SPATIAL RISK: HOW PREDATOR DISTRIBUTIONS SHAPE HABITAT USE BY AGE-0 COD

by

© Evelyn MacRobert

A Thesis submitted to the
School of Graduate Studies
In partial fulfillment of the requirements for the degree of

Master of Science
Department of Biology
Memorial University of Newfoundland

August 2020
St. John's, Newfoundland and Labrador

Abstract

The early life history stages of fish experience greater mortality rates than older conspecifics, primarily as a result of predation. Determining which habitats pose the highest predation "risk" can help in understanding habitat use by juvenile cod. In two field experiments, I examined spatial and temporal segregation of age-0 Atlantic (*Gadus morhua*) and Greenland (*Gadus macrocephalus ogac*) cod from piscivorous fishes. In Chapter 2, I used underwater video footage to construct a habitat map and locate age-0 Atlantic and Greenland cod in Newman Sound, Bonavista Bay, Newfoundland. Age-0 cod significantly associated with uniform eelgrass habitat, as opposed to less use of kelp or bare substrates, with all individuals observed within 1 m of eelgrass patches. In Chapter 3, I tested seasonal and diel habitat associations of 37 individuals of four known piscivorous fish species – age-1+ Atlantic and Greenland cod, cunner (*Tautogolabrus adspersus*), and shorthorn sculpin (*Myoxocephalus scorpius*) – using passive acoustic telemetry. Habitat use differed significantly among species. Season significantly affected habitat use for Greenland cod, cunner, and sculpin, whereas diel period significantly influenced habitat use for cunner. Greenland cod and cunner preferred eelgrass in the spring, then transitioned to deeper water habitats (kelp, sparse vegetation, and bare substrates) during summer and fall. Overall, piscivores primarily occupied shallow habitats in spring, and transitioned to deeper water habitats during summer and fall, outside the eelgrass beds frequented by age-0 cod. My thesis demonstrates spatial and temporal segregation of age-0 cod into nursery eelgrass habitat, apart from their predators.

Acknowledgements

I'll begin by thanking my supervisors, Dr. Bob Gregory and Dr. Paul Snelgrove. Without them, this project would not have been possible. Their guidance and feedback have been invaluable throughout this process. My supervisors, along with my committee member, Dr. Pierre Pepin, helped keep my thesis pointed in the right direction as I waded through copious amounts of data. I am forever grateful.

The largest undertaking of this thesis was undoubtably the field work. The field work for this thesis was more than tiny little me could possibly do alone, and the following people have my utmost gratitude in helping pull it all together. Curtis Pennell and Brianna Newton were instrumental for tagging the numerous fish needed for this study. In addition to Curtis Pennell and Brianna Newton, Shannon Anderson and Kate Dalley were a tremendous help in deploying the acoustic receiver array needed for this project to succeed. I appreciate the dedication of the entire field crew – Kate Dalley, Shannon Anderson, Phil Sargent, Brianna Newton, Dr. Bob Gregory, Emile Geissinger, Emma Cook, Chelsea Bloom, Andrew Cuff, and Paula Lundrigan – who spent hours helping collect video and bathymetry data through both blisteringly hot days and copious amounts of rain (plus that one night seine).

I would like to thank Dustin Schornagel, Danielle Quinn and Rémi Daigle for their invaluable help and expertise in R and getting me up to speed on all things coding. I also thank my colleagues in the Snelgrove lab. In particular, I thank my fellow lab mates Emma Cook and Emilie Geissinger for allowing me to bounce ideas off of them. I am also grateful to my fellow OSC grad students. Our numerous potlucks kept me sane.

This research was sponsored by the NSERC Canadian Healthy Oceans Network (CHONe) and its Partners: Department of Fisheries and Oceans Canada and INREST (representing the Port of Sept-Îles and City of Sept-Îles). Through CHONe, I presented my work on multiple occasions, and networked with researchers across Canada. Fisheries and Oceans Canada provided the equipment, boat time, and expertise needed to complete this thesis, in addition to transportation and accommodations in TNNP.

Last but not least, I would like to thank my family for always cheering for me from the sidelines. Their support could be felt from miles away.

Table of Contents

List of Tables

List of Figures

List of Appendices

Chapter 1 : The role of habitat in mortality and predation

Habitat selection by prey species reflects a trade-off between foraging and predation risk as individuals seek to maximize growth while minimizing mortality (Werner and Gilliam 1984). Prey species respond to perceived risk by altering their behaviour (Lima and Dill 1990), in response to predator species (Savino and Stein 1989; Laurel and Brown 2006) or predator behaviour (Gotceitas *et al*. 1995). Resource availability, condition (starvation level) of the individual, and risk level (assessed in terms of encounter rates, escape rate, and time of vulnerability) also play a role in these decisions (Lima and Dill 1990; Hugie and Dill 1994). When considering habitat selection of predators and prey in the context of Evolutionary Game Theory (an equilibrium in behavioural strategies that can persist in a population; Maynard Smith 1982), evidence suggests that individuals select habitat solely on habitat riskiness (Hugie and Dill 1994). As such, prey select productive habitat in the absence of predators, but select more protective habitats in the presence of a predator despite lower productivity (Hugie and Dill 1994).

Atlantic cod (*Gadus morhua*) and Greenland cod (*Gadus macrocephalus ogac*) inhabit the Northern Atlantic Ocean, with overlapping geographic ranges along the eastern coast of Canada (Scott and Scott 1988). Atlantic cod occur along the northern boundary of the Atlantic Ocean from the Baltic Sea west along Iceland and Greenland to Baffin Island, and along the eastern coast of North America from Labrador to New England (Scott and Scott 1988; Rose 2007). This species also occurs along the European coast in the Norwegian and Baltic seas, and into the Bay of Biscay (Scott and Scott 1988). Greenland cod are distributed from Alaska to Greenland along the Arctic coast of Canada (Scott and Scott 1988; Rose 2007) and as far south as Nova Scotia (Mikhail and Welch 1989). Atlantic and Greenland cod co-occur off the coast of Newfoundland, Canada.

In Newfoundland, Atlantic and Greenland cod spawn as early as February (Scott and Scott 1988) in both inshore and offshore water (Anderson *et al.* 1995). Pelagic Atlantic cod eggs hatch into pelagic larvae (Templeman 1981) that are transported by currents (Pepin and Helbig 2011) and winds (Ings *et al.* 2008) toward nursery habitat (Dalley and Anderson 1997; Ings *et al.* 1997). Greenland cod spawn demersal eggs that attach to kelp or rocks (Rose 2007), and hatch into pelagic larvae (Mikhail and Welch 1989). Both species settle as juveniles into nursery eelgrass habitats (Ings *et al.* 1997, 2008; Grant and Brown 1998a); doing so in a single ‘pulse’ in July or August in Greenland cod (Laurel *et al.* 2003b; Ings *et al.* 2008), and in multiple (up to five) pulses from July to November in Atlantic cod (Methven and Bajdik 1994; Grant and Brown 1998a; Ings *et al.* 2008). Settlement of juveniles into eelgrass nursery beds provides food (Sogard 1997; Renkawitz *et al.* 2011) and cover from predation (Gotceitas *et al.* 1997; Linehan *et al.* 2001; Laurel *et al.* 2003a; Gorman *et al.* 2009). Age-0 cod remain in nursery habitat for their first year, feeding predominantly on crustacean zooplankton, including cladocerans and copepods, and benthic invertebrates (Lough *et al.* 1989; Keats and Steele 1992; Grant and Brown 1998b; Renkawitz *et al.* 2011). After spending their first year in coastal shallows, age-1 cod move into the surrounding environment to occupy deeper water (Gregory and Anderson 1997; Shapiera *et al.* 2014), and toward the outer shelf at age-2 (Anderson and Gregory 2000), using cobble and macroalgae habitats as cover (Gregory and Anderson 1997). At age-3, juvenile cod begin seasonal migrations offshore (Anderson and Gregory 2000), inhabiting offshore habitats similar to that of adults (Taggart *et al.* 1994).

Natural mortality in fishes varies greatly over their life history, but highest mortality typically occurs before maturity and decreases with age as body size increases (Peterson and Wroblewski 1984; Houde 1987; Julliard *et al.* 2001). The limited mobility of early life history stages – eggs and larvae – leaves them more susceptible to predation, compared to larger, morphologically more developed individuals (Hewitt *et al.* 1985). Starvation can also contribute to high mortality in larvae (Miller and Kendall 2009). Mortality decreases as larvae develop into juveniles, corresponding to increases in size and mobility and the behavioural ability of individuals to find refuge in protective habitat (Houde 1987; Sogard 1997; Miller and Kendall, 2009).

