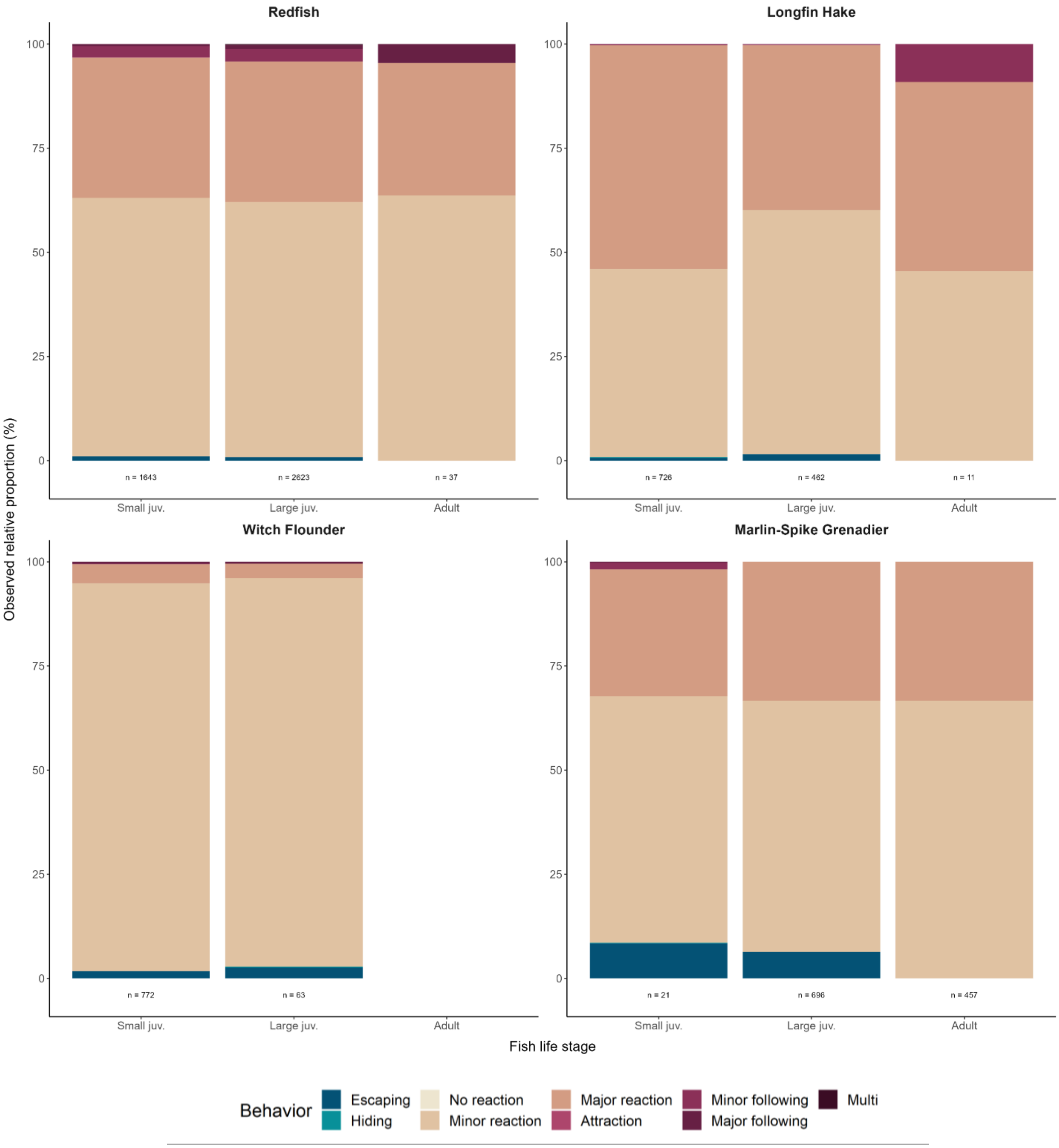
Appendix 4-16 | Patterns of observed response behaviors of fish in relation to fish locomotion per fish taxon. See Table 4-2 for detail of fish reactions and Table 4-3 of fish locomotion categories.



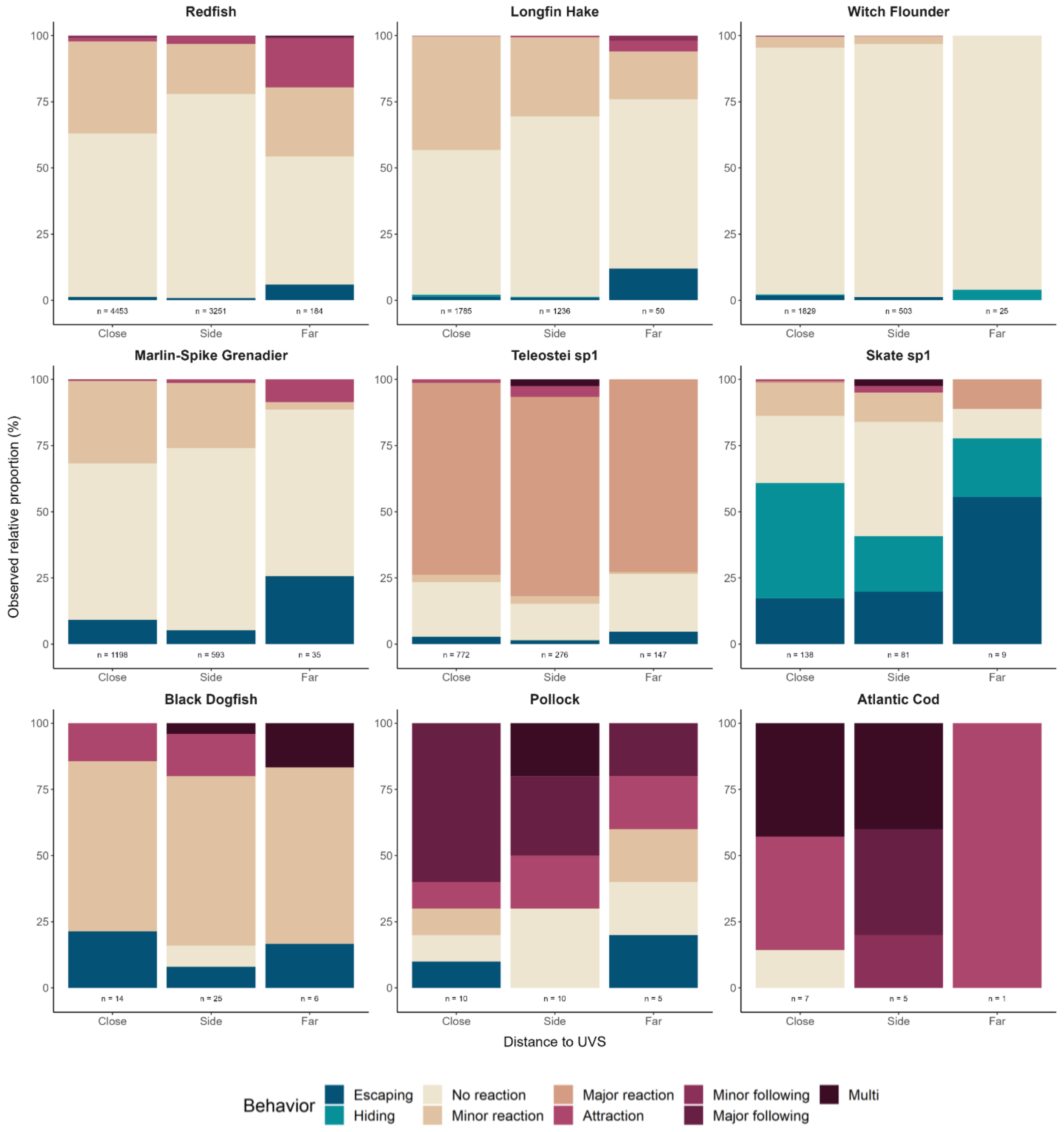
Appendix 4-17 | Patterns of observed response behaviors of fish in relation to fish total density per fish taxon. See Table 4-2 for detail of fish reactions and Table 4-3 of fish density categories.



Appendix 4-18 | Patterns of observed response behaviors of fish in relation to fish life stage per fish taxon. See Table 4-2 for detail of fish reactions and Table 4-3 of fish life stages.



Appendix 4-19 | Patterns of observed response behaviors of fish in relation to fish distance to UVS per fish taxon. See Table 4-2 for detail of fish reactions and Table 4-3 of distance categories.



Appendix 4-20 | Patterns of observed response behaviors of fish in relation to fish reaction timing per fish taxon. See Table 4-2 for detail of fish reactions and Table 4-3 of timing categories.

Appendix 4-21 | Redfish multinomial logistic regression model summary. *Neutral* was used as the reference response factor.

Factor	Category	Avoidance			Attraction		
		Coefficient	SE	p-value	Coefficient	SE	p-value
	(Intercept)	-428.38	0.79	-	-65.36	0.75	-
Technical							
UVS type	CAMPOD	-1.59	1.47	0.2819	-0.97	0.72	0.1761
UVS speed	Low	-2.9	1.18	0.0138*	0.15	0.83	0.8552
	Medium	-2.34	1.31	0.0728	-2.1	1.3	0.1058
	High	-1.73	1.5	0.2485	0.79	0.88	0.3718
UVS altitude	Low	-0.01	1.06	0.9893	-1.03	0.6	0.0868
	Medium	-0.81	1.6	0.611	-1.33	0.91	0.1442
	High	0.18	1.48	0.9051	-88.4	NA	NA
Survey operation	Invest.	354.69	1.44	-	-491.45	NA	NA
	Sampl.	0	NA	NA	0	NA	NA
	In maint.	353.7	1.11	-	-3.16	1.37	0.0206*
	Transect	353.57	0.58	-	-1.42	1.11	0.1997
	Transit	353.85	0.65	-	-1.66	1.15	0.1504
	Drifting	-97.85	NA	NA	-226.45	NA	NA
	Off bot.	353.74	1.21	-	-1	1.29	0.4384
Environmental							
Time of day	Night	-0.88	1.06	0.4096	-1.41	0.67	0.0345*
Benthic habitat type	Acti	199.65	0.56	-	-1.22	0.58	0.0357*
	Kopho	199.09	1.01	-	0.02	0.72	0.9813
	Sclerac	198.98	0.48	-	-1.67	0.48	< 0.001***
	Flab	185.21	0.59	-	-2.81	0.88	0.0014**
	Penna	186.8	0.6	-	-1.51	0.98	0.1251
Bottom type	Soft neg.	-1.09	0.73	0.1361	-0.52	0.35	0.1357
	Soft pos.	6.51	NA	NA	7.72	NA	NA
	Soft mixed	-233.77	NA	NA	-250.68	NA	NA
	Hard	-103.62	NA	NA	-111.62	NA	NA
Depth (m)	200-250	54.31	NA	NA	-14.63	NA	NA
	250-300	-23.76	NA	NA	-212.22	NA	NA
	300-350	-149.2	0.67	-	56.28	0.63	-
	350-400	-149.01	0.58	-	56.57	0.51	-
	400-455	-161.99	0.54	-	56.03	0.56	-
Fish *in-situ* behavior							
Fish altitude	On seafloor	-156.3	0.52	-	-35.97	0.43	-
	Above SF	-153.88	0.68	-	-34.82	0.49	-
	UVS level	0	NA	NA	0	0	NA

	Above UVS	0	NA	NA	0	0	NA
Fish activity	Resting	-1.85	1.11	0.0953	-0.53	0.42	0.2048
	Low BM	-230.47	NA	NA	-3.41	1.78	0.0552
	Medium BM	0.92	2.69	0.7308	-0.66	1.67	0.6917
	High BM	1.54	1.2	0.1965	-0.49	1.47	0.74
Fish locomotion	Hovering	1.13	2.58	0.6633	1.58	1.64	0.3349
	Drifting	0.4	NA	NA	-103.87	NA	NA
	Swimming	-1.85	1.29	0.1509	2.46	1.47	0.0937
Fish-related							
Fish density	Low	0.28	0.8	0.7211	0.24	0.47	0.6129
	Medium	0.37	0.79	0.6427	0.01	0.49	0.9792
	High	1.21	0.86	0.1618	0.2	0.54	0.7133
	Very high	-0.62	1.59	0.696	-0.75	0.73	0.3034
Fish life stage	Large juv.	-0.03	0.48	0.9445	0.69	0.31	0.0276*
	Adult	-228.58	NA	NA	1.96	1.7	0.2509
Distance to UVS	Side	0.14	0.68	0.8341	2.19	0.34	< 0.001***
	Far	-0.37	1.15	0.7478	1.6	0.68	0.0197
Reaction timing	Before	194.39	0.95	-	48.82	0.59	-
	During	193.02	0.54	-	45.2	0.35	-
	After	196.22	0.58	-	48.74	0.42	-
	Bef./Dur.	0	NA	NA	0	NA	NA
	Dur./Aft.	3.53	NA	NA	582.76	NA	NA
	Bef./Aft.	0	NA	NA	0	NA	NA

Appendix 4-22 | Longfin Hake multinomial logistic regression model summary. *Neutral* was used as the reference response factor.