High mortality rates continue beyond the larval stage into juvenile cod, largely as a result of predation (Houde 1987; Sogard 1997; Anderson and Gregory 2000; Miller and Kendall 2009). In order to reduce predation risk, juveniles may alter their behaviour by schooling or selecting habitat that offers protection from predators. Many aquatic species forage in vegetation as an antipredation strategy; however, this behaviour may result in a trade-off between feeding and predation risk (reviewed by Lima and Dill 1990). Additionally, species-specific behaviour may also depend on the foraging behaviour of dominant predators (Savino and Stein 1989). Juvenile cod often settle in structured habitats, such as eelgrass (Gotceitas *et al.* 1997; Linehan *et al.* 2001; Laurel *et al.* 2003b), kelp (Gotceitas *et al.* 1995), and cobble (Gotceitas and Brown 1993; Fraser *et al.* 1996), as refuge from predation. Decreased predator mobility (Gotceitas and Colgan 1989), prey visibility (Lindholm *et al.* 1999), and capture success (Gotceitas and Colgan 1989; Tupper and Boutilier 1995a; Gotceitas *et al.* 1997) all reduce predation rate in structured environments. Higher predation rates commonly occur in less structured habitats, such as sandy seabed (Tupper and Boutilier 1995b; Linehan *et al*. 2001). When occupying unstructured habitats, age-0 cod may alter their behaviour by forming schools to reduce predation risk (Laurel *et al.* 2004). In coastal Newfoundland, age-0 cod may saturate available eelgrass beds before utilizing other, less favorable habitats (Grant and Brown 1998a; Anderson and Gregory 2000), suggesting either active habitat selection or high mortality rates outside eelgrass beds.

A wide diversity of predators target juvenile fishes, including birds, marine mammals, invertebrates, and larger fish, including conspecifics (Scott and Scott 1988; Linehan *et al.* 2001; Laurel *et al.* 2003b; Miller and Kendall 2009). Fish predation tends to be gape-limited, with piscivores consuming prey up to half their own body length (Paradis *et al.* 1996; Sogard 1997), but most fish predators are three to four times larger than their prey (Bogstad *et al.* 1994). This size window leaves age-0 Atlantic cod susceptible to older cod age classes, such as age-1 and 2 (Grant and Brown 1998b). As juveniles grow, increased body size leads to decreased predation (Houde 1987; Sogard 1997). This reduction in predation pressure gives larger juveniles (age 1-2) the freedom to move away from eelgrass beds, so that age-1 Atlantic cod occur in greater numbers in non-vegetated areas than in eelgrass (Cote *et al.* 2013).

In Newman Sound, Newfoundland, cunner (*Tautogolabrus adspersus*), sculpin (*Myoxocephalus scorpius*), white hake (*Urophycis tenuis*) and older conspecifics all potentially feed on age-0 Atlantic and Greenland cod (Linehan *et al.* 2001; Laurel *et al.* 2003a). Although previous research identified older conspecifics of both species as predominant predators of juvenile cod in nursery habitats (Bogstad *et al.* 1994), tethering studies in Newman Sound suggest that cunner and sculpin also play a large role (Laurel *et al.* 2003a); e.g., up to 50% of predator attacks in shallow water (< 3 m) can be attributed to cunner (Linehan *et al.* 2001).

Piscivores – like older cod – may inhabit deeper water as a result of temperature preferences (Clark and Green 1991), or to avoid their own predators (e.g., river otters; Cote *et al.*

2008). In order to avoid predators, some species of piscivorous fish undergo diel movements (Keats 1990; Linehan *et al.* 2001; Ivanova *et al.* 2018). Despite the restriction that vegetation places on the movements of larger-bodied fishes (Gotceitas and Colgan 1989), nearshore eelgrass beds are still occupied by these predators (Linehan *et al.* 2001; Laurel *et al.* 2003a). In Newman Sound, age-1 and -2 Atlantic and Greenland cod move into shallow water at night to forage (Keats 1990; Linehan *et al.* 2001). Sculpin also increase foraging activity at night (Linehan *et al.* 2001; Landry *et al.* 2019). Habitat preferences for age-1+ Atlantic and Greenland cod include kelp (Gotceitas *et al.* 1997), whereas sculpin frequent both bare substrates and eelgrass (Linehan *et al.* 2001; Laurel *et al.* 2003a). Cunner defend territories at various depths (0.7-13.0 m: Pottle and Green 1979a), predominantly on rocky substrates (Pottle and Green 1979b; Tupper and Boutilier 1997).

While there is overwhelming evidence demonstrating the importance of eelgrass beds for reducing predator-induced mortality on juvenile cod, predation nevertheless occurs in these habitats. Determining which habitat types pose the highest predation “risk” can help our understanding of the ecology of juvenile cod. Highest predator density occurs over large eelgrass patches (Laurel *et al.* 2003a; Gorman *et al.* 2009), despite greater predation rates in smaller patches (Laurel *et al.* 2003a). If age-0 cod respond to predator presence (Ryan *et al.* 2012), then the movements of those predators may shape their distribution within the eelgrass beds. However, just as prey move freely to avoid their predators, these predators also move freely and follow their prey (Hugie and Dill 1994). In order to examine the spatial segregation of age-0 cod from their predators, I conducted two field experiments to address “two sides of the same coin”. The first experiment examined the distribution of age-0 cod within eelgrass habitat. The second investigated the habitat use of piscivorous fishes within this habitat among seasons and diel periods.

In Chapter 2, I examine habitat use by age-0 Atlantic and Greenland juvenile cod in Newman Sound, Bonavista Bay, Newfoundland. Using underwater video footage collected from August through October 2016, I describe vegetation and mineral substrate within my study area, and construct a habitat map. I then locate age-0 cod within that area to determine the association of juvenile cod across habitat types. I also locate and determine habitat associations for larger piscivorous fish species known to predate of age-0 cod. Based on past research conducted in Newman Sound, I expected that juvenile cod would strongly associate with eelgrass.

In Chapter 3, I use acoustic telemetry data to determine the habitats occupied by four piscivorous fish species – age-1+ Atlantic cod, age-1+ Greenland cod, cunner, and shorthorn sculpin – collected from May through November 2016 – and overlay the spatial detections onto the habitat map from Chapter 2. Specifically, I determine habitat use based on frequency of positions as a proxy for habitat preference, and examine this use in relation to season and diel period. Previous telemetry studies in Newman Sound focused on age-1 to -3 Greenland cod (Shapiera *et al.* 2014) and age-2 to -3 Atlantic cod (e.g. Cote *et al.* 2003, 2004). Other survey data collected by SCUBA (Keats 1990; Cote *et al.* 2001) and by tethering (Linehan *et al.* 2001; Laurel *et al.* 2003a) indicate habitat use by age-1 cod, sculpin, and cunner, but do not fully explore temporal patterns in habitat use by season or diel period. I conducted my experiment to increase understanding of seasonal and diel variations in predator habitat association. In Newman Sound, kelp and sand habitats generally occur in deeper water than eelgrass. As such, I expected piscivores would predominantly occupy deeper waters.

I conclude with Chapter 4, where I discuss how the results of my two data chapters offer insight into how predators influence habitat selection by age-0 cod by using proportional habitat use by these predators as a proxy for habitat riskiness. Additionally, I discuss the implications of segregation of predator and prey, both spatially and temporally.

References

Anderson, J. T., Dalley, E. L., and Carscadden, J. E. (1995). Abundance and distribution of pelagic 0-group cod (*Gadus morhua*) in Newfoundland waters: inshore versus offshore. Canadian Journal of Fisheries and Aquatic Sciences 52, 115–125. doi:10.1139/f95-011

Anderson, J. T., and Gregory, R. S. (2000). Factors regulating survival of northern cod (NAFO 2J3KL) during their first 3 years of life. ICES Journal of Marine Science 57, 349–359. doi:10.1006/jmsc.1999.0530

Bogstad, B., Lilly, G. R., Mehl, S., Pálsson, Ó. K., and Stefánsson, G. (1994). Cannibalism and year-class strength in Atlantic cod (*Gadus morhua* L.) in Arcto-boreal ecosystems (Barents Sea, Iceland, and eastern Newfoundland). ICES Marine Science Symposia 198, 576–599.

Clark, D. S., and Green, J. M. (1991). Seasonal variation in temperature preference of juvenile Atlantic cod (*Gadus morhua*), with evidence supporting an energetic basis for their diel vertical migration. Canadian Journal of Zoology 69, 1302–1307. doi:10.1139/z91-183

Cote, D., Gregory, R. S., Morris, C. J., Newton, B. H., and Schneider, D. C. (2013). Elevated habitat quality reduces variance in fish community composition. Journal of Experimental Marine Biology and Ecology 440, 22–28. doi:10.1016/j.jembe.2012.11.006

Cote, D., Gregory, R. S., and Stewart, H. M. J. (2008). Size-selective predation by river otter (*Lontra canadensis*) improves refuge properties of shallow coastal marine nursery habitats. Canadian Journal of Zoology 86, 1324–1328. doi:10.1139/Z08-120

Cote, D., Moulton, S., Frampton, P. C. B., Scruton, D. A., and McKinley, R. S. (2004). Habitat use and early winter movements by juvenile Atlantic cod in a coastal area of Newfoundland. Journal of Fish Biology 64, 665–679. doi:10.1111/j.1095-8649.2004.00331.x

Cote, D., Moulton, S., Scruton, D. A., and McKinley, R. S. (2001). Microhabitat use of juvenile Atlantic cod in a coastal area of Bonavista Bay, Newfoundland. Transactions of the American Fisheries Society 130, 1217–1223. doi:10.1577/1548-8659(2001)130<1217:MUOJAC>2.0.CO;2

Cote, D., Ollerhead, L. M. N., Scruton, D. A., and McKinley, R. S. (2003). Microhabitat use of juvenile Atlantic cod in a coastal area of Newfoundland determined by 2D telemetry. Marine Ecology Progress Series 265, 227–234. doi:10.3354/meps265227

Dalley, E. L., and Anderson, J. T. (1997). Age-dependent distribution of demersal juvenile Atlantic cod (*Gadus morhua*) in inshore/offshore northeast Newfoundland. Canadian Journal of Fisheries and Aquatic Sciences 54, 168–176. doi:10.1139/cjfas-54-S1-168

Fraser, S., Gotceitas, V., and Brown, J. A. (1996). Interactions between age-classes of Atlantic cod and their distribution among bottom substrates. Canadian Journal of Fisheries and Aquatic Sciences 53, 305–314. doi:10.1139/f95-183

Gorman, A. M., Gregory, R. S., and Schneider, D. C. (2009). Eelgrass patch size and proximity to the patch edge affect predation risk of recently settled age 0 cod (*Gadus*). Journal of Experimental Marine Biology and Ecology 371, 1–9. doi:10.1016/j.jembe.2008.12.008

Gotceitas, V., and Brown, J. A. (1993). Substrate selection by juvenile Atlantic cod (*Gadus morhua*): effects of predation risk. Oecologia 93, 31–37.