Factor	Category	Avoidance			Attraction		
		Coefficient	SE	p-value	Coefficient	SE	p-value
	(Intercept)	-30.28	101.71	0.7659	-30.57	219.05	0.889
Technical							
UVS type	CAMPOD	1.73	3.8	0.6486	-22.59	44.68	0.6132
UVS speed	Low	-13.34	20.85	0.5223	12.18	384.17	0.9747
	Medium	-12.18	20.93	0.5606	-33.63	581.94	0.9539
	High	-20.39	50.63	0.6872	-6.41	NA	NA
UVS altitude	Low	18.97	39.13	0.6279	6.83	219.04	0.9751
	Medium	19.25	39.28	0.624	-4.92	NA	NA
	High	-3.17	1.82	0.0812	-1.62	NA	NA
Survey operation	Invest.	-17.24	81.85	0.8331	-0.58	NA	NA
	Sampl.	0	NA	NA	0	NA	NA
	In maint.	-0.53	230.61	0.9982	-0.39	NA	NA
	Transect	-8.52	53.43	0.8733	-22.98	297.96	0.9385
	Transit	-3.53	53.42	0.9473	-20.48	492.35	0.9668
	Drifting	-0.93	NA	NA	-4.14	581.94	0.9943
	Off bot.	5.44	53.87	0.9195	18.2	182.73	0.9207
Environmental							
Time of day	Night	15.17	20.52	0.4598	-26.02	0.02	-
Benthic habitat type	Acti	3.72	3.69	0.3132	-2.63	182.72	0.9885
	Kopho	-27.06	156.84	0.863	-3.95	NA	NA
	Sclerac	-19	57.08	0.7393	-15.21	0.01	-
	Flab	-5.37	60.01	0.9287	-15.46	310.35	0.9603
	Penna	4.99	59.83	0.9335	-3.34	238.71	0.9888
Bottom type	Soft neg.	0.91	2.2	0.6776	14.7	198.91	0.9411
	Soft pos.	-0.29	NA	NA	-0.26	NA	NA
	Soft mixed	-16.01	348.02	0.9633	-3.49	NA	NA
	Hard	-15.13	66.09	0.8189	-2.65	NA	NA
Depth (m)	200-250	-0.39	NA	NA	-0.39	NA	NA
	250-300	-7.53	431.86	0.9861	-1.16	NA	NA
	300-350	-16.51	104.84	0.8749	-7.94	198.92	0.9681
	350-400	2.37	103.68	0.9817	7.9	316.27	0.9801
	400-455	-8.17	159.72	0.9592	-28.91	222.14	0.8965
Fish *in-situ* behavior							
Fish altitude	On seafloor	-20.8	52.39	0.6913	-18.35	349.5	0.9581
	Above SF	-9.21	51.33	0.8575	-11.96	403.78	0.9764
	UVS level	0	NA	NA	0	NA	NA

	Above UVS	0	0	1	0	0	NA
Fish activity	Resting	-0.39	NA	NA	-0.39	NA	NA
	Low BM	-20.46	103.69	0.8436	-19.64	0.05	-
	Medium BM	-7.4	98.8	0.9403	-2.62	NA	NA
	High BM	-16.27	100.58	0.8715	15.76	301.53	0.9583
Fish locomotion	Hovering	11.46	98.86	0.9077	-9.44	NA	NA
	Drifting	-0.08	NA	NA	-15.82	NA	NA
	Swimming	20.51	100.67	0.8386	19.09	301.5	0.9495
Fish-related							
Fish density	Low	1.2	1.75	0.4928	12.32	455.68	0.9784
	Medium	-12.93	30.11	0.6675	2.04	839.27	0.9981
	High	18.63	20.62	0.366	-4.08	NA	NA
	Very high	-5.89	75.99	0.9382	-1.1	0.08	< 0.001***
Fish life stage	Large juv.	1.74	2.7	0.518	-12.69	232.57	0.9565
	Adult	-1.59	NA	NA	60.05	368.92	0.8707
Distance to UVS	Side	-20.6	143.03	0.8855	1.44	430.48	0.9973
	Far	14.02	136.95	0.9185	-4.58	168.23	0.9783
Reaction timing	Before	54.26	146.4	0.7109	42.1	168.23	0.8024
	During	40.28	164.71	0.8068	0.2	723.41	0.9998
	After	66.21	200.08	0.7407	-0.13	NA	NA
	Bef./Dur.	0	NA	NA	0	NA	NA
	Dur./Aft.	0	0	1	0	NA	NA
	Bef./Aft.	0	0	1	0	NA	NA

Appendix 4-23 | Witch Flounder multinomial logistic regression model summary. *Neutral* was used as the reference response factor.

Factor	Category	Avoidance			Attraction		
		Coefficient	SE	p-value	Coefficient	SE	p-value
	(Intercept)	-175.5	171.19	0.3053	-145.06	67.9	0.0326*
Technical							
UVS type	CAMPOD	-5.64	454.79	0.9901	-24.97	121.24	0.8368
UVS speed	Low	115.69	219.87	0.5988	11.94	118.16	0.9195
	Medium	110.65	501.66	0.8254	-25.33	84.83	0.7652
	High	115.7	219.87	0.5987	-23.05	2.4	< 0.001***
UVS altitude	Low	19.43	447.38	0.9654	104.77	339.86	0.7579
	Medium	54.98	767.06	0.9429	191.89	132.33	0.147
	High	53.33	344.35	0.8769	117.15	NA	NA
Survey operation	Invest.	255.46	32.84	< 0.001***	3.7	NA	NA
	Sampl.	0	0	1	0	NA	NA
	In maint.	-140.84	NA	NA	-215.46	NA	NA
	Transect	177.84	408.82	0.6636	63.03	67.52	0.3506
	Transit	151.43	273.04	0.5792	-68.39	NA	NA
	Drifting	1.77	NA	NA	6.63	NA	NA
	Off bot.	102.74	NA	NA	69.23	0.91	-
Environmental							
Time of day	Night	21.37	414.59	0.9589	42.52	156.84	0.7863
Benthic habitat type	Acti	-50.14	0.05	-	-65.08	NA	NA
	Kopho	-1.84	500.49	0.9971	16.96	1.06	< 0.001***
	Sclerac	17.53	304.4	0.9541	33.22	173.61	0.8482
	Flab	-22.25	339.72	0.9478	-55.35	310.94	0.8587
	Penna	-28.36	2.92	< 0.001***	15.71	2.44	< 0.001***
Bottom type	Soft neg.	-21.9	188.46	0.9075	-2.57	175.91	0.9883
	Soft pos.	0	0	1	0	NA	NA
	Soft mixed	87.18	306.83	0.7763	63.28	72.07	0.3799
	Hard	37.93	NA	NA	43.35	NA	NA
Depth (m)	200-250	-12.23	0.03	-	-3.16	NA	NA
	250-300	3.23	NA	NA	-6.94	NA	NA
	300-350	-88.92	479.38	0.8528	-98.85	311.19	0.7507
	350-400	-22.34	564.43	0.9684	-8.38	82.09	0.9187
	400-455	-55.25	234.58	0.8138	-27.72	205.71	0.8928
Fish *in-situ* behavior							

Fish altitude	On seafloor	-175.5	171.19	0.3053	-145.06	67.9	0.0326*
	Above SF	0	0	1	0	NA	NA
	UVS level	0	NA	NA	0	NA	NA
	Above UVS	0	NA	NA	0	NA	NA
Fish activity	Resting	0	NA	NA	0	NA	NA
	Low BM	0	0	1	0	NA	NA
	Medium BM	0	NA	NA	0	NA	NA
	High BM	0	0	1	0	NA	NA
Fish locomotion	Hovering	0	NA	NA	0	NA	NA
	Drifting	0	0	1	0	NA	NA
	Swimming	0	0	1	0	NA	NA
Fish-related							
Fish density	Low	-46.94	361.82	0.8968	-35.62	286.97	0.9012
	Medium	-13.73	436.06	0.9749	10.89	129.24	0.9328
	High	-33.9	514.73	0.9475	-8.68	166.48	0.9584
	Very high	-132.91	NA	NA	36.64	NA	NA
Fish life stage	Large juv.	31.25	183.44	0.8647	49.98	182.09	0.7837
	Adult	0	NA	NA	0	NA	NA
Distance to UVS	Side	11	244.19	0.9641	-51.02	NA	NA
	Far	24.03	276.75	0.9308	42.14	NA	NA
Reaction timing	Before	0	NA	NA	0	NA	NA
	During	75.76	303.93	0.8031	20	NA	NA
	After	186.8	301.46	0.5355	235.88	195.65	0.228
	Bef./Dur.	0	NA	NA	0	NA	NA
	Dur./Aft.	0	NA	NA	0	NA	NA
	Bef./Aft.	0	NA	NA	0	NA	NA

Appendix 4-24 | Marlin-Spike Grenadier multinomial logistic regression model summary. *Neutral* was used as the reference response factor.

Factor	Category	Avoidance			Attraction		
		Coefficient	SE	p-value	Coefficient	SE	p-value
	(Intercept)	-14971.3	0.63	-	-5204.49	79.56	-
Technical							
UVS type	CAMPOD	-4.42	1.37	0.013**	8088.21	NA	NA
UVS speed	Low	-1695.73	0.55	-	5683.7	47.74	-
	Medium	-1693.95	0.8	-	-2394.3	127.3	< 0.001***
	High	-1694.74	0.74	-	-23593.87	NA	NA
UVS altitude	Low	-0.04	0.76	0.9626	-9703.69	NA	NA
	Medium	0.97	1.54	0.5286	-8523.77	NA	NA
	High	-11482.47	NA	NA	10417.7	127.3	-
Survey operation	Invest.	-6889.37	NA	NA	941.38	NA	NA
	Sampl.	0	0	1	0	NA	NA
	In maint.	22449.58	NA	NA	1528.46	NA	NA
	Transect	13020.35	0.43	-	-8996.39	47.74	-
	Transit	13018.82	0.49	-	5244.78	127.3	-
	Drifting	294.87	NA	NA	789.25	NA	NA
	Off bot.	-7761.87	NA	NA	-5829.09	NA	NA
Environmental							
Time of day	Night	0.31	0.58	0.5919	-546.77	47.74	< 0.001***
Benthic habitat type	Acti	-0.04	1.06	0.9673	-9892.28	NA	NA
	Kopho	0.36	1.16	0.7562	7923.05	NA	NA
	Sclerac	-0.89	1	0.3719	-3427.07	NA	NA
	Flab	3.12	1.97	0.1126	2022.28	127.3	< 0.001***
	Penna	4.6	2.16	0.0331*	-5931.31	47.74	-
Bottom type	Soft neg.	-0.66	0.45	0.1411	11177.71	NA	NA
	Soft pos.	-15780.64	NA	NA	1103.38	NA	NA
	Soft mixed	0.64	1.27	0.6111	28007.43	NA	NA
	Hard	-21117.7	NA	NA	1341.09	NA	NA
Depth (m)	200-250	2271.05	NA	NA	8372.87	NA	NA
	250-300	-20059.61	NA	NA	-4961.05	NA	NA
	300-350	937.62	0.9	-	-7977.88	79.56	-
	350-400	936.94	1.02	-	8705.97	NA	NA
	400-455	942.7	1.27	-	-9344.4	NA	NA
Fish *in-situ* behavior							
Fish altitude	On seafloor	-7485.19	0.84	-	-19066.31	NA	NA
	Above SF	-7486.11	0.83	-	13861.83	79.56	-
	UVS level	0	NA	NA	0	NA	NA

	Above UVS	0	NA	NA	0	NA	NA
Fish activity	Resting	0	NA	NA	0	NA	NA
	Low BM	-9781.41	0.74	-	-20600.97	NA	NA
	Medium BM	-9781.61	0.78	-	-21636.39	NA	NA
	High BM	-9781.42	0.79	-	-8669.74	127.3	-
Fish locomotion	Hovering	9780.93	0.68	-	-15354.78	NA	NA
	Drifting	9782.16	0.95	-	-22011.5	NA	NA
	Swimming	9782.33	0.93	-	-1049	127.3	-
Fish-related							
Fish density	Low	0.56	0.48	0.2509	3175.06	127.3	< 0.001***
	Medium	0.26	0.56	0.649	150.17	NA	NA
	High	0.93	0.9	0.3032	9958.94	NA	NA
	Very high	-3518.89	NA	NA	3105.1	NA	NA
Fish life stage	Large juv.	0.66	0.85	0.4324	-12563.31	NA	NA
	Adult	-8073.93	NA	NA	-3916.09	NA	NA
Distance to UVS	Side	0.91	0.58	0.1143	8411.86	NA	NA
	Far	7761.8	NA	NA	5499.88	NA	NA
Reaction timing	Before	10189.73	1	-	21315.25	NA	NA
	During	10190.21	0.5	-	9111.97	47.74	-
	After	10192.97	0.62	-	26806.97	NA	NA
	Bef./Dur.	0	NA	NA	0	NA	NA
	Dur./Aft.	0	NA	NA	0	NA	NA
	Bef./Aft.	0	NA	NA	0	NA	NA

Appendix 4-25 | Teleostei sp1 multinomial logistic regression model summary. *Neutral* was used as the reference response factor.

Factor	Category	Avoidance			Attraction		
		Coefficient	SE	p-value	Coefficient	SE	p-value
	(Intercept)	-23.28	106.06	0.8263	-13.86	65.9	0.8334
Technical							
UVS type	CAMPOD	-0.89	1.92	0.6411	-4.03	3.91	0.302
UVS speed	Low	19.64	35.37	0.5788	-2.42	1.47	0.0982
	Medium	27.79	35.42	0.4326	2.72	3.43	0.4277
	High	19.89	35.37	0.574	-1.78	1.36	0.1913
UVS altitude	Low	0.58	0.75	0.4416	-1.84	0.87	0.0339*
	Medium	3.43	1.36	0.0117*	-9.65	93.4	0.9178
	High	-5.32	55.57	0.9238	-9.41	111.71	0.9329
Survey operation	Invest.	8.06	42.61	0.85	3.92	1.97	0.0463*
	Sampl.	-16.62	0.34	-	1	2.29	0.664
	In maint.	-5.36	398.65	0.9893	-7.59	48.62	0.8759
	Transect	8.02	42.58	0.8506	1.25	1.54	0.4161
	Transit	6.15	42.59	0.8851	0.76	1.67	0.6488
	Drifting	0	0	1	0	NA	NA
	Off bot.	-10.7	76.87	0.8892	-7.51	541.1	0.9889
Environmental							
Time of day	Night	1.01	1.7	0.553	1.38	1.35	0.3041
Benthic habitat type	Acti	11.89	295.79	0.9679	12.26	337.63	0.971
	Kopho	-2.58	19.34	0.894	-6.88	2.33	0.0032**
	Sclerac	12.26	295.8	0.9669	-10.44	1.79	< 0.001***
	Flab	-1.94	2.41	0.4219	-1.51	1.9	0.4255
	Penna	3.18	2.38	0.1821	-1.46	1.95	0.4547
Bottom type	Soft neg.	-0.14	0.93	0.8807	-0.03	0.9	0.9761
	Soft pos.	-0.55	112.48	0.9961	-8.06	360.55	0.9822
	Soft mixed	-6.98	95.94	0.942	-8.76	129.26	0.9459
	Hard	-10.04	147.69	0.9458	1.2	2.08	0.5638
Depth (m)	200-250	0	NA	NA	0	NA	NA
	250-300	-1.17	450.41	0.9979	-0.08	326.41	0.9998
	300-350	-3	134.53	0.9822	-0.27	122.4	0.9982
	350-400	-4.37	134.53	0.9741	-2.27	122.4	0.9852
	400-455	-14.74	262.18	0.9552	-11.24	262.58	0.9659
Fish *in-situ* behavior							
Fish altitude	On seafloor	-20.36	86.53	0.8139	-1.39	16.5	0.9329
	Above SF	-21.44	86.54	0.8043	-5.94	16.51	0.719

	UVS level	-18.35	86.53	0.8321	-3.63	16.49	0.8259
	Above UVS	-14.33	86.48	0.8684	-2.77	16.5	0.8668
Fish activity	Resting	0	NA	NA	0	0	1
	Low BM	-7.53	68.91	0.913	-5.59	194.79	0.9771
	Medium BM	-10.86	68.91	0.8748	-2.68	603.93	0.9965
	High BM	-9.6	68.88	0.8891	2.83	133.51	0.9831
Fish locomotion	Hovering	4.93	68.91	0.943	-6.19	159.94	0.9691
	Drifting	-11.14	1.47	-	-0.53	144.84	0.9971
	Swimming	1.7	68.89	0.9804	1.44	133.51	0.9914
Fish-related							
Fish density	Low	-0.96	0.65	0.1384	0.15	0.94	0.8747
	Medium	-0.25	0.68	0.7111	0.56	0.98	0.5677
	High	-1.38	1.25	0.2695	1.61	1.12	0.1504
	Very high	11.6	2.71	< 0.001***	-15.52	NA	NA
Distance to UVS	Side	0.6	0.76	0.4358	0.42	0.68	0.544
	Far	1.97	0.86	0.0214*	-10.47	54.3	0.8471
Reaction timing	Before	15.47	80.81	0.8481	14.21	116.65	0.9031
	During	16.24	80.81	0.8407	13.2	116.65	0.9099
	After	14	80.82	0.8625	15.54	116.65	0.894
	Bef./Dur.	-0.07	NA	NA	34.78	226.5	0.878
	Dur./Aft.	-0.07	NA	NA	26.93	145.93	0.8536
	Bef./Aft.	0	NA	NA	0	NA	NA

Appendix 4-26 | Skate sp1 multinomial logistic regression model summary. *Neutral* was used as the reference response factor.

Factor	Category	Avoidance			Attraction		
		Coefficient	SE	p-value	Coefficient	SE	p-value
	(Intercept)	-78.14	1.17	-	-19.48	157.2	0.9014
Technical							
UVS type	CAMPOD	-2.11	1.1	0.055	-49.39	NA	NA
UVS speed	Low	1.94	1.77	0.2719	-26.49	157.08	0.8661
	Medium	0.86	1.81	0.6353	13.31	NA	NA
	High	-0.38	1.79	0.8333	18.07	0.12	-
UVS altitude	Low	-1.55	1.44	0.2802	-45.46	157.2	0.7724
	Medium	-2.03	1.59	0.2033	-41.09	NA	NA
	High	-0.33	2.11	0.8761	-3.92	NA	NA
Survey operation	Invest.	51.36	NA	NA	-9.99	NA	NA
	Sampl.	0	NA	NA	0	NA	NA
	In maint.	32.91	1.48	< 0.001***	-6.23	NA	NA
	Transect	32.85	0.76	-	5.85	157.09	0.9703
	Transit	33.46	0.83	-	12.36	0.11	-
	Drifting	0	NA	NA	0	NA	NA
	Off bot.	-20.77	NA	NA	-8.56	NA	NA
Environmental							
Time of day	Night	-1.16	1.08	0.2836	-94.69	NA	NA
Benthic habitat type	Acti	-1.39	1.56	0.3739	-44.61	NA	NA
	Kopho	-1.01	1.96	0.6049	30.91	NA	NA
	Sclerac	-2.63	1.44	0.0685	-21.95	NA	NA
	Flab	-0.08	3.99	0.9846	5.63	0.19	< 0.001***
	Penna	0.04	4	0.9925	-46	0	0
Bottom type	Soft neg.	-0.61	0.65	0.3513	3.07	0.41	< 0.001***
	Soft pos.	-13.74	NA	NA	-32.22	NA	NA
	Soft mixed	-1.29	1.47	0.3802	-0.88	NA	NA
	Hard	69.84	0	0	-11.72	NA	NA
Depth (m)	200-250	0	NA	NA	0	NA	NA
	250-300	0	0	1	0	NA	NA
	300-350	-26.34	1.76	< 0.001***	-30.06	0.11	-
	350-400	-26.99	1.74	< 0.001***	-2.41	0.08	< 0.001***
	400-455	-24.82	2.45	< 0.001***	12.99	157.01	0.9341
Fish *in-situ* behavior							

Fish altitude	On seafloor	-14.54	1.17	< 0.001***	11.56	157.2	0.9414
	Above SF	-60.18	NA	NA	-25.66	NA	NA
	UVS level	0	0	1	0	NA	NA
	Above UVS	0	0	1	0	NA	NA
Fish activity	Resting	0	NA	NA	0	NA	NA
	Low BM	0.41	NA	NA	4.94	NA	NA
	Medium BM	-59.09	NA	NA	5.31	NA	NA
	High BM	-3.82	0.82	< 0.001***	13.92	NA	NA
Fish locomotion	Hovering	-59.27	NA	NA	-43.88	NA	NA
	Drifting	0	NA	NA	0	NA	NA
	Swimming	0.75	0.82	0.3623	66.39	NA	NA
Fish-related							
Fish density	Low	-0.27	1	0.7887	33.11	157.08	0.8331
	Medium	-1	1.14	0.3798	23.64	0.11	-
	High	-2.24	1.38	0.1027	19.78	NA	NA
	Very high	0.36	NA	NA	-20.21	NA	NA
Distance to UVS	Side	-0.31	0.66	0.6405	9.53	156.79	0.9515
	Far	-1.04	2.04	0.608	-30.07	NA	NA
Reaction timing	Before	90.31	1.1	-	45.83	NA	NA
	During	89.69	0.91	-	8.74	157.09	0.9556
	After	164.83	NA	NA	192.89	NA	NA
	Bef./Dur.	0	NA	NA	0	NA	NA
	Dur./Aft.	10.81	NA	NA	93.7	NA	NA
	Bef./Aft.	0	NA	NA	0	NA	NA

Appendix 4-27 | Black Dogfish multinomial logistic regression model summary. *Neutral* was used as the reference response factor.

Factor	Category	Avoidance			Attraction		
		Coefficient	SE	p-value	Coefficient	SE	p-value
	(Intercept)	11.88	0.12	-	-27.63	0.23	-
Technical							
UVS type	CAMPOD	15.48	0.12	-	2.69	0.23	< 0.001***
UVS speed	Low	-47.96	NA	NA	28.18	1.15	< 0.001***
	Medium	28.72	0.12	-	29.77	1.06	< 0.001***
	High	-41.6	NA	NA	31.93	1.3	< 0.001***
UVS altitude	Low	13.66	0.12	-	-31.06	0.23	-
	Medium	-1.78	NA	NA	3.43	NA	NA
	High	0	NA	NA	0	NA	NA
Survey operation	Invest.	0	NA	NA	0	NA	NA
	Sampl.	0	NA	NA	0	NA	NA
	In maint.	0	NA	NA	0	NA	NA
	Transect	11.88	0.12	-	-27.63	0.23	-
	Transit	0	NA	NA	0	NA	NA
	Drifting	0	NA	NA	0	NA	NA
	Off bot.	0	NA	NA	0	NA	NA
Environmental							
Time of day	Night	-3.6	NA	NA	-30.32	NA	NA
Benthic habitat type	Acti	-45.62	NA	NA	-20.67	NA	NA
	Kopho	-3.6	NA	NA	-30.32	NA	NA
	Sclerac	0	NA	NA	0	NA	NA
	Flab	0	NA	NA	0	NA	NA
	Penna	0	NA	NA	0	NA	NA
Bottom type	Soft neg.	-102.8	NA	NA	-1.65	1.63	0.3096
	Soft pos.	0	NA	NA	0	NA	NA
	Soft mixed	91.03	NA	NA	-34.61	NA	NA
	Hard	-56.79	NA	NA	-94.51	NA	NA
Depth (m)	200-250	-24.7	NA	NA	-16.22	NA	NA
	250-300	0	NA	NA	0	NA	NA
	300-350	0	NA	NA	0	NA	NA
	350-400	0	NA	NA	0	NA	NA
	400-455	36.58	0.12	-	-11.41	0.23	-
Fish *in-situ* behavior							
Fish altitude	On seafloor	-16.89	NA	NA	-45.28	NA	NA
	Above SF	19.98	0.12	-	-38.94	0.23	-
	UVS level	4.23	NA	NA	18.34	NA	NA

	Above UVS	4.55	NA	NA	38.25	NA	NA
Fish activity	Resting	0	NA	NA	0	NA	NA
	Low BM	0	NA	NA	0	NA	NA
	Medium BM	1.47	NA	NA	-23.44	NA	NA
	High BM	-36.49	0.12	-	39.26	0.23	-
Fish locomotion	Hovering	0	NA	NA	0	NA	NA
	Drifting	0	NA	NA	0	NA	NA
	Swimming	-35.01	0.12	-	15.82	0.23	-
Fish-related							
Fish density	Low	-55.19	NA	NA	0.48	1.86	0.7955
	Medium	0	NA	NA	0	NA	NA
	High	0	NA	NA	0	NA	NA
	Very high	0	NA	NA	0	NA	NA
Distance to UVS	Side	-61.21	0.12	-	-1.86	2.04	0.3624
	Far	-7.61	NA	NA	-1.28	3.18	0.688
Reaction timing	Before	4.23	NA	NA	18.34	NA	NA
	During	-5.8	0.12	-	50.13	0.23	-
	After	0	NA	NA	0	NA	NA
	Bef./Dur.	0	NA	NA	0	NA	NA
	Dur./Aft.	0	NA	NA	0	NA	NA
	Bef./Aft.	4.55	NA	NA	38.25	NA	NA

Appendix 4-28 | Pollock multinomial logistic regression model summary. *Neutral* was used as the reference response factor.

Factor	Category	Avoidance			Attraction		
		Coefficient	SE	p-value	Coefficient	SE	p-value
	(Intercept)	-0.55	13850.47	1	0.65	16645.18	1
Technical							
UVS type	CAMPOD	-1.58	15530.29	0.99	-2.69	16567.33	0.99
UVS speed	Low	-5.41	33073.73	0.99	-11.25	24978.22	0.99
	Medium	-0.46	38401.53	1	1.54	32760.33	1
	High	-7.57	31222.81	0.99	0.03	31407.69	1
UVS altitude	Low	3.18	63931.26	1	-0.45	74798.13	1
	Medium	-3.97	9358.89	0.99	-8.25	69976.35	0.99
	High	0.24	18383.33	1	1.44	30085.31	1
Survey operation	Invest.	0.5	31538.39	1	0.75	34750.03	1
	Sampl.	0	NA	NA	0	NA	NA
	In maint.	0	NA	NA	0	NA	NA
	Transect	-0.59	10892.16	1	-4.42	24778.52	0.99
	Transit	-2.3	29519.33	0.99	-1.04	43359.66	1
	Drifting	0	0	1	0	NA	NA
	Off bot.	1.85	21620.84	0.99	5.37	20528.74	0.99
Environmental							
Time of day	Night	-4.21	77575.96	1	-11.43	55193.84	0.99
Benthic habitat type	Acti	1.03	41021.67	1	4.16	47598.78	0.99
	Kopho	0	NA	NA	0	NA	NA
	Sclerac	-1.01	23391.61	1	2.69	43842.75	1
	Flab	-4.79	22926.34	0.99	9.67	27588.52	0.99
	Penna	6.47	6001.11	0.99	-1.62	1759.39	0.99
Bottom type	Soft neg.	-3.3	113622.99	1	-1.79	5609.34	0.99
	Soft pos.	0	0	1	0	NA	NA
	Soft mixed	0.66	27.98	0.98	1.38	126754.99	1
	Hard	-0.78	76297.53	1	-9.75	20790.23	0.99
Depth (m)	200-250	13.2	29236.15	0.99	-2.14	10.58	0.99
	250-300	0	NA	NA	0	NA	NA
	300-350	-10.45	28149.05	0.99	-3.58	30821.88	0.99
	350-400	5.52	23676.29	0.99	2.31	30500.92	0.99
	400-455	-0.75	16129.14	1	4.78	15565.12	0.99
Fish *in-situ* behavior							
Fish altitude	On seafloor	5.73	4708.52	0.99	-0.67	NA	NA
	Above SF	-0.79	30905.07	1	-10.27	31500.11	0.99
	UVS level	-1.98	81019.78	1	3.67	11274.07	0.99

	Above UVS	-3.51	46826.14	0.99	7.92	34898.14	0.99
Fish activity	Resting	0	NA	NA	0	0	NA
	Low BM	-8.06	585.45	0.99	-0.72	7399	0.99
	Medium BM	0	0	1	0	NA	NA
	High BM	1.78	12992.57	0.99	2.04	22354.83	0.99
Fish locomotion	Hovering	-8.06	585.45	0.99	-0.72	7399	0.99
	Drifting	0	0	1	0	NA	NA
	Swimming	1.78	12992.57	0.99	2.04	22354.83	0.99
Fish-related							
Fish density	Low	3.14	55248.21	1	9.34	84691.65	0.99
	Medium	3.14	40650.24	0.99	-7.9	39284.92	0.99
	High	0	NA	NA	0	NA	NA
	Very high	-0.85	31053.11	1	-1.83	40787.55	1
Distance to UVS	Side	-0.49	114708.81	1	3.72	5517.8	0.99
	Far	-1.34	29005.95	1	-1.25	34817.45	1
Reaction timing	Before	0.53	19686.63	1	3.41	33057.47	0.99
	During	3.44	58733.13	1	9.79	36526.03	0.99
	After	5.73	4708.52	0.99	-0.67	NA	NA
	Bef./Dur.	0.68	52137.02	1	3.87	41340.66	0.99
	Dur./Aft.	4.52	113603.54	1	28.41	1485.91	0.99
	Bef./Aft.	-0.09	40197.98	1	8.47	19664.26	0.99

Appendix 5-1 | Number of fish individuals sampled per taxon and per survey. Total_F: total number of fish sampled per taxon. The 13 top species (above red line) represent each at least 1 % of total abundance.