Gotceitas, V., and Colgan, P. (1989). Predator foraging success and habitat complexity: quantitative test of the threshold hypothesis. Oecologia 80, 158–166. doi:10.1007/BF00380145

Gotceitas, V., Fraser, S., and Brown, J. A. (1995). Habitat use by juvenile Atlantic cod (*Gadus morhua*) in the presence of an actively foraging and non-foraging predator. Marine Biology 123, 421–430. doi:10.1007/BF00349220

Gotceitas, V., Fraser, S., and Brown, J. A. (1997). Use of eelgrass beds (*Zostera marina*) by juvenile Atlantic cod (Gadus morhua). Canadian Journal of Fisheries and Aquatic Sciences 54, 1306–1319. doi:10.1139/f97-033

Grant, S. M., and Brown, J. a. (1998a). Diel foraging cycles and interactions among juvenile Atlantic cod (*Gadus morhua*) at a nearshore site in Newfoundland. Canadian Journal of Fisheries and Aquatic Sciences 55, 1307–1316. doi:10.1139/cjfas-55-6-1307

Grant, S. M., and Brown, J. A. (1998b). Nearshore settlement and localized populations of age 0 Atlantic cod (*Gadus morhua*) in shallow coastal waters of Newfoundland. Canadian Journal of Fisheries and Aquatic Sciences 55, 1317–1327.

Gregory, R. S., and Anderson, J. T. (1997). Substrate selection and use of protective cover by juvenile Atlantic cod *Gadus morhua* in inshore waters of Newfoundland. Marine Ecology Progress Series 146, 9–20. doi:10.3354/meps146009

Hewitt, R. P., Theilacker, G. H., and Lo, N. C. H. (1985). Causes of mortality in young jack mackerel. Marine Ecology - Progress Series 26, 1–10. doi:10.3354/meps026001

Houde, E. D. (1987). Fish early life dynamics and recruitment variability. American Fisheries Society Symposium 2, 17–29.

Hugie, D. M., and Dill, L. M. (1994). Fish and game: a theoretic approach to habitat selection by predators and prey. Journal of Fish Biology 45, 151–169.

Ings, D. W., Gregory, R. S., and Schneider, D. C. (2008). Episodic downwelling predicts recruitment of Atlantic cod, Greenland cod and white hake to Newfoundland coastal waters. Journal of Marine Research 66, 529–561.

Ings, D. W., Schneider, D. C., and Methven, D. a. (1997). Detection of a recruitment signal in juvenile Atlantic cod (*Gadus morhua*) in coastal nursery areas. Canadian Journal of Fisheries and Aquatic Sciences 54, 25–29. doi:10.1139/cjfas-54-S1-25

Ivanova, S. V., Kessel, S. T., Landry, J., O'Neill, C., McLean, M. F., Espinoza, M., Vagle, S., Hussey, N. E., and Fisk, A. T. (2018). Impact of vessel traffic on the home ranges and movement of shorthorn sculpin (*Myoxocephalus scorpius*) in the nearshore environment of the high Arctic. Canadian Journal of Fisheries and Aquatic Sciences 75, 2390–2400. doi:10.1139/cjfas-2017-0418

Julliard, R., Stenseth, N. C., Gløsæter, J., Lekve, K., Fromentn, J.-M., and Danielssen, D. S. (2001). Natural mortality and fishing mortality in a coastal cod population: A release-recapture experiment. Ecological Applications 11, 540–558.

Keats, D. W. (1990). A nocturnal inshore movement of juvenile cod *Gadus morhua* L. in eastern Newfoundland. Journal of Experimental Marine Biology and Ecology 139, 167–173. doi:10.1016/0022-0981(90)90144-2

Keats, D. W., and Steele, D. H. (1992). Diurnal feeding of juvenile cod (*Gadus morhua*) which migrate into shallow water at night in eastern Newfoundland. Journal of Northwest Atlantic Fishery Science 13, 7–14. doi:10.2960/J.v13.a1

Landry, J. J., Kessel, S. T., McLean, M. F., Ivanova, S. V., Hussey, N. E., O’Neill, C., Vagle, S., Dick, T. A., and Fisk, A. T. (2019). Movement types of an arctic benthic fish, shorthorn sculpin (*Myoxocephalus scorpius*), during open-water periods in response to biotic and abiotic factors1. Canadian Journal of Fisheries and Aquatic Sciences 76, 626–635. doi:10.1139/cjfas-2017-0389

Laurel, B. J., and Brown, J. A. F. (2006). Influence of cruising and ambush predators on 3-dimensional habitat use in age 0 juvenile Atlantic cod *Gadus morhua*. 329, 34–46. doi:10.1016/j.jembe.2005.08.003

Laurel, B. J., Gregory, R. S., and Brown, J. A. (2003a). Predator distribution and habitat patch area determine predation rates on age-0 juvenile cod *Gadus* spp. Marine Ecology Progress Series 251, 245–254. doi:Doi 10.3354/Meps251245

Laurel, B. J., Gregory, R. S., and Brown, J. A. (2003b). Settlement and distribution of age-0 juvenile cod, *Gadus morhua* and *G. ogac*, following a large-scale habitat manipulation. Marine Ecology Progress Series 262, 241–252. doi:10.3354/meps262241

Laurel, B. J., Gregory, R. S., Brown, J. A., Hancock, J. K., and Schneider, D. C. (2004). Behavioural consequences of density-dependent habitat use in juvenile cod *Gadus morhua* and *G. ogac*: the role of movement and aggregation. Marine Ecology Progress Series 272, 257–270. doi:10.3354/meps272257

Lima, S. L., and Dill, L. M. (1990). Behavioral decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology 68, 619–640. doi:10.1139/z90-092

Lindholm, J. B., Auster, P. J., and Kaufman, L. S. (1999). Habitat-mediated survivorship of juvenile (0-year) Atlantic cod *Gadus morhua*. Marine Ecology Progress Series 180, 247–255. doi:10.3354/meps180247

Linehan, J. E., Gregory, R. S., and Schneider, D. C. (2001). Predation risk of age-0 cod (*Gadus*) relative to depth and substrate in coastal waters. Journal of Experimental Marine Biology and Ecology 263, 25–44. doi:10.1016/S0022-0981(01)00287-8

Lough, R. G., Valentine, P. C., Potter, D. C., Auditore, P. J., Bolz, G. R., Neilson, J. D., and Perry, R. I. (1989). Ecology and distribution of juvenile cod and haddock in relation to sediment type and bottom currents on eastern Georges Bank. Marine Ecology Progress Series 56, 1–12.

Maynard Smith, J. (1982). 'Evolution and the Theory of Games'. (Cambridge University Press: Cambridge.)

Methven, D. A., and Bajdik, C. (1994). Temporal variation in size and abundance of juvenile Atlantic cod (*Gadus morhua*) at an inshore site off eastern Newfoundland. Canadian Journal of Fisheries and Aquatic Sciences 51, 78–90.

Mikhail, M. Y., and Welch, H. E. (1989). Biology of Greenland cod, *Gadus ogac*, at Saqvaqjuac, northwest coast of Hudson Bay. Environmental Biology of Fishes 26, 49–62.

Miller, B. S., and Kendall, A. W. (2009). 'Early life history of marine fishes'. University of California Press. doi:10.5860/choice.47-2003

Paradis, A. R., Pepin, P., and Brown, J. A. (1996). Vulnerability of fish eggs and larvae to predation: review of the influence of the relative size of prey and predator. Canadian Journal of Fisheries and Aquatic Sciences 53, 1226–1235. doi:10.1139/f96-051

Pepin, P., and Helbig, J. A. (2011). Distribution and drift of Atlantic cod (*Gadus morhua*) eggs and larvae on the northeast Newfoundland Shelf. Canadian Journal of Fisheries and Aquatic Sciences 54, 670–685. doi:10.1139/f96-317

Peterson, I., and Wroblewski, J. S. (1984). Mortality rate of fishes in the pelagic ecosystem. Canadian Journal of Fisheries and Aquatic Sciences 41, 1117–1120. doi:10.1139/f84-131

Pottle, A., and Green, M. (1979a). Territorial behaviour of the north temperate labrid, *Tautogolabrus adspersus*. Canadian Journal of Zoology 57, 2337–2347.

Pottle, R. A., and Green, J. M. (1979b). Field observations on the reproductive behaviour of the cunner, *Tautogolabrus adspersus* (Walbaum), in Newfoundland. Canadian Journal of Zoology 57, 247–256.