Scientific name	Common name/ Taxon	Survey								Total_F	%
		T2015	T2016Ap	T2016Au	T2017	T2018	T2019	R2017	C2018		
Sebastes mentella	Deep Water Redfish	9575	13847	6916	9548	12348	76878	9909	2046	141067	57
Merluccius bilinearis	Silver Hake	6995	4205	505	5333	9411	7411	82	117	34059	14
Urophycis chesteri	Longfin Hake	1439	2393	743	2803	2256	2399	1984	1110	15127	6
Glyptocephalus cynoglossus	Witch Flounder	2008	2170	748	2279	2037	1919	1413	949	13523	5
Nezumia bairdii	Marlin-Spike Grenadier	896	722	495	1269	1473	977	1292	540	7664	3
Myctophidae	Lanternfish	664	206	1745	441	626	260	0	0	3942	2
Centroscyllium fabricii	Black Dogfish	354	626	21	534	1119	1029	1	44	3728	1
Merluccius albidus	Offshore Silver Hake	0	8	3	0	209	3413	0	0	3633	1
Myxine glutinosa	Atlantic Hagfish	560	535	0	479	1006	621	149	142	3492	1
Squalus acanthias	Spiny Dogfish	5	4	0	2	3	2465	0	2	2481	1
Hippoglossoides platessoides	American Plaice	120	430	29	391	1378	89	0	0	2437	1
Amblyraja radiata	Thorny Skate	212	338	77	1173	394	133	0	0	2327	1
Gadus morhua	Atlantic Cod	423	1179	6	264	58	313	13	0	2256	1
Ammodytes dubius	Sand Lance	1665	49	0	0	0	0	0	0	1714	<1
Paralepididae	Barracudina	10	3	1499	0	0	0	0	0	1512	<1
Urophycis tenuis	White Hake	259	269	173	250	275	191	28	0	1445	<1
Teleostei spp.	Teleostei sp1	0	0	0	0	0	0	1212	21	1233	<1
Argentina silus	Atlantic Argentine	9	28	168	32	512	292	33	83	1157	<1
Reinhardtius hippoglossoides	Greenland Halibut	138	122	13	132	236	119	0	0	760	<1
Limanda ferruginea	Yellowtail Flounder	6	529	0	194	8	0	0	0	737	<1
Enchelyopus cimbrius	Fourbeard Rockling	6	24	42	21	174	109	119	171	666	<1
Lycenchelys verrillii	Verrill's Wolf Eel	0	0	0	0	0	1	509	104	614	<1
Malacoraja senta	Smooth Skate	81	101	19	133	107	87	0	0	528	<1
Clupea harengus	Atlantic Herring	97	77	4	27	188	6	0	0	399	<1
Notolepis rissoi kroyeri	Scaled Lancetfish	70	63	4	77	53	40	0	0	307	<1
Rajidae spp.	Skate sp1	0	0	0	0	0	0	181	47	228	<1
Melanostigma atlanticum	Soft Eelpout	133	11	0	10	20	16	0	0	190	<1
Lophius americanus	Monkfish	16	22	18	40	37	25	6	8	172	<1

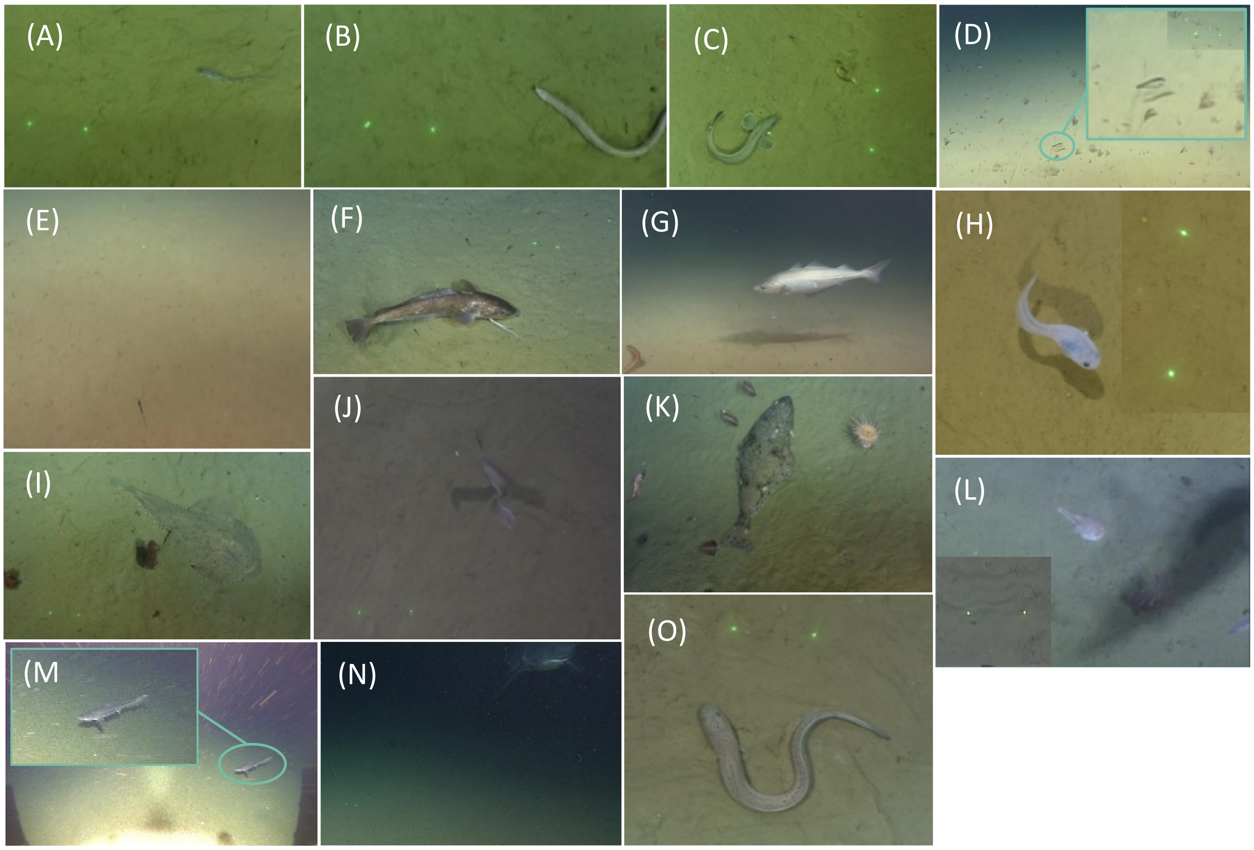
Nemichthys scolopaceus	Atlantic Snipe Eel	30	18	16	29	51	15	0	0	159	<1
Melanogrammus aeglefinus	Haddock	3	107	0	4	3	25	0	0	142	<1
Lycenchelys paxillus	Northern Wolf Eel	3	103	0	5	2	8	0	0	121	<0.1
Pollachius virens	Pollock	28	3	2	4	8	47	19	4	115	<0.1
Stomias boa ferox	Boa Dragonfish	32	0	50	0	22	0	0	0	104	<0.1
Nemichthyidae	Snipe Eel	0	0	104	0	0	0	0	0	104	<0.1
Artediellus uncinatus	Atlantic Hookear Sculpin	30	0	23	20	16	2	0	0	91	<0.1
Hippoglossus hippoglossus	Atlantic Halibut	3	40	1	4	16	10	2	1	77	<0.1
Actino sp. indet.	Actino sp1	0	0	0	0	0	0	67	6	73	<0.1
Triglops murrayi	Moustache Sculpin	20	0	0	48	0	5	0	0	73	<0.1
Hemitripterus americanus	Sea Raven	45	9	0	10	5	4	0	0	73	<0.1
Etrumeus sadina	Round Herring	0	0	0	71	0	0	0	0	71	<0.1
Chauliodus sloani	Viperfish	4	2	27	31	2	1	0	0	67	<0.1
Liparis fabricii	Gelatinous Seasnail	1	4	7	28	0	1	17	5	63	<0.1
Gaidropsarus ensis	Threebeard Rockling	36	7	0	14	0	1	0	0	58	<0.1
Eumicrotremus spinosus	Spiny Lumpfish	21	0	0	30	0	5	0	0	56	<0.1
Argentina striata	Striated Argentine	0	0	0	51	0	0	0	0	51	<0.1
Lycodes sp.	Eelpout	0	2	1	26	7	14	0	0	50	<0.1
Aspidophoroides monopterygius	Common Alligatorfish	10	15	2	18	0	2	0	0	47	<0.1
Myoxocephalus scorpius	Shorthorn Sculpin	2	40	0	0	0	5	0	0	47	<0.1
Anarhichas lupus	Striped Wolffish	0	2	21	1	5	18	0	0	47	<0.1
Paraliparis copei	Blacksnout Seasnail	0	0	0	0	13	21	0	0	34	<0.1
Synaphobranchus kaupii	Longnose Eel	1	9	0	3	11	9	0	0	33	<0.1
Myoxocephalus octodecemspinosus	Longhorn Sculpin	13	4	0	1	0	8	0	0	26	<0.1
Serrivomer beanii	Shortnose Snipe Eel	11	1	1	6	2	4	0	0	25	<0.1
Mallotus villosus	Capelin	0	11	0	9	0	1	0	0	21	<0.1
Alosa pseudoharengus	Alewife	2	2	0	1	0	15	0	0	20	<0.1
Helicolenus dactylopterus	Blackbelly Rosefish	1	0	2	7	6	4	0	0	20	<0.1
Poromitra capito	Ridgehead	20	0	0	0	0	0	0	0	20	<0.1
Lycodes esmarki	Esmark's Eelpout	1	4	0	1	4	8	0	0	18	<0.1
Boreogadus saida	Arctic Cod	0	5	0	12	0	0	0	0	17	<0.1
Unidentified fish	Actino spp.	0	0	0	0	0	0	5	11	16	<0.1
Coryphaenoides rupestris	Roundnose Grenadier	0	0	13	0	0	0	0	0	13	<0.1
Anarhichas denticulatus	Broadhead Wolffish	3	2	0	2	1	3	0	0	11	<0.1
Cryptacanthodes maculatus	Wrymouth	2	3	1	2	0	2	1	0	11	<0.1
Zoarcidae	Zoarcidae	0	0	0	0	0	0	7	3	10	<0.1

Dibranchus atlanticus	Atlantic Batfish	1	0	1	1	2	0	3	0	8	<0.1
Sternoptychidae	Silver Hatchetfish	2	0	5	1	0	0	0	0	8	<0.1
Bathyraja spinicauda	Spinytail Skate	1	1	0	1	2	3	0	0	8	<0.1
Paralepis atlantica	Short Barracudina	0	0	0	0	7	0	0	0	7	<0.1
Macrozoarces americanus	Ocean Pout	6	0	0	0	1	0	0	0	7	<0.1
Scomber scombrus	Atlantic Mackerel	0	0	0	3	2	1	0	0	6	<0.1
Malacosteus niger	Stoplight Loosejaw	1	0	0	2	2	0	0	0	5	<0.1
Anarhichas minor	Spotted Wolffish	1	0	0	0	3	1	0	0	5	<0.1
Eumesogrammus praecisus	Fourline Snakeblenny	0	0	0	4	0	0	0	0	4	<0.1
-	Unidentified Grenadier	0	0	0	0	0	0	0	4	4	<0.1
Argyropelecus aculeatus	Silver Atlantic Hatchetfish	0	1	0	0	0	3	0	0	4	<0.1
Urophycis chuss	Red Hake	0	0	3	0	0	0	0	0	3	<0.1
Raja laevis	Barndoor Skate	0	0	2	1	0	0	0	0	3	<0.1
Ceratias holboelli	Deepsea Angler	1	0	0	0	0	0	0	0	1	<0.1
Cottunculus microps	Deepsea Arctic Sculpin	0	0	1	0	0	0	0	0	1	<0.1
Astronesthes richardsoni	Scaled Dragonfish	1	0	0	0	0	0	0	0	1	<0.1
Simenchelyidae	Snubnose Eel	1	0	0	0	0	0	0	0	1	<0.1
Coryphaenoides guentheri	Günther's Grenadier	0	0	0	0	1	0	0	0	1	<0.1
Lamna nasus	Porbeagle Shark	0	0	0	0	0	0	1	0	1	<0.1
Percoidea	Sea Bass	0	1	0	0	0	0	0	0	1	<0.1
Ceratiidae	Sea Devils	0	0	0	1	0	0	0	0	1	<0.1
Raja ocellata	Winter Skate	0	0	0	0	0	1	0	0	1	<0.1
Gasterosteiformes	Sticklebacks	1	0	0	0	0	0	0	0	1	<0.1
Lycenchelys verrillii	Verrill's Wolf Eel	0	0	0	0	0	1	0	0	1	<0.1

Appendix 5-2 | Results of PERMANOVAs performed on fish assemblages per benthoscape and per survey (factor) within benthoscapes.

Benthoscape	Factor	Df	Sum of Sqs	R^2	F	P
All	Benthoscape	7	5.09	0.18	7.4	< 0.001***
	Residuals	240	23.73	0.82		
	Total	247	28.82	1		
All	Survey	7	8.02	0.28	13.22	< 0.001***
	Residuals	240	20.8	0.72		
	Total	247	28.82	1		
Slope pockmarks	Survey	6	0.9	0.25	1.59	0.021*
	Residuals	29	2.7	0.75		
	Total	35	3.6	1		
Slope dense pockmarks	Survey	7	1.73	0.54	4.84	< 0.001***
	Residuals	29	1.48	0.46		
	Total	36	3.2	1		
Deep iceberg scours	Survey	7	2.9	0.51	8.9	< 0.001***
	Residuals	61	2.84	0.49		
	Total	68	5.74	1		
Deep dense pockmarks	Survey	6	2.69	0.58	10.48	< 0.001***
	Residuals	45	1.93	0.42		
	Total	51	4.62	1		

Appendix 5-3 | Frame captures from underwater video of the 15 other fish taxa observed during the video surveys sorted in descending order of abundance. (A) Wolf Eelpout (*Lycenchelys vyerrillii*), (B) Hagfish (*Myxine glutinosa*), (C) Fourbeard Rockling (*Enchelyopus cimbrius*), (D) Greater Argentine (*Argentina silus*), (E) Actino sp1, (F) White Hake (*Urophycis tenuis*), (G) Pollock (*Pollachius virens*), (H) Snailfish sp1 (Liparidae sp. indet.), (I) Monkfish (*Lophius americanus*), (J) Zoarcidae sp1, (K) Atlantic Halibut (*Hippoglossus hippoglossus*), (L) Batfish sp1 (*Dibranchus* sp. indet.), (M) Spiny Dogfish (*Squalus acanthias*), (N) Porbeagle (*Lamna nasus*), (O) Wrymouth (*Cryptacanthodes maculata*). Distance between lasers: 10 cm.