Renkawitz, M. D., Gregory, R. S., and Schneider, D. C. (2011). Habitat dependant growth of three species of bottom settling fish in a coastal fjord. Journal of Experimental Marine Biology and Ecology 409, 79–88. doi:10.1016/j.jembe.2011.08.004

Rose, G. A. (2007). 'Cod: The ecological history of the North Atlantic fisheries'. (Breakwater Books Ltd.: St. John's, NL.)

Ryan, M. R., Killen, S. S., Gregory, R. S., and Snelgrove, P. V. R. (2012). Predators and distance between habitat patches modify gap crossing behaviour of juvenile Atlantic cod (*Gadus morhua,* L. 1758). Journal of Experimental Marine Biology and Ecology 422–423, 81–87. doi:10.1016/j.jembe.2012.04.017

Savino, J. F., and Stein, R. A. (1989). Behavioural interactions between fish predators and their prey: effects of plant density. Animal Behaviour 37, 311–321. doi:10.1016/0003-3472(89)90120-6

Scott, W., and Scott, M. (1988). 'Atlantic fishes of Canada'. Canadian Bulletin of Fisheries and Aquatic Sciences 219.

Shapiera, M., Gregory, R. S., Morris, C. J., Pennell, C. J., and Snelgrove, P. V. R. (2014). Season and site fidelity determine home range of dispersing and resident juvenile Greenland cod

Gadus ogac in a Newfoundland fjord. Marine Ecology Progress Series 503, 235–246. doi:10.3354/meps10729

Sogard, S. M. (1997). Size-selective mortality in the juvenile stage of teleost fishes: a review. Bulletin of Marine Science 60, 1129–1157.

Taggart, C. T., Anderson, J., Bishop, C., Colbourne, E., Hutchings, J., Lilly, G., Morgan, J., Murphy, E., Myers, R., Rose, G., and Shelton, P. (1994). Overview of cod stocks, biology, and environment in the Northwest Atlantic region of Newfoundland, with emphasis on northern cod. ICES Marine Science Symposium 198, 140–157.

Templeman, W. (1981). Vertebral numbers in Atlantic cod, *Gadus morhua*, of the Newfoundland and adjacent areas, 1947-71, and their use for delineating cod stocks. Journal of Northwest Atlantic Fishery Science 2, 21–45. doi:10.2960/j.v2.a3

Tupper, M., and Boutilier, R. G. (1995a). Effects of habitat on settlement, growth, and postsettlement survival of Atlantic cod (*Gadus morhua*). Canadian Journal of Fisheries and Aquatic Sciences 52, 1834–1841. doi:10.1139/f95-176

Tupper, M., and Boutilier, R. G. (1997). Effects of habitat on settlement, growth, predation risk and survival of a temperate reef fish. Marine Ecology Progress Series 151, 225–236. doi:10.3354/meps151225

Tupper, M., and Boutilier, R. G. (1995b). Size and priority at settlement determine growth and competitive success of newly settled Atlantic cod. Marine Ecology Progress Series 118, 295–300. doi:10.3354/meps118295

Werner, E. E., and Gilliam, J. F. (1984). The ontogenetic niche and species interactions in size-structures populations. Annual Review of Ecology, Evolution and Systems 15, 393–425.

Co-Authorship Statement

The research described in Chapter 2 was designed by Evelyn MacRobert, in collaboration with Dr. Bob Gregory and Dr. Paul Snelgrove. Evelyn MacRobert collected and analysed the data, and prepared the thesis. Dr. Bob Gregory and Dr. Paul Snelgrove contributed ideas and advised on data processing. Evelyn MacRobert will be lead author on any manuscripts arising from this thesis, and will include those collaborators who have contributed significantly to the manuscripts as co-authors.

Chapter 2 : Habitat use by age-0 Atlantic (*Gadus morhua*) and Greenland (*G. macrocephalus ogac*) cod in coastal Newfoundland

Abstract

The early life history stages of fish experience greater mortality rates than older conspecifics, primarily as a result of size-selective predation. In order to maximize survival, juveniles of many fish species choose nursery habitats that provide food and reduce predation risk by impeding predator movements. However, mortality remains high even in these protective environments. In Newfoundland, juvenile Atlantic cod (*Gadus morhua*) settle from the plankton into coastal nearshore nursery habitat in pulses from July through November, whereas Greenland cod (*Gadus macrocephalus ogac*) settle in a single pulse in July or August. Age-0 cod remain in this nursery habitat for their first year of life. In order to characterize their habitat association following settlement, I conducted video transects in Newman Sound, Bonavista Bay, Newfoundland during August, September, and October of 2016. Multiple discrete habitats characterize the chosen site, Newbridge Cove – eelgrass, kelp, and sparse vegetation – bounded by areas of bare substrate. I reviewed the transect videos to create a habitat map of the site and to identify habitat association of juvenile cod and their predators. Eelgrass occurred in nearshore depths less than 7 m. Kelp often occurred adjacent to eelgrass, extending into 9 m deep water. Sparse vegetation and bare substrate surrounded eelgrass and kelp patches. Age-0 cod significantly associated with eelgrass habitat, with all individuals observed within 1 m of eelgrass patches. Older piscivorous conspecifics, white hake (*Urophycis tenuis*), and sculpin (*Myoxocephalus scorpius*) were observed too infrequently in the videos to determine habitat associations, but I observed both species in kelp, and hake in eelgrass. Cunner (*Tautogolabrus adspersus*) significantly associated with kelp. My results demonstrate that juvenile cod selected

uniform eelgrass, suggesting that occupying this habitat benefits age-0 cod. Piscivores were rarely observed in eelgrass, suggesting that one benefit may be spatial segregation of age-0 cod from their predators.

Introduction

Juveniles of Atlantic (*Gadus morhua*) and Greenland (*Gadus macrocephalus ogac*) cod utilize nursery habitat as a source of food (Sogard 1997; Renkawitz *et al.* 2011) and refuge from predators (Houde 1987; Gotceitas *et al.* 1997; Linehan *et al.* 2001; Laurel *et al.* 2003a; Gorman *et al.* 2009). Following spawning as early as February, eggs of Atlantic and Greenland cod (Scott and Scott 1988) hatch into pelagic larvae (Templeman 1981; Mikhail and Welch 1989). Currents (Pepin and Helbig 2011) and winds (Ings *et al.* 2008) transport Atlantic cod larvae towards nursery habitat (Dalley and Anderson 1997; Ings *et al.* 1997). Upon hatching, the pelagic larvae develop into demersal juveniles and settle into coastal nursery habitat. In Newfoundland and elsewhere, cod favour eelgrass as nursery habitat (Tveite 1984; Gotceitas *et al.* 1997; Laurel *et al.* 2004; Cote *et al.* 2013) with young-of-the-year cod settling into eelgrass beds (Laurel *et al.* 2004) before moving into other habitats as they develop and grow (Anderson and Gregory 2000). Age-0 Greenland cod settle into eelgrass in a single recruitment 'pulse' in July/August (Laurel *et al.* 2003b; Ings *et al.* 2008), whereas the extended spawning season of Atlantic cod (Hardy 1978) results in age-0s settling in multiple recruitment 'pulses' (as many as five) from early July to mid-November (Methven and Bajdik 1994; Grant and Brown 1998).

Juvenile fish experience higher rates of mortality than older conspecifics (Peterson and Wroblewski 1984; Anderson and Gregory 2000), and predation drives much of juvenile mortality (Houde 1987; Chen and Watanabe 1989; Tupper and Boutilier 1995a). As such, strategies for mitigating predation likely play a large role in juvenile fish survival. Structurally complex habitat, such as eelgrass, kelp, and cobble, reduce predation mortality by decreasing predator mobility (Gotceitas and Colgan 1989), visibility (Lindholm *et al.* 1999), and capture success (Gotceitas and Colgan 1989; Tupper and Boutilier 1995a) as a result of leaf density and spatial complexity (Gotceitas et al. 1997; Lindholm et al. 1999). Higher predation rates occur in habitats such as bare sand (Tupper and Boutilier 1995a; Linehan *et al.* 2001), which lacks structure in which juveniles can hide while increasing the distance at which predators may detect them (Lindholm *et al.* 1999). Cobble physically prevents larger predators from accessing juveniles which may hide in interstitial spaces (Gotceitas *et al.* 1995) whereas vegetative habitat obscures juveniles from a predator's view (Lindholm *et al.* 1999) and provides obstructive cover (Gotceitas and Colgan 1989).

Eelgrass patches of intermediate complexity support higher abundances of age-0 cod than small or large beds (Thistle *et al.* 2010), despite lower predation rates in large patches (Laurel *et al.* 2003a). Given higher predation risk along patch edges (Gorman *et al.* 2009), elevated abundances of juvenile cod in patchy eelgrass may reflect a trade-off between refuge from predators and food availability. Patchy eelgrass allows juveniles to forage in sandy areas for benthic invertebrates and zooplankton (Thistle *et al.* 2010), while also providing access to refuge from predators. Habitat depth also influences predation rates. Outside eelgrass beds, mortality rates increase with depth (Linehan *et al.* 2001) where larger piscivorous fishes (e.g., age-1+ juvenile cod) occur during the day (Methven and Bajdik 1994).

Purpose and Hypotheses

This chapter examines the habitat association of juvenile cod and their predators based on video transects, and also serves as context for Chapter 3, where I specifically investigate habitat use by predators of juvenile cod. In order to determine if age-0 cod and their predators segregate spatially, I first created a habitat map of my study site in Newbridge Cove, Newman Sound, to investigate habitat associations of age-0 cod and their predators in contrasting habitats. Given evidence of the vital role that eelgrass nursery habitat plays in reducing predation rate on juvenile Atlantic and Greenland cod, I predicted that age-0 individuals would occur primarily over eelgrass and that their predators would be primarily in non-eelgrass habitats.

Methods

Study Area

Newman Sound, a fjord located on the north east coast of Newfoundland, Canada in Bonavista Bay, measures 22 km long and 2 km wide, with a total area of 44 km^2. A shallow sill (18 m depth) divides the fjord into an inner and outer basin, with maximum depths of 55 m and 300 m respectively. Subtidal habitat consists primarily of eelgrass (*Zostera marina*), kelp (*Saccharina latissima*), and bottom covered with sparse vegetation. Four temperature loggers placed in the sound at 3-m depth indicated that mean daily temperature in shallows occupied by age 0 juveniles ranged from 1.3 °C to 16.8 °C between May 1 and November 28, 2016.

The study site, Newbridge Cove (48.5838° N, 53.9269° W), is located along the northern shore of the inner basin of Newman Sound (Figure 2.1). I selected this site because of its multiple vegetation types – eelgrass, kelp, and sparse vegetation – and published accounts by my colleagues (e.g., Warren *et al.* 2010; Gregory *et al.* 2019). Juvenile movements between sites increase where continuous shoreline habitats occur (Laurel *et al.* 2004); therefore, I chose this study site for its discrete pockets of vegetative habitat bounded by open areas of sand and cobble, presumably less desirable habitats for age-0 cod. This lack of habitat continuity, in addition to well-documented site fidelity by juvenile cod (Tupper and Boutilier 1995a, 1995b) reduced the need to consider movements of age-0 cod in and out of the study site.

Video Transects

In order to determine habitat and location of age-0 cod within Newbridge Cove, I collected video footage along transects (Figure 2.2). Transects were spaced 25 m apart, and collected in a grid format to account for any spatial gradients that may be present either along the shoreline or with increasing depth. I collected video on eight 200 m transects parallel to shore and seven 250 m transects perpendicular to shore (Figure 2.2). The perpendicular transects extended from within 25 m of the shoreline to the 10 m isobath. I collected transect videos up to three times throughout the season, during the day, to account for any habitat saturation effects that may occur over the course of the season. Each collection period lasted one or two days each – August 17-18, September 27-28 and October 20, 2016, and took ~4 hours to collect a full set of transects. I could not control for variations in tidal height because of time limitations during the sampling periods. Because recruitment pulses of juvenile cod and habitat saturation may lead to reduced site fidelity (Laurel *et al.* 2004), I collected video imagery at an additional five 100 m transects adjacent to the site in September and October, 2016 to confirm the absence of age-0 cod in the areas surrounding the focal study site.

I used two cameras for video sampling – a waterproof live feed camera with white LED lights and a GoPro camera (either a Hero 3+ or Hero 4) in a waterproof casing – affixed to a polyethylene frame (Figure 2.3) towed behind a 5.5 m open fibreglass-hulled boat, powered using a 75 hp Honda outboard engine. Three zinc weights totalling 3.6 kg sank the frame, and I controlled the distance to the bottom using a 1-m long chain. I used the live feed camera to observe the habitat in real time through a portable DVD player, enabling me to raise and lower the camera as needed to avoid collisions with obstacles (e.g., boulders). This approach reduced net avoidance problems, and allowed sampling of complex habitats that might damage other types of gear (e.g. seining). Video collection by SCUBA divers provides representative fish assemblages compared to traditional underwater visual surveys (Pelletier *et al*. 2011) and I expected this finding to apply to my towed video camera as well.

High resolution video was recorded with a GoPro camera in 1080p HD format, which captured images of the seafloor 1 m in width. I linked these videos to GPS data recorded during my video collection. I reviewed the GoPro videos and recorded timestamps every time vegetation composition changed. Vegetation – eelgrass beds, kelp beds, and sparse vegetation – that covered 50% or more of the video frame was recorded as “primary” vegetation. Vegetation covering less than 50% of the video frame was recorded as “secondary” vegetation. A given frame could potentially contain both primary and secondary vegetation, or neither. I also recorded primary and secondary substrates – sand, cobble, and boulder. The number of timestamps recorded for each transect ranged from 2 to 27.

All fish observed in these videos were identified, and the habitat occupied by the individuals was recorded. Juvenile count data included both age-0 Atlantic and Greenland cod, because I could not distinguish the two species on video. At this lifestage, age-0 juvenile cod share an ecological niche (Linehan *et al.* 2001) and are challenging to visually distinguish because of similarities in morphology (size, shape, and colour; Methven and McGowan 1998) and the resolution limitations of the video imagery. Seine hauls, which surveyed an area of approximately 880 m^2 (55 m from shore by 16 m across shore; Schneider *et al.* 1997; Laurel *et al.* 2003a), conducted at Newbridge Cove during the study period provided estimates of the ratios of the two species. The ratio of Greenland to Atlantic age-0 cod varied from 2.7:1 in August to 1:5 for September and October. Therefore, age-0 cod observed in August transects were likely Greenland cod, whereas age-0 cod observed in September and October were likely Atlantic cod.

Bathymetry Collection and Habitat Mapping

I collected bathymetric data for a stretch of shoreline 1 km in length by 500 m (at the widest point) centered on Newbridge Cove using a single-beam echo-sounder. These data were standardized to correct for tidal height using tide chart data from the Canadian Hydrographic Service (CHS; tides.gc.ca) for Newman Sound. I downloaded data from CHS as hourly Height Above Datum (HAD), then interpolated to determine HAD to the nearest minute relevant to my video collections. I interpolated a bathymetric data surface (5 m cells) from the standardized sounder data by modeling the data as a triangulated irregular network (TIN), using point samples as nodes to create Delaunay triangles, where each triangle represents a linear interpolation surface of these nodes (ArcGIS 10.5).

I calculated GPS coordinates for the habitat observations using R (R Core Team 2019) by linking observations to the GPS data recorded during video collection by time stamp. Using the "Feature to Polygon" tool to convert the point data of primary vegetation and primary substrate to polygons, I constructed a habitat map in ArcMap 10.5. I adjusted the polygons by hand to remove overlap of the vegetation polygons and to smooth edges. After mapping primary substrate, I combined the vegetation and substrate polygons to create the final map, plotting coordinates of age-0 cod on the map to visualize habitat associations at the scale of habitat patches (~10s of meters).

Statistical analysis

I determined habitat associations of age-0 cod using chi-square tests with expected values that represented the proportion of habitat area represented on the habitat map, because total observations of cod were limited (50 individuals). I calculated p-values using Monte Carlo simulations with 2000 iterations, because many cell values were small (< 5 individuals). Tests were conducted for overall association, as well as weekly association. I followed all significant tests with post-hoc tests to determine significant pairs, using the R package *chisq.posthoc.test* (Ebbert 2019), with p-values adjusted using the Benjamini and Hochberg (1995) procedure of false discovery rate. I analyzed habitat associations for predator species observed in the videos in the same way.

Results

Habitat Mapping

Eelgrass and sand habitats were located near shore and restricted to depths less than 7 m, covering an area of 14,633 m^2 with an average depth of 4.6 m (Figure 2.4). Kelp beds and sand extended along the shelf encompassing a total area of 29,011 m^2, but limited to depths less than 9 m with a mean depth of 5.9 m. A small portion (5%; 1,500 m^2) of the kelp beds overlapped cobble and boulder substrates. Sparse vegetation occurred over both sandy and rocky areas to the maximum depth of the survey area (10 m), and covered an area of 131,072 m^2. Roughly a third (39,964 m^2) of the sparse vegetation occurred on cobble substrate whereas the rest (91,108 m^2) occurred over sand (Figure 2.4). Bare sand (4,925 m^2) and bare cobble (11,293 m^2) occurred along the shoreline (< 4 m deep) as well as along the seaward edge of the areas with sparse vegetation (> 8 m) and extended outward to the end of the shelf.

Habitat Association of Age-0 Cod

I observed a total of 50 age-0 Atlantic and Greenland cod in all my video transects – four in August, 30 in September, and 16 in October (Figure 2.5). Seine hauls in the study area (e.g., Gregory et al. 2019) indicated that the ratio of Greenland to Atlantic age-0 cod varied throughout my study period in 2016. In August, this ratio was 2.7:1. The abundance of Atlantic cod in the seine hauls increased throughout the season, resulting in a ratio of 1:5 for September and October as additional pulses of age-0 Atlantic cod settled into my study area.

Age-0 cod associated significantly with eelgrass ($X^2 = 479.1$, df = 3, $p < 0.001$; Table 2.1a, b) and sand ($X^2 = 19.4$, df = 3, $p = 0.012$; Table 2.1c, d). Vegetation and substrate use did not noticeably change between sampling months. Most of the 50 age-0 cod observations occurred in eelgrass habitat with sand substrate – either inside eelgrass patches or within one meter of a patch. Four individual cod occurred over kelp and one occurred over sparse vegetation (Figure 2.5). Most individuals (40) were observed in uniform eelgrass patches, with no secondary vegetation (Figure 2.5).