Appendix 5-4 | Percentage of dissimilarity extracted from the SIMPER analysis between surveys within benthoscapes based on forth-root transformed fish densities.

Benthoscape	Survey	Survey						
		T2015	T2016$_{Ap}$	T2016$_{Au}$	T2017	T2018	T2019	R2017
All	T2016$_{Ap}$	39	-					
	T2016$_{Au}$	56	55	-				
	T2017	39	35	55	-			
	T2018	40	36	55	36	-		
	T2019	43	38	58	39	39	-	
	R2017	57	48	58	49	48	49	-
	C2018	47	45	57	46	44	46	28
Slope pockmarks	T2016$_{Ap}$	45	-					
	T2016$_{Au}$	46	54	-				
	T2017	39	44	47	-			
	T2018	40	43	49	37	-		
	T2019	40	45	47	38	39	-	
	R2017	NA	NA	NA	NA	NA	NA	-
	C2018	49	56	50	47	45	47	NA
Slope dense pockmarks	T2016$_{Ap}$	28	-					
	T2016$_{Au}$	48	44	-				
	T2017	28	26	44	-			
	T2018	31	29	45	26	-		
	T2019	29	30	47	28	30	-	
	R2017	49	47	52	46	44	48	-
	C2018	47	43	50	40	39	45	25
Deep iceberg scours	T2016$_{Ap}$	31	-					
	T2016$_{Au}$	47	46	-				
	T2017	31	27	48	-			
	T2018	31	26	46	25	-		
	T2019	37	30	50	32	31	-	
	R2017	54	43	56	47	44	45	-
	C2018	46	37	50	40	34	39	28
Deep dense pockmarks	T2016$_{Ap}$	26	-					
	T2016$_{Au}$	66	68	-				
	T2017	23	23	65	-			
	T2018	27	26	65	22	-		
	T2019	28	39	69	25	24	-	
	R2017	NA	NA	NA	NA	NA	NA	-
	C2018	43	29	70	40	40	42	NA

Appendix 5-5 | Average contribution (%) to dissimilarity between survey assemblages of fish taxa that contributed to less than 1 % (all surveys combined).

Taxon	Survey				Total
	Trawls *vs.* Trawls	$T2016_{Au}$ *vs.* Trawls	Trawls *vs.* UVSs	R2017 *vs.* C2018	
Soft Eelpout	1.4	0.6	0.6	NA	0.9
Boa Dragonfish	0.9	1.2	0.6	NA	0.9
Blacksnout Seasnail	1.0	0.8	0.7	NA	0.9
Offshore Silver Hake	1.2	0.7	0.5	NA	0.8
Unidentified Grenadier	NA	NA	0.8	1.1	0.8
Viperfish	0.6	1.6	0.4	NA	0.7
Haddock	1.1	0.5	0.4	NA	0.7
Spiny Dogfish	0.8	0.3	0.7	1.2	0.7
Threebeard Rockling	0.9	0.5	0.4	NA	0.7
Yellowtail Flounder	0.9	0.5	0.4	NA	0.7
Longnose Eel	0.8	0.4	0.3	NA	0.5
Sea Raven	0.8	0.4	0.3	NA	0.5
Eelpout	0.7	0.4	0.3	NA	0.5
Northern Wold Eel	0.8	0.3	0.3	NA	0.5
Esmark's Eelpout	0.7	0.3	0.3	NA	0.5
Porbeagle Shark	NA	NA	0.4	0.7	0.4
Striped Wolffish	0.5	0.7	0.3	NA	0.4
Round Herring	0.5	0.4	0.3	NA	0.4
Shortnose Snipe Eel	0.7	0.4	0.2	NA	0.4
Wrymouth	0.5	0.3	0.4	0.7	0.4
Striated Argentine	0.4	0.4	0.4	NA	0.4
Spiny Lumpfish	0.5	0.3	0.2	NA	0.4
Moustache Sculpin	0.4	0.3	0.2	NA	0.3
Common Alligatorfish	0.5	0.3	0.2	NA	0.3
Atlantic Hookear Sculpin	0.4	0.6	0.2	NA	0.3
Broadhead Wolffish	0.5	0.2	0.2	NA	0.3
Atlantic Batfish	0.2	0.2	0.4	1.0	0.3
Shorthorn Sculpin	0.4	0.2	0.2	NA	0.3
Capelin	0.4	0.2	0.2	NA	0.3
Blackbelly Rosefish	0.4	0.3	0.2	NA	0.3
Arctic Cod	0.3	0.2	0.2	NA	0.3
Silver Hatchetfish	0.2	0.4	0.2	NA	0.3
Spinytail Skate	0.4	0.2	0.1	NA	0.2
Verrill's Wolf Eel	0.1	0.1	0.0	4.1	0.2
Longhorn Sculpin	0.3	0.2	0.2	NA	0.2
Alewife	0.3	0.2	0.2	NA	0.2
Red Squirrel Hake	NA	0.2	0.2	NA	0.2
Ridgehead	0.2	0.2	0.2	NA	0.2
Roundnose Grenadier	NA	0.2	0.2	NA	0.2

Loosejaw	0.2	0.2	0.1	NA	0.2
Atlantic Mackerel	0.2	0.1	0.1	NA	0.2
Atlantic Silver Hatchetfish	0.2	0.2	0.1	NA	0.2
Barndoor Skate	0.1	0.2	0.1	NA	0.2
Ocean Pout	0.2	0.1	0.1	NA	0.1
Snakeblenny Fourline	0.2	0.1	0.1	NA	0.1
Spotted Wolffish	0.2	0.1	0.1	NA	0.1
Deepsea Angler	0.1	0.1	0.1	NA	0.1
Scaled Dragonfish	0.2	0.1	0.1	NA	0.1
Deepsea Arctic Sculpin	NA	0.1	0.1	NA	0.1
Snubnose Eels	0.1	0.1	0.1	NA	0.1
Günther's Grenadier	0.1	0.1	0.1	NA	0.1
Sea Bass	0.1	0.1	0.1	NA	0.1
Winter Skate	0.1	0.1	0.1	NA	0.1
Sticklebacks	0.1	0.1	0.1	NA	0.1
Sea Devils	0.1	0.1	0.1	NA	0.1

Appendix 5-6 | Contribution (%) of seven fish taxa to dissimilarity between surveys within benthoscapes. The fish taxa were selected as they were the most abundant taxa among all surveys, among the taxa that contributed the most to dissimilarity between surveys, and were identified during the trawl and UVS surveys.

		Benthoscape																				
		All							Slope pockmarks							Slope dense pockmarks						
Taxon	**Survey**	T2015	T2016$_{Ap}$	T2016$_{Au}$	T2017	T2018	T2019	R2017	T2015	T2016$_{Ap}$	T2016$_{Au}$	T2017	T2018	T2019	R2017	T2015	T2016$_{Ap}$	T2016$_{Au}$	T2017	T2018	T2019	R2017
Silver Hake	T2016$_{Ap}$	7.8	-						10.2	-						9.4	-					
	T2016$_{Au}$	7.6	7.4	-					10.8	11.1	-					8.2	6.8	-				
	T2017	7.6	7.2	6.6	-				11.8	11.5	11.5	-				9	6.6	6.4	-			
	T2018	8.5	8.2	7.9	8	-			11.2	11.3	13.8	13.9	-			10.3	9.1	11.9	9.6	-		
	T2019	7.4	7.2	7.1	6.9	8	-		10	10.6	11	12.6	11.3	-		10.2	8.5	9.2	8.6	8	-	
	R2017	5.2	5.3	2.9	4.7	5.8	5.4	-	NA	NA	NA	NA	NA	NA	-	7.5	6.3	4.4	6.3	9.8	8.1	-
	C2018	4.8	4.5	5.7	4.3	5.5	4.8	7.7	5	5.8	6.1	7.6	6.6	4.8	NA	4.8	3.7	4.1	3.6	7.2	5.3	9.9
Redfish	T2016$_{Ap}$	5.9	-						6.1	-						3.9	-					
	T2016$_{Au}$	6.1	6.2	-					7.1	6.1	-					2.9	3.3	-				
	T2017	5.5	5.2	5.4	-				6.9	4.6	5.7	-				2.8	2.5	2.9	-			
	T2018	5.5	4.6	5.7	4.8	-			6.1	4.3	4.1	5	-			9.6	6.6	7	8.2	-		
	T2019	9.7	8.3	9.3	9.5	8.9	-		11.7	9.1	9.5	10.2	8.9	-		6.8	8.3	5.6	8.2	13.3	-	
	R2017	7.4	5.8	8.7	7.2	6.6	6.4	-	NA	NA	NA	NA	NA	NA	-	4.6	3.8	4.7	4	4	6.2	-
	C2018	5	3.2	6.3	4.6	4.2	6.1	7.7	5.2	5.3	2.1	4.9	4	7.5	NA	5.7	4.2	5.6	4.9	4	7.8	5.2
	T2016$_{Ap}$	2.8	-						5	-						2.4	-					
	T2016$_{Au}$	8.9	7.7	-					8.7	6.3	-					10.1	9.9	-				
	T2017	2.3	0.9	8.3	-				5	1	7.4	-				NA	2.5	10.5	-			
	T2018	2.4	1.1	8.1	0.4	-			5.4	1.9	6.1	1.5	-			NA	2.4	10.9	NA	-		
	T2019	1.9	0.8	7.6	NA	0.3	-		5	1	7.5	NA	1.5	-		NA	2.2	10	NA	NA	-	
	R2017	8.9	9.3	4.4	9.7	9.7	9.5	-	NA	NA	NA	NA	NA	NA	-	13.2	12.6	6.8	13.8	14.8	13.3	-
	C2018	4.6	4	4.2	4.1	4.2	4	10.5	5.6	3.5	3.1	5	3.9	5	NA	3.9	4.3	6	4.4	4.7	3.9	18.3
Longfin Hake	T2016$_{Ap}$	5	-						4.9	-						6.9	-					
	T2016$_{Au}$	4.6	5.1	-					3.1	4.7	-					4.9	4	-				
	T2017	5.5	4.3	5.5	-				6.6	6.4	6.5	-				9.3	3	5.2	-			
	T2018	4.6	3.8	4.9	4.1	-			4.5	5.4	3.8	6.6	-			6.7	1.9	4.4	3.2	-		
	T2019	4.5	4.1	4.6	4.3	3.8	-		4.5	5.2	3.8	6.8	5.1	-		8.5	2.9	4.9	3.4	3.4	-	
	R2017	5.8	4.3	7	4.3	4.5	4.7	-	NA	NA	NA	NA	NA	NA	-	8.5	5.7	7.7	4.6	6	4.7	-
	C2018	6.8	5.2	8.1	5.2	5.6	5.6	4.1	7.4	7	8.5	6	7.3	7.9	NA	9.7	6.6	9	5.5	7.3	5.2	4.6
Marlin- Spike Grenadier	T2016$_{Ap}$	4.2	-						5.2	-						2.3	-					
	T2016$_{Au}$	3.8	3.3	-					2.9	5.2	-					2.9	2.7	-				
	T2017	4.3	4.1	3.7	-				2.2	5.4	2.6	-				3	2.1	2.7	-			
	T2018	4.6	4.3	3.9	4	-			4.7	5.5	4.7	4.8	-			4.5	3.8	3.7	2.8	-		
	T2019	3.7	3.5	3.1	3.3	3.8	-		2.5	5	3	2.7	4.8	-		3	2.4	2.9	2.6	3.8	-	
	R2017	5.8	5.9	6.4	4.9	5.1	5.5	-	NA	NA	NA	NA	NA	NA	-	6.8	6.7	6.7	5.8	5.2	6.1	-
	C2018	5.5	5.6	6	4.5	4.9	5	3.4	6.7	7.2	7	5.5	8	7.1	NA	5.4	5.3	5.4	4.3	3.5	4.8	4.7

Black Dogfish	T2016$_{Ap}$	5.6	-						2.8	-							6.7	-					
	T2016$_{Au}$	2.6	4.1	-					NA	2.7	-						2.9	4.5	-				
	T2017	5.3	6.3	4	-				2.5	3.9	2.4	-					4.2	6.5	1.2	-			
	T2018	5.9	6.8	4.7	6.8	-			0.9	3	0.7	3	-				4.1	6.3	NA	1.8	-		
	T2019	5.3	6.2	4.3	5.9	6.5	-		2.1	3.7	1.9	3.8	2.5	-			6.3	7.3	3	5.3	4.4	-	
	R2017	1.8	3.2	1	3	3.5	3.5	-	NA	NA	NA	NA	NA	NA	-		1.9	3	NA	0.8	NA	2.2	-
	C2018	3	4.3	2.5	4.1	4.9	4.4	3.4	2.3	2.5	2.5	3.2	2.3	3.1	NA		2.4	3.7	NA	1.1	NA	2.6	NA
Skate sp1	T2016$_{Ap}$	5.1	-						5.3	-							7.6	-					
	T2016$_{Au}$	5.7	6	-					5	5	-						6.9	7.2	-				
	T2017	5.7	5.2	6.8	-				5.7	3.6	4.8	-					6.9	7.8	5.5	-			
	T2018	4.9	4.6	6.1	5	-			5.3	3.3	4.6	4	-				6.9	7.7	5.3	4.6	-		
	T2019	4.7	4.7	4.9	5.1	4.5	-		5.4	4.8	4	4.8	4.8	-			5.8	6.7	6.1	5.5	5.7	-	
	R2017	2.2	2.1	3.9	2.2	2	2.3	-	NA	NA	NA	NA	NA	NA	-		2.2	2.9	4.2	2.3	2.9	2	-
	C2018	3.5	3.9	3.6	4.3	3.9	3.3	3.5	3.7	3.8	3.4	4.1	4.4	3.6	NA		3.4	4.2	4.4	2.6	2.7	3	3.2
Witch Flounder	T2016$_{Ap}$	3.6	-						4.2	-							3.7	-					
	T2016$_{Au}$	5	4.7	-					3.4	4	-						4	4	-				
	T2017	3.6	2.5	4.5	-				4	3.5	4.6	-					3.6	2.7	3.2	-			
	T2018	3.8	3	4.2	2.8	-			4.3	4.1	4.7	3	-				7	7.4	2.6	6.6	-		
	T2019	3.7	3.1	4	2.9	3	-		3.5	3.6	3.3	3.2	3.8	-			4.3	3.9	2.7	3.1	4.6	-	
	R2017	4.7	4.1	6.8	4.1	4.6	4.7	-	NA	NA	NA	NA	NA	NA	-		3.8	3.9	6.2	4.5	8	5	-
	C2018	5.2	4.4	7.5	4.4	5.3	5.1	2.2	3.5	2.9	5	1.7	2.2	3	NA		5.1	5.5	8.3	6.6	11.2	6.7	1.3
Atlantic Cod	T2016$_{Ap}$	4.4	-						8	-							4.9	-					
	T2016$_{Au}$	3	2.6	-					8.8	7.3	-						3.3	2.3	-				
	T2017	4.2	4.5	2.2	-				7	6.6	3.6	-					4.7	3.7	1.4	-			
	T2018	3.5	3.7	1.4	3.3	-			6.2	6.1	2.7	3.2	-				5	2.9	0.7	1.6	-		
	T2019	3.6	3.8	1.8	3.4	2.6	-		8.9	8.1	4.4	5.6	5	-			3.9	3.6	2.1	3.1	2.8	-	
	R2017	2.4	2.7	2.2	2.6	2.4	2.4	-	NA	NA	NA	NA	NA	NA	-		2.1	1.9	1.4	1.5	1.4	1.7	-
	C2018	2.4	2.4	0.5	1.9	1.1	1.5	3.9	6.4	5.6	0.9	2.8	2.6	2.9	NA		2.9	1.8	0.6	1	NA	1.7	2.3