Habitat Association of Predator Species

I observed few predators in my video transects, except for cunner which were observed 1904 times (Figure 2.5). Cunner significantly associated with kelp ($X^2 = 811.64$, df = 3, $p < 0.001$; Table 2.2a, b) and sand ($X^2 = 79.272$, df = 3, $p = 0.0001$; Table 2.2c, d). Habitat use did not noticeably change among sampling periods. Cunner used both uniform vegetation patches (i.e., no secondary vegetation), as well as areas with kelp and sparse vegetation as secondary vegetation (Figure 2.5)

I observed too few age-1+ cod (7), sculpin (1), or hake (3) to detect significant differences in habitat associations. All observations of age-1+ cod and sculpin occurred over sparsely vegetated habitats, with some individuals occurring in areas with kelp as secondary vegetation. Hake were observed in eelgrass, kelp, and sparse vegetation in equal proportions; with no distinct preferences among secondary vegetation types (Figure 2.5).

Discussion

Age-0 Atlantic and Greenland cod were significantly associated with eelgrass habitat in this study, but not with kelp or sparse vegetation, strongly suggesting highest cod abundances occurred in eelgrass habitat. Despite increasing observations over the course of the study, habitat association did not change, suggesting that habitat saturation did not occur. This finding confirms previous studies in Newfoundland (Gotceitas *et al.* 1997; Laurel *et al.* 2003b; Schneider *et al.* 2008) and elsewhere (Tupper and Boutilier 1995a), however age-0 cod have also been observed associating with kelp in depths greater than 10 m (Cote *et al.* 2001), beyond the extent of my survey. Unlike beach seines, my video system allowed greater spatial resolution of habitat association, and also allowed me to examine more than two habitat types both together and separately. Age-0 cod preferred uniform habitats (e.g., eelgrass beds) with no secondary vegetation or substrates. However, in years of strong recruitment to the nearshore, age-0 cod also school over barren seabeds, presumably once eelgrass beds become saturated (Laurel *et al.* 2004). In my study, age-0 cod were rarely observed outside of eelgrass beds and although high predation rates outside eelgrass beds (Linehan *et al*. 2001) may result in this pattern, there was no evidence of habitat saturation.

I rarely observed piscivorous fishes in eelgrass habitats. Piscivorous age-1+ cod were only observed in sparse vegetation. Age-1+ cod generally occur in deeper water during the day

(Methven and Bajdik 1994; Cote *et al.* 2001), associating with rocky substrates, kelp, and gravel seabeds (Keats *et al.* 1987; Gotceitas *et al.* 1997; Gregory and Anderson 1997). Previous studies attribute this behaviour to avoidance of avian (e.g., mergansers, osprey, and terns) and terrestrial (e.g., otters) predators (Linehan *et al.* 2001; Schneider *et al.* 2008; Cote *et al.* 2008a, 2008b), during the day. In my study, the sparsely vegetated habitats where I observed age-1+ cod during the day largely occurred at depths greater than eelgrass beds, suggesting that age-0 cod are spatial separated from their older conspecifics during the day. At night, age-1+ cod move into shallow water (Keats 1990; Cote *et al*. 2001; Linehan *et al*. 2001) to forage (Pihl, 1982), potentially increasing predation risk for age-0 cod. Diel patterns of habitat use for piscivorous fishes were not examined in this study, but are examined further in Chapter 3.

Cunner associated with uniform and mixed (i.e., with secondary vegetation) kelp and sand habitats, but not any other habitat, in contrast to reports of cunner being associated with rock reefs, boulder-strewn substrate, and exposed bedrock (Pottle and Green 1979a, 1979b; Tupper and Boutilier 1997). The cunner in my study were generally small juveniles, similar to those reported in previous work on their distribution (Joseph *et al.* 2006), and may not be piscivorous; instead feeding on zooplankton and benthic invertebrates (Levin 1994). However, I also observed cunner large enough to be piscivorous based on previous studies (> 11 cm SL; Linehan *et al*. 2001; Gorman *et al*. 2009). Large cunner occupy deep water (Linehan *et al.* 2001) and they are less abundant at night than during the day (Linehan *et al.* 2001; Joseph *et al.* 2006) because of their quiescent behaviour (Pottle and Green 1979a), but they nevertheless can represent the dominant predator of age-0 cod in shallow (< 3 m) water during the day (Linehan *et al.* 2001). The few sculpin and hake I observed precluded determination of habitat associations for these species, however those I observed were distributed across various habitats. Hake use eelgrass as nursery habitat (Joseph *et al.* 2006; Ings *et al.* 2008), and laboratory studies suggest that shorthorn sculpin primarily occupy sand substrate except when prey (age-0 cod) are present, when sculpin "hide" in eelgrass to ambush their prey (Laurel and Brown 2006). The association of predators with non-eelgrass habitats, combined with the strong association of age-0 with eelgrass I observed here, implies spatial separation of juvenile cod in nursery habitat from their predators at the scale of habitat patches.

In my study, I observed a limited number of juvenile cod (50 individuals). Despite the high resolution of the habitat association data I captured with my video transects, the narrow field of vision of the camera (~ 1 m) may have resulted in missed observations. Additionally, the structure of kelp arguably creates pockets of refuge that may obscure juveniles from view. However, I deployed my camera at a downward facing angle that enabled observation of movement in the area ahead of the camera. When moving through kelp, none of the movements ahead of the camera indicated fish escaping into refugia in response to the approach of the camera. Nevertheless, I acknowledge that I may have missed seeing some individuals when I collected my video imagery. The potential for refuge to obscure individuals was reduced in sparsely vegetated and barren sand habitats. While I cannot discount avoidance behaviours entirely, the strong presence of cunner in sparse vegetation suggests that this potential bias was limited.

Structurally complex habitats, such as cobble, macroalgae, moderate to dense eelgrass, and rock reefs provide protection from predation by reducing encounter rates (Lindholm *et al.* 1999), restricting predator movements (Savino and Stein 1982), and decreasing their capture success (Gotceitas and Colgan 1989; Tupper and Boutilier 1995a; Gotceitas *et al.* 1997). In structurally simple habitat (e.g., sand) juvenile fish sometimes form aggregations as a behavioural tactic to reduce risk from piscivorous fishes (Laurel *et al.* 2004). Given a choice between eelgrass and cobble, juvenile cod in laboratory experiments choose cobble in the presence of a predator unless eelgrass blade density exceeded 1000 stems m^{-2} (Gotceitas *et al.* 1997). Below this density, age-0 cod choose cobble substrate, where they can hide in interstitial spaces (Gotceitas and Brown 1993; Gotceitas *et al.* 1995; Fraser *et al.* 1996), increasing their survival (Tupper and Boutilier 1995b). The mottled colouration of juveniles may provide further "camouflage" from visual predators by helping them blend in with pebble substrate (Lough *et al.* 1989). In the absence of eelgrass, juvenile cod may find refuge from predators in either macroalgae or cobble (Gjøsæter 1987; Gotceitas and Brown 1993; Gotceitas *et al.* 1995; Gregory and Anderson 1997). Most habitat selection studies examine uniform habitat patches. In my study, age-0 cod were associated with uniform eelgrass patches, indicating a preference for this habitat at my study site and suggesting that mixed vegetation habitats (i.e., habitat with secondary vegetation) may offer fewer cover benefits.

In addition to providing a refuge from predators, eelgrass supports higher juvenile cod growth rates compared to other habitats (e.g., cobble: Tupper and Boutilier 1995b; Renkawitz *et al.* 2011). Trade-offs between protection from predators and access to food may lead age-0 cod to choose patchy eelgrass of intermediate complexity (Thistle *et al.* 2010) despite increased predation rates in such habitats (Laurel *et al*. 2003b; Gorman *et al*. 2009). Eelgrass provides habitat for many invertebrates (Orth *et al.* 1984) at densities greater than surrounding habitat (Sogard 1992; Hasegawa *et al.* 2008), and it has been suggested that sandy bottom functions as an important feeding habitat by providing opportunities to forage (Borg *et al.* 1997; Thistle *et al*. 2010). In my study, age-0 cod that were not in eelgrass were always within 1 m their primary habitat. In the absence of predators, laboratory studies have demonstrated that habitat preference of age-0 switches from coarse (cobble, gravel) to fine (sand) mineral substrates (Fraser *et al.* 1996). However, in my study, cunner (a common predator of age-0 cod) were frequently observed in habitats outside eelgrass beds. Juvenile cod may forage in bare sand (Borg *et al.* 1997), however, the trade-off between refuge and food may explain why I observed a few age-0 cod individuals adjacent to eelgrass beds.

Conclusion

I characterized habitat associations of age-0 Atlantic and Greenland cod with eelgrass beds, kelp beds, sparse vegetation, and bare substrate in a spatially discrete site. Age-0 cod significantly associated with shallow water eelgrass beds and sand substrate located in water less than 7 m deep, consistent with the importance of eelgrass beds as a nursery habitat in coastal waters. Cunner significantly associated with kelp beds surrounding eelgrass habitat. The low frequency of observation of older piscivorous conspecifics, sculpin, and hake precluded determination of habitat associations. The few observations of these predators indicated nearly complete absence in eelgrass habitat, where almost all my age 0 cod were found. This pattern implies spatial segregation of juveniles from their predators, and that habitat adjacent to eelgrass carries greater risk of mortality by piscivorous fishes.

References

Anderson, J. T., and Gregory, R. S. (2000). Factors regulating survival of northern cod (NAFO 2J3KL) during their first 3 years of life. ICES Journal of Marine Science 57, 349–359. doi:10.1006/jmsc.1999.0530

Benjamini, Y., and Hochberg, Y. (1995). Controlling the false discovery rate: a practical and powerful approach to multiple testing. Journal of Royal Statistical Society. Series B (Methodological) 57, 289–300.

Borg, Å., Pihl, L., and Wennhage, H. (1997). Habitat choice by juvenile cod (*Gadus morhua* L.) on sandy soft bottoms with different vegetation types. Helgoländer Meeresuntersuchungen 51, 197–212.

Chen, S., and Watanabe, S. (1989). Age dependence of natural mortality coefficient in fish population dynamics. Nippon Suisan Gakkaishi 55, 205–208. doi:10.2331/suisan.55.205

Cote, D., Gregory, R. S., Morris, C. J., Newton, B. H., and Schneider, D. C. (2013). Elevated habitat quality reduces variance in fish community composition. Journal of Experimental Marine Biology and Ecology 440, 22–28. doi:10.1016/j.jembe.2012.11.006

Cote, D., Gregory, R. S., and Stewart, H. M. J. (2008a). Size-selective predation by river otter (*Lontra canadensis*) improves refuge properties of shallow coastal marine nursery habitats. Canadian Journal of Zoology 86, 1324–1328. doi:10.1139/Z08-120

Cote, D., Moulton, S., Scruton, D. A., and McKinley, R. S. (2001). Microhabitat use of juvenile Atlantic cod in a coastal area of Bonavista Bay, Newfoundland. Transactions of the American Fisheries Society 130, 1217–1223. doi:10.1577/1548-8659(2001)130<1217:MUOJAC>2.0.CO;2

Cote, D., Stewart, H. M. J., Gregory, R. S., Gosse, J., Reynolds, J. J., Stenson, G. B., and Miller, E. H. (2008b). Prey selection by marine-coastal river otters (*Lontra canadensis*) in Newfoundland, Canada. Journal of Mammalogy 89, 1001–1011. doi:10.1644/07-MAMM-A-192.1

Dalley, E. L., and Anderson, J. T. (1997). Age-dependent distribution of demersal juvenile Atlantic cod (*Gadus morhua*) in inshore/offshore northeast Newfoundland. Canadian Journal of Fisheries and Aquatic Sciences 54, 168–176. doi:10.1139/cjfas-54-S1-168

Ebbert, D. (2019). ‘chisq.posthoc.test’: A post hoc analysis for Pearson’s chi-squared test for count data. Available at: https://cran.r-project.org/package=chisq.posthoc.test

Fraser, S., Gotceitas, V., and Brown, J. A. (1996). Interactions between age-classes of Atlantic cod and their distribution among bottom substrates. Canadian Journal of Fisheries and Aquatic Sciences 53, 305–314. doi:10.1139/f95-183

Gjøsæter, J. (1987). Habitat selection and inter year class interaction in young cod (*Gadus morhua)* in aquaria. Flødevigen Rapportser 1, 27–36.

Gorman, A. M., Gregory, R. S., and Schneider, D. C. (2009). Eelgrass patch size and proximity to the patch edge affect predation risk of recently settled age 0 cod (*Gadus*). Journal of Experimental Marine Biology and Ecology 371, 1–9. doi:10.1016/j.jembe.2008.12.008

Gotceitas, V., and Brown, J. A. (1993). Substrate selection by juvenile Atlantic cod (*Gadus morhua):* effects of predation risk. Oecologia 93, 31–37.

Gotceitas, V., and Colgan, P. (1989). Predator foraging success and habitat complexity: quantitative test of the threshold hypothesis. Oecologia 80, 158–166. doi:10.1007/BF00380145

Gotceitas, V., Fraser, S., and Brown, J. A. (1995). Habitat use by juvenile Atlantic cod (*Gadus morhua*) in the presence of an actively foraging and non-foraging predator. Marine Biology 123, 421–430. doi:10.1007/BF00349220

Gotceitas, V., Fraser, S., and Brown, J. A. (1997). Use of eelgrass beds (*Zostera marina*) by juvenile Atlantic cod (*Gadus morhua*). Canadian Journal of Fisheries and Aquatic Sciences 54, 1306–1319. doi:10.1139/f97-033

Grant, S. M., and Brown, J. A. (1998). Diel foraging cycles and interactions among juvenile Atlantic cod (*Gadus morhua*) at a nearshore site in Newfoundland. Canadian Journal of Fisheries and Aquatic Sciences 55, 1307–1316. doi:10.1139/cjfas-55-6-1307

Gregory, R. S., and Anderson, J. T. (1997). Substrate selection and use of protective cover by juvenile Atlantic cod *Gadus morhua* in inshore waters of Newfoundland. Marine Ecology Progress Series 146, 9–20. doi:10.3354/meps146009

Gregory, R.S., K.L. Dalley, B.H. Newton, P.S. Sargent, E.L.L. Cooke. (2019). Relative strength of three cohorts (2015-17) of Atlantic cod, from nearshore surveys of demersal age 0 & 1 juveniles in Newman Sound, Bonavista Bay. DFO CSAS Res. Doc. 2019/012.

Hardy, J. D. Jr. (1978). Development of fishes of the Mid-Atlantic Bight. An atlas of egg, larval and juvenile stages. Vol. 2. Anguillidae through Syngnathidae. U.S. Fish Wildlife Service, Biological Services Program FSW/OBS-78/12: 458 p.

Hasegawa, N., Hori, M., and Mukai, H. (2008). Seasonal changes in eelgrass functions: current velocity reduction, prevention of sediment resuspension, and control of sediment-water column nutrient flux in relation to eelgrass dynamics. Hydrobiologia 596, 387–399. doi:10.1007/s10750-007-9111-4

Houde, E. D. (1987). Fish early life dynamics and recruitment variability. American Fisheries Society Symposium 2, 17–29.

Ings, D. W., Gregory, R. S., and Schneider, D. C. (2008). Episodic downwelling predicts recruitment of Atlantic cod, Greenland cod and white hake to Newfoundland coastal waters. Journal of Marine Research 66, 529–561.

Ings, D. W., Schneider, D. C., and Methven, D. a. (1997). Detection of a recruitment signal in juvenile Atlantic cod (*Gadus morhua*) in coastal nursery areas. Canadian Journal of Fisheries and Aquatic Sciences 54, 25–29. doi:10.1139/cjfas-54-S1-25

Joseph, V., Locke, A., and Godin, J. G. J. (2006). Spatial distribution of fishes and decapods in eelgrass (*Zostera marina* L.) and sandy habitats of a New Brunswick estuary, eastern Canada. Aquatic Ecology 40, 111–123. doi:10.1007/s10452-005-9027-x

Keats, D. W. (1990). A nocturnal inshore movement of juvenile cod *Gadus morhua* L. in eastern Newfoundland. Journal of Experimental Marine Biology and Ecology 139, 167–173. doi:10.1016/0022-0981(90)90144-2

Keats, D. W., and Steele, D. H. (1992). Diurnal feeding of juvenile cod (*Gadus morhua*) which migrate into shallow water at night in eastern Newfoundland. Journal of Northwest Atlantic Fishery Science 13, 7–14. doi:10.2960/J.v13.a1

Keats, D. W., Steele, D. H., and South, G. R. (1987). The role of fleshy macroalgae in the ecology of juvenile cod (*Gadus morhua* L.) in inshore waters off eastern Newfoundland. Canadian Journal of Fisheries and Aquatic Sciences 65, 49–53. doi:10.1139/z87-008

Laurel, B. J., and Brown, J. A. F. (2006). Influence of cruising and ambush predators on 3-dimensional habitat use in age 0 juvenile Atlantic cod *Gadus morhua*. Journal of Experimental Marine Biology and Ecology 329, 34–46. doi:10.1016/j.jembe.2005.08.003

Laurel, B. J., Gregory, R. S., and Brown, J. A. (2003a). Predator distribution and habitat patch area determine predation rates on age-0 juvenile cod *Gadus* spp. Marine Ecology Progress Series 251, 245–254. doi:Doi 10.3354/Meps251245

Laurel, B. J., Gregory, R. S., and Brown, J. A. (2003b). Settlement and distribution of age-0 juvenile cod, *Gadus morhua* and *G. ogac*, following a large-scale habitat manipulation. Marine Ecology Progress Series 262, 241–252. doi:10.3354/meps262241

Laurel, B. J., Gregory, R. S., Brown, J. A., Hancock, J. K., and Schneider, D. C. (2004). Behavioural consequences of density-dependent habitat use in juvenile cod *Gadus morhua* and *G. ogac*: the role of movement and aggregation. Marine Ecology Progress Series 272, 257–270. doi:10.3354/meps272257

Levin, P.S., (1994). Small-scale recruitment variation in a temperate fish: the roles of macrophytes and food supply. Environmental Biology of Fishes 40, 271–281

Lindholm, J. B., Auster, P. J., and Kaufman, L. S. (1999). Habitat-mediated survivorship of juvenile (0-year) Atlantic cod *Gadus morhua*. Marine Ecology Progress Series 180, 247–255. doi:10.3354/meps180247

Linehan, J. E., Gregory, R. S., and Schneider, D. C. (2001). Predation risk of age-0 cod (*Gadus*) relative to depth and substrate in coastal waters. Journal of Experimental Marine Biology and Ecology 263, 25–44. doi:10.1016/S0022-0981(01)00287-8

Lough, R. G., Valentine, P. C., Potter, D. C., Auditore, P. J., Bolz, G. R., Neilson, J. D., and Perry, R. I. (1989). Ecology and distribution of juvenile cod and haddock in relation to sediment type and bottom currents on eastern Georges Bank. Marine Ecology Progress Series 56, 1–12.