		Benthoscape													
		Deep iceberg scours							Deep dense pockmarks						
Taxon	**Survey**	T2015	T2016$_{Ap}$	T2016$_{Au}$	T2017	T2018	T2019	R2017	T2015	T2016$_{Ap}$	T2016$_{Au}$	T2017	T2018	T2019	R2017
Silver Hake	T2016$_{Ap}$	6.2	-						4.1	-					
	T2016$_{Au}$	6.7	6.1	-					7.7	5.5	-				
	T2017	6.2	5	8.1	-				5.2	4.4	5.7	-			
	T2018	6.5	5.4	8.5	4.2	-			7	5.6	4	4	-		
	T2019	6.2	6.3	6	5.8	6.2	-		3.9	3.5	4.7	1.8	3.2	-	
	R2017	3.5	3.6	2.1	4.3	4.7	4.3	-	NA	NA	NA	NA	NA	NA	-
	C2018	4.2	4.1	3.8	4.5	5.7	5.2	4.4	2.4	4.3	7.8	5.1	6.8	4.6	NA
Redfish	T2016$_{Ap}$	8	-						3.5	-					
	T2016$_{Au}$	5.9	7.4	-					8.5	8.4	-				
	T2017	5.4	5.8	5.2	-				4.2	3.9	8.3	-			
	T2018	5.9	6.8	6	4.9	-			4.6	5.2	6.6	4.8	-		

	T2019	9.6	6.6	9.2	8	9.2	-		13.8	13.7	14.7	17	20.2	-	
	R2017	9.2	7.6	10.8	9	9.8	5.7	-	NA	NA	NA	NA	NA	NA	-
	C2018	4.3	3	5.3	2.6	3.8	4.8	12.2	1.9	2.2	5.1	1.7	1.2	9.8	NA
Teleostei sp1	T2016$_{Ap}$	1.6	-						NA	-					
	T2016$_{Au}$	10.2	9	-					7.5	7.1	-				
	T2017	NA	1.8	9.6	-				NA	NA	8	-			
	T2018	NA	1.9	10.5	NA	-			NA	NA	7.8	NA	-		
	T2019	NA	1.5	8.6	NA	NA	-		NA	NA	6.6	NA	NA	-	
	R2017	7.1	7.6	2.5	7.7	8.5	7.9	-	NA	NA	NA	NA	NA	NA	-
	C2018	5.3	6.1	4.4	5.9	7.2	5.8	5.8	4.2	4.3	2.5	4.6	4.7	4.2	NA
Longfin Hake	T2016$_{Ap}$	5.2	-						2.8	-					
	T2016$_{Au}$	4.2	6.4	-					6.2	6.5	-				
	T2017	4.5	3.1	5.6	-				3.2	3.4	7.4	-			
	T2018	4.6	3	6.1	3.2	-			2.2	2.5	7.1	2.6	-		
	T2019	3.1	2.5	4.5	2.3	2.2	-		2.1	4.4	6.2	2.1	1.7	-	
	R2017	4.4	2.8	6.3	3.1	3.2	3.4	-	NA	NA	NA	NA	NA	NA	-
	C2018	4.8	3	7.1	3.2	3.7	3.3	3.5	7.1	NA	10.4	6.9	7	6.1	NA
Marlin- Spike Grenadier	T2016$_{Ap}$	4.3	-						3	-					
	T2016$_{Au}$	3.8	2.5	-					4.9	3.7	-				
	T2017	5.1	3.5	3.2	-				3.5	3.6	5.7	-			
	T2018	4.8	2.9	3	3.5	-			3	3.1	5.1	3.4	-		
	T2019	3.6	2.3	2.4	2.6	2.4	-		2.9	44.7	4.8	3.1	3.4	-	
	R2017	5.6	5.7	5.9	4.6	5.2	5.3	-	NA	NA	NA	NA	NA	NA	-
	C2018	5.1	4.7	5.1	3.9	4.6	4.3	4.4	6	NA	8.4	5.9	6.6	5.1	NA
Black Dogfish	T2016$_{Ap}$	2	-						8.4	-					
	T2016$_{Au}$	1	1.4	-					4.3	5.8	-				
	T2017	2.3	3	1.5	-				8.2	6.9	5.6	-			
	T2018	2.9	3.5	2.1	4.1	-			9.3	6	8.2	7.4	-		
	T2019	4.6	5.3	3.6	5.1	5.4	-		7.6	5.2	6.2	5.4	3.8	-	
	R2017	1.1	1.4	1.1	1.4	1.7	2.8	-	NA	NA	NA	NA	NA	NA	-
	C2018	0.4	1.1	0.4	1.3	2	3.9	1.5	5	2.6	6.2	3.3	1.2	1.5	NA
Skate sp1	T2016$_{Ap}$	6.1	-						3.8	-					
	T2016$_{Au}$	6	5.6	-					6.4	7.3	-				
	T2017	6.5	5.9	7	-				4.1	3.2	7.3	-			
	T2018	6	5.2	6.7	3.9	-			3.4	2.8	7.3	3.1	-		
	T2019	4.3	4.1	4.9	3.6	2.8	-		3.5	4.1	5	3.7	3.9	-	
	R2017	2.3	2.1	3	2.1	1.4	1.4	-	NA	NA	NA	NA	NA	NA	-
	C2018	3.3	3.2	3.6	4	3.8	2.6	1.7	2.2	3.2	3.6	2.6	2.7	1.7	NA
Witch Flounder	T2016$_{Ap}$	2.5	-						1.4	-					
	T2016$_{Au}$	4.5	4.7	-					5.6	5.4	-				
	T2017	2.4	2.1	4.3	-				1.8	1.8	5.8	-			
	T2018	2.8	2.5	4.8	2.8	-			2.8	3.2	4.5	3.3	-		
	T2019	2.6	2.5	4.2	2.4	2.8	-		2.1	2.4	3.9	2.3	1.9	-	
	R2017	4	4	5.8	4.3	4.3	4	-	NA	NA	NA	NA	NA	NA	-
	C2018	5.7	5.6	8	6.2	6.9	5.7	2.2	4.7	4.5	8.1	5.4	6.8	5.7	NA

Atlantic Cod	T2016$_{Ap}$	2.6	-							3.5	-					
	T2016$_{Au}$	1.2	1.9	-						1.9	0.5	-				
	T2017	2.4	3.3	1.6	-					4.2	1.6	0.3	-			
	T2018	1.1	2.7	0.5	2.2	-				3.5	1.4	0.3	1.4	-		
	T2019	1.6	2.7	1.2	2.2	1.3	-			3.1	0.8	NA	0.6	0.7	-	
	R2017	2.8	3.1	3.1	2.9	3.8	3.1	-		NA	NA	NA	NA	NA	NA	-
	C2018	0.7	1.7	0.4	1.3	NA	1	5.4		1.9	0.5	NA	0.4	0.4	NA	NA

Appendix 5-7 | Average total density of fish (ind./m^2) per benthoscape and per survey (± standard error). Total_B: average fish density per benthoscape. Total_S: average fish density per survey. Densities in bold represent the highest fish densities when compared between surveys within benthoscapes ($p < 0.05$).

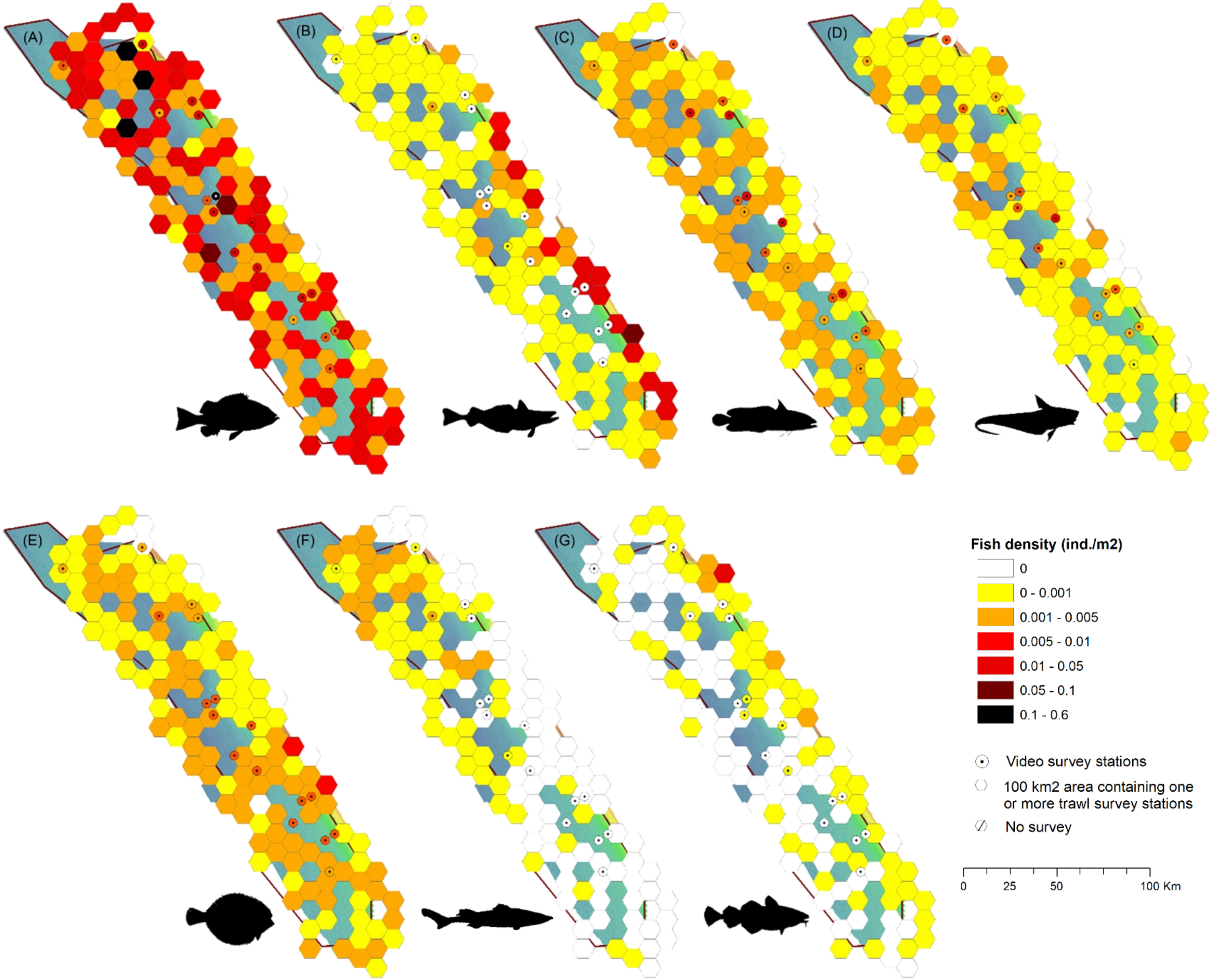
Benthoscape	**Survey**								**Total_B**
	T2015	T2016Ap	T2016Au	T2017	T2018	T2019	R2017	C2018	
Slope pockmarks	0.0202 (± 0.0046)	0.0224 (± 0.0059)	0.0168 (± 0.003)	0.0266 (± 0.009)	0.0391 (± 0.0113)	**0.1251** (± 0.0888)	NA	0.0388 (± 0.0057)	0.0437 (± 0.0163)
Slope dense pockmarks	0.0143 (± 0.006)	0.0130 (± 0.0009)	0.0102 (± 0.0013)	0.0118 (± 0.0015)	0.0274 (± 0.0088)	0.0159 (± 0.0041)	**0.0576** (± 0.0114)	0.0386 (± 0.0055)	0.0199 (± 0.0028)
Deep iceberg scours	0.0088 (± 0.0012)	0.0159 (± 0.002)	0.0080 (± 0.0012)	0.0111 (± 0.001)	0.0114 (± 0.0011)	0.0295 (± 0.0087)	**0.0705** (± 0.0153)	0.0244 (± 0.0046)	0.0175 (± 0.0024)
Deep dense iceberg scours	NA	0.0174 (± 0.0013)	0.0074 (± 0)	0.0199 (± 0)	0.0126 (± 0)	**0.0359** (± 0.0005)	NA	0.0259 (± 0)	0.0211 (± 0.0031)
Deep dense pockmarks	0.0137 (± 0.0011)	0.0145 (± 0.0011)	0.0038 (± 0.001)	0.0122 (± 0.0009)	0.0103 (± 0.0008)	**0.0690** (± 0.0258)	NA	0.0339 (± 0)	0.0192 (± 0.0045)
Total_S	0.0148 (± 0.0019)	0.0183 (± 0.0018)	0.0083 (± 0.0009)	0.0143 (± 0.0017)	0.0196 (± 0.0032)	0.0529 (± 0.0159)	**0.0650** (± 0.0103)	0.0326 (± 0.0032)	0.0231 (± 0.0028)

Appendix 5-8 | Results of ANOVAs performed on square-root transformed fish densities between surveys within benthoscapes and results of post hoc Tukey's HSD pairwise comparisons when significant differences were found.

Fish taxon	Benthoscape	Predictor	Df	Sum Sq	Mean Sq	F	Pr(>F)	Tukey test								
Redfish	Slope pockmarks	Survey	6	0.07	0.01	0.80	0.582									
		Residuals	29	0.44	0.02											
	Slope dense pockmarks	Survey	7	0.03	< 0.01	3.13	0.0139*	All trawls	<	T2018						
		Residuals	29	0.03	< 0.01					R2017 & C2018						
	Deep iceberg scours	Survey	7	0.12	0.02	10.52	< 0.001***	All trawls	<	T2019	<	R2017				
		Residuals	61	0.10	< 0.01			C2018								
	Deep dense iceberg scours	Survey	5	0.02	< 0.01	19.48	0.0171*	T2016$_{Au}$ & T2018	<	T2016$_{Ap}$ & T2017	<	T2019				
		Residuals	3	< 0.01	< 0.01					C2018						
	Deep dense pockmarks	Survey	6	0.16	0.03	10.39	< 0.001***	All trawls	<	T2019						
		Residuals	45	0.12	< 0.01			C2018								
Silver Hake	Slope pockmarks	Survey	6	0.03	< 0.01	0.58	0.74									
		Residuals	29	0.23	0.01											
	Slope dense pockmarks	Survey	7	0.02	< 0.01	1.91	0.104									
		Residuals	29	0.03	< 0.01											
	Deep iceberg scours	Survey	7	< 0.01	< 0.01	3.69	0.00217**	T2016$_{Ap}$ & T2016$_{Au}$	<	All trawls						
		Residuals	61	0.01	< 0.01			R2017 & C2018								
	Deep dense iceberg scours	Survey	5	< 0.01	< 0.01	29.50	0.00938**	All trawls	<	C2018						
		Residuals	3	< 0.01	< 0.01											
	Deep dense pockmarks	Survey	6	< 0.01	< 0.01	25.53	< 0.001***	T2016$_{Au}$ & T2018	<	T2017 & T2019	<	T2016$_{Ap}$	<	T2015	<	C2018
		Residuals	45	< 0.01	< 0.01											
Longfin Hake	Slope pockmarks	Survey	6	0.01	< 0.01	4.21	0.00366**	All trawls	<	T2017	<	C2018				
		Residuals	29	0.01	< 0.01											
	Slope dense pockmarks	Survey	7	0.02	< 0.01	10.80	< 0.001***	R2017 & C2018	<	All trawls						
		Residuals	29	0.01	< 0.01											
	Deep iceberg scours	Survey	7	0.01	< 0.01	13.63	< 0.001***	T2016$_{Au}$	<	T2015	<	All trawls	<	R2017 & C2018		
		Residuals	61	0.01	< 0.01											
	Deep dense iceberg scours	Survey	5	< 0.01	< 0.01	13.77	0.0279*	T2016$_{Ap}$ & T2019	<	All trawls	<	C2018				
		Residuals	3	< 0.01	< 0.01											
	Deep dense pockmarks	Survey	6	0.01	< 0.01	20.06	< 0.001***	T2016$_{Au}$	<	All trawls	<	C2018				
		Residuals	45	< 0.01	< 0.01											
Marlin-Spike Grenadier	Slope pockmarks	Survey	6	0.01	< 0.01	5.59	< 0.001***	All trawls	<	C2018						
		Residuals	29	< 0.01	< 0.01											
	Slope dense pockmarks	Survey	7	0.01	< 0.01	15.68	< 0.001***	All trawls	<	T2018	<	R2017				
		Residuals	29	< 0.01	< 0.01					C2018						
	Deep iceberg scours	Survey	7	0.01	< 0.01	14.39	< 0.001***	All trawls	<	R2017 & C2018						
		Residuals	61	< 0.01	< 0.01											
	Deep dense iceberg scours	Survey	5	< 0.01	< 0.01	0.70	0.66									
		Residuals	3	< 0.01	< 0.01											
	Deep dense pockmarks	Survey	6	0.01	< 0.01	13.07	< 0.001***	T2016$_{Ap}$ & T2016$_{Au}$	<	All trawls	<	C2018				
		Residuals	45	< 0.01	< 0.01											
Witch Flounder	Slope pockmarks	Survey	6	< 0.01	< 0.01	1.69	0.159									
		Residuals	29	0.01	< 0.01											
	Slope dense pockmarks	Survey	7	0.01	< 0.01	16.25	< 0.001***	All trawls	<	R2017 & C2018						
		Residuals	29	< 0.01	< 0.01											
	Deep iceberg	Survey	7	0.01	< 0.01	13.98	< 0.001***	All trawls	<	R2017 & C2018						

	scours	Residuals	61	0.01	< 0.01										
	Deep dense iceberg scours	Survey	5	< 0.01	< 0.01	21.34	0.015*	All trawls	<	C2018					
		Residuals	3	< 0.01	< 0.01										
	Deep dense pockmarks	Survey	6	0.01	< 0.01	25.47	< 0.001***	T2016$_{\text{Au}}$	<	T2016$_{\text{Ap}}$	<	T2015 & T2018	T2017 & T2019	<	C2018
		Residuals	45	< 0.01	< 0.01										
Black Dogfish	Slope pockmarks	Survey	6	< 0.01	< 0.01	0.54	0.77								
		Residuals	29	< 0.01	< 0.01										
	Slope dense pockmarks	Survey	7	< 0.01	< 0.01	0.69	0.684								
		Residuals	29	0.01	< 0.01										
	Deep iceberg scours	Survey	7	< 0.01	< 0.01	2.21	0.0457*	T2016$_{\text{Au}}$	<	All trawls	<	T2019			
		Residuals	61	< 0.01	< 0.01			R2017 & C2018							
	Deep dense iceberg scours	Survey	5	< 0.01	< 0.01	5.86	0.0883								
		Residuals	3	< 0.01	< 0.01										
	Deep dense pockmarks	Survey	6	0.01	< 0.01	6.27	< 0.001***	T2016$_{\text{Au}}$	<	T2016$_{\text{Ap}}$	<	T2018 & T2019			
		Residuals	45	0.01	< 0.01					T2015 & T2017		C2018			
Atlantic Cod	Slope pockmarks	Survey	6	0.01	< 0.01	0.90	0.509								
		Residuals	29	0.03	< 0.01										
	Slope dense pockmarks	Survey	7	< 0.01	< 0.01	0.95	0.487								
		Residuals	29	< 0.01	< 0.01										
	Deep iceberg scours	Survey	7	< 0.01	< 0.01	4.17	< 0.001***	All trawls	<	R2017					
		Residuals	61	< 0.01	< 0.01			C2018							
	Deep dense iceberg scours	Survey	5	< 0.01	< 0.01	0.26	0.911								
		Residuals	3	< 0.01	< 0.01										
	Deep dense pockmarks	Survey	6	< 0.01	< 0.01	2.81	0.021*	T2016$_{\text{Au}}$ & T2019	<	All trawls	<	T2015			
		Residuals	45	< 0.01	< 0.01			C2018							

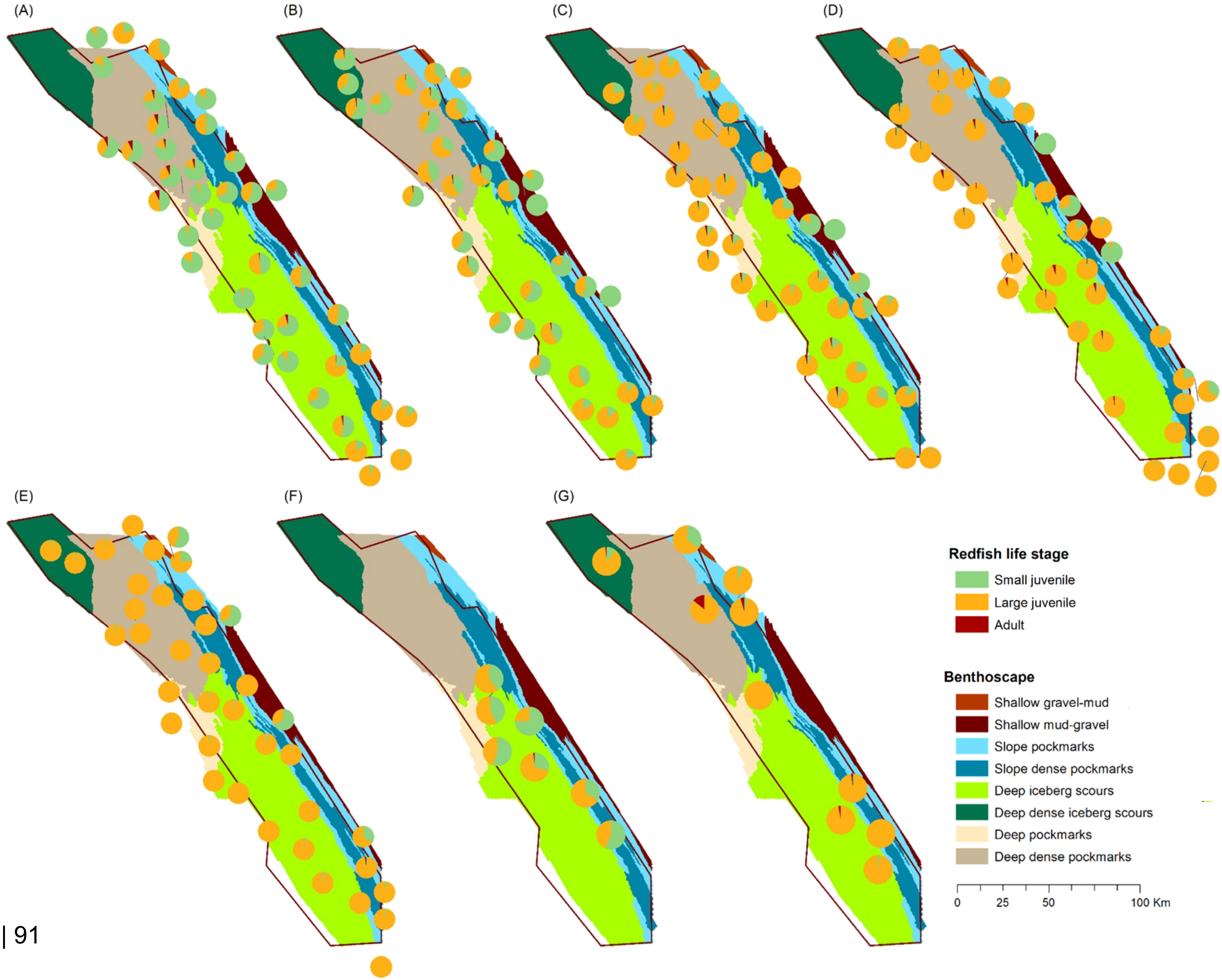
Appendix 5-9 | Average density (ind./m^2) of (A) Redfish, (B) Silver Hake, (C) Longfin Hake, (D) Marlin-Spike Grenadier, (E) Witch Flounder, (F) Black Dogfish, (G) Atlantic Cod per station surveyed by ROPOS and CAMPOD (⊙) and per station surveyed by trawls within hexagonal areas (⬡). Each cell contains one or more stations surveyed by bottom trawls between 2015 and 2019.



Appendix 5-10 | Total number of Redfish measured per life stage and per size class, per benthoscape

Life stage	Size class (cm)	Benthoscape							
		Shallow gravel-mud	Shallow mud-gravel	Slope pockmarks	Slope dense pockmarks	Deep iceberg scours	Deep dense iceberg scours	Deep pockmarks	Deep dense pockmarks
Small juvenile		139	719	832	1149	3056	490	649	2507
	[1-10]	93	246	21	4	4	0	0	6
	[10-20]	46	473	811	1145	3052	490	649	2501
Large juvenile		111	406	4397	3802	9488	1060	2137	5505
	[20-30]	110	388	4197	3441	8171	989	1801	4733
	[30-40]	1	18	200	361	1317	71	336	772
Adult	[40+]	1	1	11	26	120	14	54	158
Total		**251**	**1126**	**5240**	**4977**	**12664**	**1564**	**2840**	**8170**

Appendix 5-11 | Redfish local size structure (as percentage of life stages) per station surveyed by trawl in (A) 2015, (B) 2016, (C) 2017, (D) 2018, (E) 2019, and by UVS in (F) 2017, (G) 2018. Small juvenile: 1-20 cm in total length, Large juvenile: 20-40 cm, Adult: 40+ cm



Appendix 5-12 | Multinomial logistic regression model summaries performed on Redfish size classes between surveys and per benthoscape. The size class [1-10] was used as the reference response factor.

Benthoscape	Gear	Survey	[10-20]			[20-30]			[30-40]			[40+]		
			Coeff.	SE	p-value	Coeff.	SE	p-value	Coeff.	SE	p-value	Coeff.	SE	p-value
Slope pockmarks	Trawl	(Intercept)	5.54	1	<0.001***	6.48	1	<0.001***	3.3	1.02	0.0012***	0.7	1.23	0.5706
		T2016	-2.41	1.05	0.022*	-2.73	1.05	0.0095**	-2.34	1.08	0.0309*	-1.61	1.36	0.2363
		T2017	-1.41	1.23	0.2511	-0.79	1.23	0.517	-0.06	1.25	0.9624	-1.39	1.73	0.423
		T2018	-1.67	1.23	0.1755	0.02	1.23	0.9873	-0.21	1.25	0.8687	-1.39	1.73	0.423
		T2019	-3.01	1.08	0.0052**	-1.42	1.07	0.1839	-1.39	1.1	0.204	-1.54	1.41	0.2728
	UVS	R2017	-	-	-	-	-	-	-	-	-	-	-	-
		C2018	3.95	25.06	0.8749	4.58	25.06	0.8551	4.75	25.07	0.8496	5.75	25.09	0.8189
Slope dense pockmarks	Trawl	(Intercept)	4.27	0.58	<0.001***	4.6	0.58	<0.001***	2.96	0.59	<0.001***	-1.1	1.15	0.3419
		T2016	1.88	1.16	0.1035	2.14	1.16	0.0646	1.42	1.17	0.2239	3.66	1.55	0.0183*
		T2017	0.28	1.16	0.8083	1.74	1.16	0.1329	1.43	1.17	0.2198	1.79	1.68	0.2874
		T2018	-1.14	1.18	0.333	1.71	1.16	0.1395	0.44	1.18	0.7093	1.1	1.83	0.5482
		T2019	-1.79	1.19	0.1339	1.87	1.16	0.1062	1.33	1.17	0.2553	1.79	1.68	0.2874
	UVS	R2017	7.84	23.77	0.74	7.38	23.77	0.76	6.26	23.77	0.79	-10.2	0	0
		C2018	6.08	88.5	0.9452	9.89	88.49	0.911	9.05	88.49	0.9186	12.01	88.5	0.8921
Deep iceberg scours	Trawl	(Intercept)	6.55	0.98	<0.001***	6.64	0.98	<0.001***	5.05	0.99	<0.001***	2.6	1.02	0.0106*
		T2016	0.31	1.4	0.826	0.32	1.4	0.8196	0	1.41	0.9987	-0.04	1.45	0.9804
		T2017	-1.27	1.41	0.3665	0.41	1.41	0.7686	0.3	1.41	0.8306	0.71	1.45	0.6214
		T2018	-3.04	1.41	0.0304*	0.63	1.4	0.6509	0.46	1.4	0.7398	0.68	1.43	0.6352
		T2019	-2.91	1.42	0.0401*	1.02	1.41	0.4693	-0.43	1.41	0.7608	-0.8	1.49	0.5915
	UVS	R2017	-0.23	1.21	0.85	-0.01	1.21	0.99	0.29	1.22	0.81	0.18	1.25	0.89
		C2018	-0.69	18.8	0.9707	3.72	18.77	0.843	4.22	18.77	0.8223	3.27	18.8	0.862
Deep dense iceberg scours	Trawl	(Intercept)	4.57	0.42	0	6.07	0.4	0	3.93	0.42	0	2.5	0.49	<0.001***
		T2016	1.46	0.88	0.097	-0.95	0.88	0.2779	-0.57	0.89	0.5258	-0.31	0.96	0.748
		T2017	-0.6	0.89	0.5013	-0.92	0.88	0.2924	-1.54	0.91	0.0925	-1.81	1.08	0.0933
		T2018	-2.62	0.93	0.0049**	-1.37	0.88	0.1176	-0.94	0.9	0.2972	-1.81	1.08	0.0937
		T2019	-2.17	0.91	0.0175*	0.12	0.87	0.8877	-2.14	0.94	0.0227*	-2.5	1.22	0.0402*
	UVS	R2017	-	-	-	-	-	-	-	-	-	-	-	-
		C2018	8.49	0.37	0	9.2	0.27	0	9.12	0.38	0	8.94	0.67	0
Deep dense pockmarks	Trawl	(Intercept)	5.54	0.41	0	2.4	0.43	<0.001***	4.12	0.41	0	2.62	0.42	<0.001***
		T2016	1.19	1.08	0.2716	4.13	1.09	<0.001***	0.59	1.09	0.5851	0.22	1.11	0.8444
		T2017	-0.97	1.09	0.3714	4.87	1.09	<0.001***	1.07	1.08	0.3256	0.94	1.1	0.3922
		T2018	-1.92	1.09	0.0784	4.64	1.09	<0.001***	0.42	1.09	0.7015	0.33	1.11	0.7666
		T2019	-2.97	1.12	0.0078**	4.85	1.09	<0.001***	-1.17	1.11	0.2899	-2.61	1.48	0.0768
	UVS	R2017	-	-	-	-	-	-	-	-	-	-	-	-
		C2018	-14.12	0.01	0	5.41	13.24	0.6831	2.15	13.25	0.8713	3.94	13.25	0.7665

Appendix 5-13 | Relative representation of Redfish size classes between surveys as predicted in the multinomial models per benthoscape (p <0.05).

Benthoscape	Size class (cm)	Survey-size class relationship						
Slope pockmarks	[1-10]	No difference						
	[10-20]	T2018 T2019	<	T2017 C2018	<	T2015 T2016		
	[20-30]	T2015 T2016	<	All trawls C2018				
	[30-40]	No difference						
	[40+]	No difference						
Slope dense pockmarks	[1-10]	No difference						
	[10-20]	T2018 T2019 C2018	<	T2017	<	T2015 T2016	<	R2017
	[20-30]	R2017	<	T2015 T2016	<	T2017 T2018 T2019 C2018		
	[30-40]	T2016 T2018 R2017	<	T2015 T2017 T2019 C2018				
	[40+]	All trawls R2017	<	C2018				
Deep iceberg scours	[1-10]	No difference						
	[10-20]	T2018 T2019 C2018	<	T2017	<	T2015 T2016 R2017		
	[20-30]	T2015 T2016 R2017	<	T2017 T2018 T2019 C2018				
	[30-40]	T2015 T2016 T2019	<	T2017 T2018 R2017	<	C2018		
	[40+]	No difference						
Deep dense iceberg scours	[1-10]	No difference						
	[10-20]	T2018 T2019	<	C2018	<	T2017	<	T2016
	[20-30]	T2016	<	All trawls C2018				
	[30-40]	T2016	<	C2018				

		T2017 T2019		T2018				
	[40+]	T2019	<	All trawls C2018				
Deep dense pockmarks	[1-10]			No difference				
	[10-20]	T2019 C2018	<	T2017 T2018	<	T2016	<	T2015
	[20-30]	T2015	<	T2016	<	T2017 T2018 T2019 C2018		
	[30-40]	T2016 T2018 T2019	<	T2017	<	T2015 C2018		
	[40+]	T2019		T2015 T2016 T2017 T2018	<	C2018		

Appendix 5-14 | ROPOS and CAMPOD imagery system technical specifications.

Imagery	Specifications	Underwater Video System	
		ROPOS	CAMPOD
Downward-looking videos	Format	mpg	mov
	Size (1 file)	4 GB	31.7 GB
	Length (1 file)	11 minutes	10 minutes
	Resolution (pixels)	1920 x 1080	1920 x 1080
	Frame rate (frame/s)	30	60
	Camera	Zoom-capable HD camera	HD camera
Forward-looking videos	Format	mpg	mov
	Size (1 file)	4 GB	8.6 GB
	Length (1 file)	11 minutes	10 minutes
	Resolution (pixels)	1920 x 1080	1920 x 1080
	Frame rate (frame/s)	30	30
	Camera	Zoom-capable HD camera	HD camera
Still images	Format	jpeg	jpeg
	Size (1 file)	17 to 19 MB	21 MB
	Length (1 file)	NA	NA
	Resolution (pixels)	7360 x 4912	7360 x 4912
	Frame rate (frame/s)	NA	NA
	Camera	Nikon D810	Nikon D810

Chapter 6

Appendix 6-1 | List of deep-sea marine protected and conserved areas in the Canadian Atlantic and Arctic that protect groundfish, fish benthic habitats or corals and sponges (retrieved from DFO's Canada's marine protected and conserved areas), their conservation targets (CT) and their monitoring indicators. MPA: Marine Protected Area, MR: Marine Refuge.

Site	MCA	Conservation targets	Relevant indicator	Ecological component	Source
Laurentian Channel	MPA	• Sea pens • Black Dogfish • Smooth Skate • Porbeagle Shark • Northern Wolffish • Leatherback Turtle • Benthic habitats • Biodiversity	Direct • Species richness • Diversity • Biomass, abundance/density, size distribution, geospatial distribution and taxonomic diversity and richness Indirect • Fauna assemblage composition • Infaunal and epifaunal composition associated with CT • Trophic structure associated with CT • Prey/predator biomass associated with CT	• CWCs provide ecologically important benthic habitats for many species	• DFO website • Lewis et *al*. (2016)
St Anns Bank	MPA	• All benthic, demersal and pelagic habitats • High biodiversity areas • Biological productivity	• Diversity and community composition of the benthos, abundance or biomass and size composition of selected benthic taxa • Fish population abundance, biomass, size distribution, fecundity • Fauna assemblage composition	• CWCs provide ecologically important benthic habitat for many species • Presence of CWCs, sea pens and sponges	• DFO website • Kenchington (2014)
The Gully	MPA	• Cetaceans and their habitats	• Coral distribution, diversity, density	• Presence of CWCs,	• DFO website • DFO (2010c)

		• Benthic habitats and communities • Commercial and non-commercial marine resources	and size structure by species • Proportions of live and dead corals by species • Relative abundances, size distributions, and diversity of selected groundfish	including sea pens • Provide ecologically important benthic habitat for many species	
Emerald Basin	Sponge Conservation Area (MR)	• *Vazella pourtalesi* glass sponges	NA	• Provide ecologically important benthic habitat for many species	• DFO website
Sambro Bank	Sponge Conservation Area (MR)	• *Vazella pourtalesi* glass sponges	NA	• Provide ecologically important benthic habitat for many species	• DFO website
Western/Emerald Banks	MR	• *Groundfish species and their benthic habitats* • *Important benthic habitats for Haddock*	NA	• Significant spawning and nursery ground for Haddock	• DFO website
Eastern Canyons	MR	• CWCs (*e.g., Paragorgia, Primnoa, Keratoisis)* • *Desmophyllum pertusum* (*Lophelia pertusa*) coral reefs • Deep-water frontier area (*i.e.*, marine area without history of fishing in Canadian waters)	NA	• Only known living *Desmophyllum pertusum* coral reef in Canadian Atlantic • CWCs provide ecologically important benthic habitat for many species	• DFO website
Division 3O (Grand Banks)	Coral closure (MR)	• CWCs sea pens, and sponges	NA	• Provide ecologically important benthic habitat for many species	• DFO website
Funk Island	Deep Closure (MR)	• Atlantic Cod and their benthic habitat	NA	• Protection of Atlantic Cod habitats benefits other species of	• DFO website

				commercial interest	
Northeast Newfoundland Slope	Closure (MR)	• CWCs and sponges • Biodiversity	NA	• Provide ecologically important benthic habitat for many species	• DFO website
Hawke Channel	Closure (MR)	• Atlantic Cod and their benthic habitat	NA	• Protection of Atlantic Cod habitats benefits other species of commercial interest	• DFO website
Hopedale Saddle	Closure (MR)	• CWCs and sponges • Biodiversity	NA	• Provide ecologically important benthic habitat for many species • Benefits Beluga population	• DFO website
Hatton Basin	Conservation Area (MR)	• CWCs and sponges • Sensitive benthic habitats	NA	• Provide ecologically important benthic habitat for many species • Benefits Narwhal population	• DFO website
Davis Strait	Conservation Area (MR)	• CWCs, sea pens and sponges • Sensitive benthic habitats	NA	• Provide ecologically important benthic habitat for many species	• DFO website
Disko Fan	Conservation Area (MR)	• Narwhal and their habitats (*e.g.*, CWC habitats) • CWCs	NA	• CWCs provide ecologically important benthic habitat for many species	• DFO website

Appendix 6-2 | List of recommendations provided throughout the manuscript regarding fish ecology, fish monitoring and conservation area management.

Theme	Recommendation	Chapter
Ecology	• Consider the spatial configuration of the small-scale habitat characteristics within the broader-scale landscape to predict fish distribution and assess small-scale habitat associations	Chapter 2
	• Integrate proximity between habitats of different complexity to predict fish distribution and assess small-scale habitat associations	Chapter 2
	• Assess the influence of seasonality and time of day on fish density and fish size	Chapters 2 & 3
	• Assess the influence of additional abiotic parameters on fish density: bottom current or topography, size or density of abiotic habitat features, and habitat cover	Chapter 2
	• Assess the influence of additional biotic parameters on fish density: fish size, prey-predator interactions, habitat cover	Chapter 2
	• Increase the study area extent - inside and in the vicinity of the MPA - to delimit boundaries of benthic habitat types, and survey benthic habitat type diversity (especially in the shallow parts of the channel)	Chapter 2
	• Conduct further research on the distributions of Sandlance and Barracudina to improve taxonomic identification and understanding of their ecological role as key forage fish in the MPA	Chapter 2
	• Assess the influence of food supply availability, quality and quantity in relation to intra and inter-competition on fish size	Chapter 3
	• Assess the influence of individual invertebrate taxon density at the small scale on fish size	Chapter 3
	• Assess the influence of additional biotic parameters on fish size: individual invertebrate taxon density, spatial extent of benthic habitat types, medium to large-scale distribution of microhabitats, prey-predator interactions	
	• Collect more data in *Kophobelemnon*-dominated habitats to fill data gaps present in this study	Chapter 3
	• Assess the influence of additional ecological parameters on fish reaction: taxon-specific density, prey-predator interactions as presence/absence data and/or specific densities of known prey or predators of the fish of interest	Chapter 4
Monitoring	• Follow a standardized sampling approach between surveys, between dives and between habitats to maximize unbiased and balanced assessments	Chapter 4

	• Integrate how long a fish is seen in the FoV, how and when the UVS is detected, and the timing of the response behavior	Chapter 4
	• Allow for an acclimation period where no data is collected at the beginning of video transects	Chapter 4
	• Prefer slow UVS speeds and longer transects to allow fish to acclimate to the presence of the UVSs	Chapter 4
	• Collaborate with taxonomists to improve faunal identification	All
	• Use the same survey gear from one survey to another. If not conduct surveys during the same months to reduce seasonality bias and compare fish assemblage characteristics	Chapters 3 & 5
	• Conduct a dedicated survey during which UVSs and bottom trawls be deployed in trawlable habitats to complement *in-situ* visual data with biological data to enable the creation of a local baseline on fish taxon size at maturity and help with fish identification at a low taxonomic level	All
	• Integrate fish mobility and time of day when designing the sampling strategy	Chapter 3
	• Maintain speeds of 1-2 km/h and an altitude of 1-3 m above seafloor during UVS surveys	Chapter 5
	• Follow a straight-line trajectory, across depth, and try as much as possible to survey multiple substrates or and habitats	Chapter 5
	• Use still images and continuous videos together as complementary methods to improve fish assessment	Chapter 5
	• UVS selected for survey should be equipped with both forward and downward-facing cameras and lasers for FoV measurements, density calculations and size measurements	Chapters 3, 4 & 5
	• UVS selected for survey should be equipped with appropriate lighting to help with fauna identification	Chapter 5
	• When selecting camera systems for benthic surveys, consider both survey system technical specifications and capabilities (*e.g.*, camera field of view, laser scaling), as well as both the at-sea imagery data management and the subsequent set-up of image analysis facilities	Chapter 5
Conservation	• Conduct UVS surveys in all benthoscapes for a better assessment of fish distribution within the MPA from multiple survey gear types	Chapter 5
	• Survey preferred areas of distribution of conservation target fish species based on previous DFO trawl survey data	Chapters 2 & 5
	• Integrate fish into survey design	Chapter 5
	• Monitor both coral and non-coral habitats	Chapters 2, 3 & 4