Methven, D. A., and Bajdik, C. (1994). Temporal variation in size and abundance of juvenile Atlantic cod (*Gadus morhua*) at an inshore site off eastern Newfoundland. Canadian Journal of Fisheries and Aquatic Sciences 51, 78–90.

Methven, D. A., and McGowan, C. (1998). Distinguishing small juvenile Atlantic cod (*Gadus morhua*) from Greenland cod (*Gadus ogac*) by comparing meristic characters and discriminant function analyses of morphometric data. Canadian Journal of Zoology 76, 1054–1062. doi:10.1139/z98-046

Mikhail, M. Y., and Welch, H. E. (1989). Biology of Greenland cod, *Gadus ogac*, at Saqvaqjuac, northwest coast of Hudson Bay. Environmental Biology of Fishes 26, 49–62.

Orth, R. J., Heck, K. L. J., and van Montfrans, J. (1984). Faunal communities in seagrass beds: a review of the influence of plant structure and prey characteristics on predator-prey relationships. Estuaries 7, 339–350.

Pelletier, D., Leleu, K., Mou-Tham, G., Guillemot, N., and Chabanet, P. (2011). Comparison of visual census and high definition video transects for monitoring coral reef fish assemblages. Fisheries Research 107, 84-93.

Pepin, P., and Helbig, J. A. (2011). Distribution and drift of Atlantic cod (*Gadus morhua*) eggs and larvae on the northeast Newfoundland Shelf. Canadian Journal of Fisheries and Aquatic Sciences 54, 670–685. doi:10.1139/f96-317

Peterson, I., and Wroblewski, J. S. (1984). Mortality rate of fishes in the pelagic ecosystem. Canadian Journal of Fisheries and Aquatic Sciences 41, 1117–1120. doi:10.1139/f84-131

Pihl, L. (1982). Food intake of young cod and flounder in a shallow bay on the Swedish west coast. Netherlands Journal of Sea Research 15, 419–432. doi:10.1016/0077-7579(82)90068-0

Pottle, A., and Green, M. (1979a). Territorial behaviour of the north temperate labrid, *Tautogolabrus adspersus*. Canadian Journal of Zoology 57, 2337–2347.

Pottle, R. A., and Green, J. M. (1979b). Field observations on the reproductive behaviour of the cunner, *Tautogolabrus adspersus* (Walbaum), in Newfoundland. Canadian Journal of Zoology 57, 247–256.

R Core Team (2019). R: A Language and Environment for Statistical Computing. Available at: https://www.r-project.org/

Renkawitz, M. D., Gregory, R. S., and Schneider, D. C. (2011). Habitat dependant growth of three species of bottom settling fish in a coastal fjord. Journal of Experimental Marine Biology and Ecology 409, 79–88. doi:10.1016/j.jembe.2011.08.004

Savino, J. F., and Stein, R. A. (1982). Predator-prey interaction between largemouth bass and bluegills as influenced by simulated, submersed vegetation. Transactions of the American Fisheries Society 111, 255–266. doi:10.1577/1548-8659(1982)111<255

Schneider, D. C., Methven, D. A., and Dalley, E. L. (1997). Geographic contraction in juvenile fish: a test with northern cod (*Gadus morhua*) at low abundances. Canadian Journal of Fisheries and Aquatic Science 54, 187–199.

Schneider, D. C., Norris, M. J., and Gregory, R. S. (2008). Predictive analysis of scale-dependent habitat association: Juvenile cod (*Gadus* spp.) in eastern Newfoundland. Estuarine, Coastal and Shelf Science 79, 71–78. doi:10.1016/j.ecss.2008.03.005

Scott, W., and Scott, M. (1988). ‘Atlantic fishes of Canada’. Canadian Bulletin of Fisheries and Aquatic Sciences 219.

Sogard, S. M. (1997). Size-selective mortality in the juvenile stage of teleost fishes: a review. Bulletin of Marine Science 60, 1129–1157.

Sogard, S. M. (1992). Variability in growth rates of juvenile fishes in different estuarine habitats. Marine Ecology Progress Series 85, 35–53.

Templeman, W. (1981). Vertebral numbers in Atlantic cod, *Gadus morhua*, of the Newfoundland and adjacent areas, 1947-71, and their use for delineating cod stocks. Journal of Northwest Atlantic Fishery Science 2, 21–45. doi:10.2960/j.v2.a3

Thistle, M. E., Schneider, D. C., Gregory, R. S., and Wells, N. J. (2010). Fractal measures of habitat structure: maximum densities of juvenile cod occur at intermediate eelgrass complexity. Marine Ecology Progress Series 405, 39–56. doi:10.3354/meps08511

Tupper, M., and Boutilier, R. G. (1995a). Effects of habitat on settlement, growth, and postsettlement survival of Atlantic cod (*Gadus morhua*). Canadian Journal of Fisheries and Aquatic Sciences 52, 1834–1841. doi:10.1139/f95-176

Tupper, M., and Boutilier, R. G. (1997). Effects of habitat on settlement, growth, predation risk and survival of a temperate reef fish. Marine Ecology Progress Series 151, 225–236. doi:10.3354/meps151225

Tupper, M., and Boutilier, R. G. (1995b). Size and priority at settlement determine growth and competitive success of newly settled Atlantic cod. Marine Ecology Progress Series 118, 295–300. doi:10.3354/meps118295

Tveite, S. (1984). 0-group cod investigations on the Norwegian Skagerrak coast. In ‘The Propagation of Cod, *Gadus morhua* L.’ (Eds E. Dahl, D. S. Danielssen, E. Moksness, and P. Solemdal.) pp. 581–590. (Flød. Rapp.)

Warren, M.A., R.S. Gregory, B.J. Laurel, and P.V.R. Snelgrove. (2010). Increasing density of juvenile Atlantic (*Gadus morhua*) and Greenland cod (*G. ogac*) in association with spatial expansion and recovery of eelgrass (*Zostera marina*) in a coastal nursery habitat. Journal of Experimental Marine Biology and Ecology 394, 154-160.

Tables and Figures

Table 2.1a: Chi-squared results for association between primary vegetation and presence of age-0 cod (*Gadus* spp.). Bold font indicates a significant p-value.

	Age-0 cod			
Vegetation	Observed	Expected	Chi-Square	P
Eelgrass	45	3.8	479.1	**<0.001**
Kelp	4	7.6		
Sparse Vegetation	1	34.2		
Bare Substrate/no Vegetation	0	4.3		

Table 2.1b: Post-hoc test of association between primary vegetation and presence of age-0 cod (*Gadus* spp.). P-values were adjusted using the Benjamini and Hochberg (1995) procedure for false discovery rate. Bold font indicates a significant p-value.

Vegetation	Residuals	Adjusted P
Eelgrass	8.23	**<0.0001**
Kelp	-1.13	1.0
Sparse Vegetation	-6.96	**<0.0001**
Bare Substrate/no Vegetation	-2.11	0.28

Table 2.1c: Chi-squared results for association between primary substrate and presence of age-0 cod (*Gadus* spp.). Bold font indicates a significant p-value.

	Age-0 cod			
Substrate	Observed	Expected	Chi-Square	P
Sand	50	36.0	19.396	**0.012**
Cobble	0	13.7		
Boulder	0	0.3		

Table 2.1d: Post-hoc test of association between primary substrate and presence of age-0 cod (*Gadus* spp.). P-values were adjusted using the Benjamini and Hochberg (1995) procedure for false discovery rate. Bold font indicates a significant p-value.

Substrate	Residuals	Adjusted P
Sand	4.03	**<0.001**
Cobble	-3.96	**<0.001**
Boulder	-0.5	1.0

Table 2.2a: Chi-squared results for association between primary vegetation and presence of cunner (*Tautogolabrus adspersus*). Bold font indicates a significant p-value.

	Cunner			
Habitat	Observed	Expected	Chi-Square	P
Eelgrass	89	145.8	811.64	**<0.001**
Kelp	711	289.2		
Sparse Vegetation	1104	1301.0		
Bare Substrate/no Vegetation	6	161.6		

Table 2.2b: Post-hoc test of association between primary vegetation and presence of cunner (*Tautogolabrus adspersus*). P-values were adjusted using the Benjamini & Hochberg (1995) procedure for false discovery rate. Bold font indicates a significant p-value.

Vegetation	Residuals	Adjusted P
Eelgrass	-3.88	**<0.001**
Kelp	15.41	**<0.0001**
Sparse Vegetation	-6.88	**<0.0001**
Bare Substrate/no Vegetation	-12.34	**<0.0001**

Table 2.2c: Chi-squared results for association between primary substrate and presence of cunner (*Tautogolabrus adspersus*). Bold font indicates a significant p-value.

	Cunner			
Substrate	Observed	Expected	Chi-Square	P
Sand	1542	1371.8	79.272	**<0.0001**
Cobble	368	522.6		
Boulder	0	9.5		

Table 2.2d: Post-hoc test of association between primary substrate and presence of cunner (*Tautogolabrus adspersus*). P-values were adjusted using the Benjamini and Hochberg (1995) procedure for false discovery rate. Bold font indicates a significant p-value.

Substrate	Residuals	Adjusted P
Sand	6.31	**<0.0001**
Cobble	-8.3	**<0.0001**
Boulder	-3.09	0.008

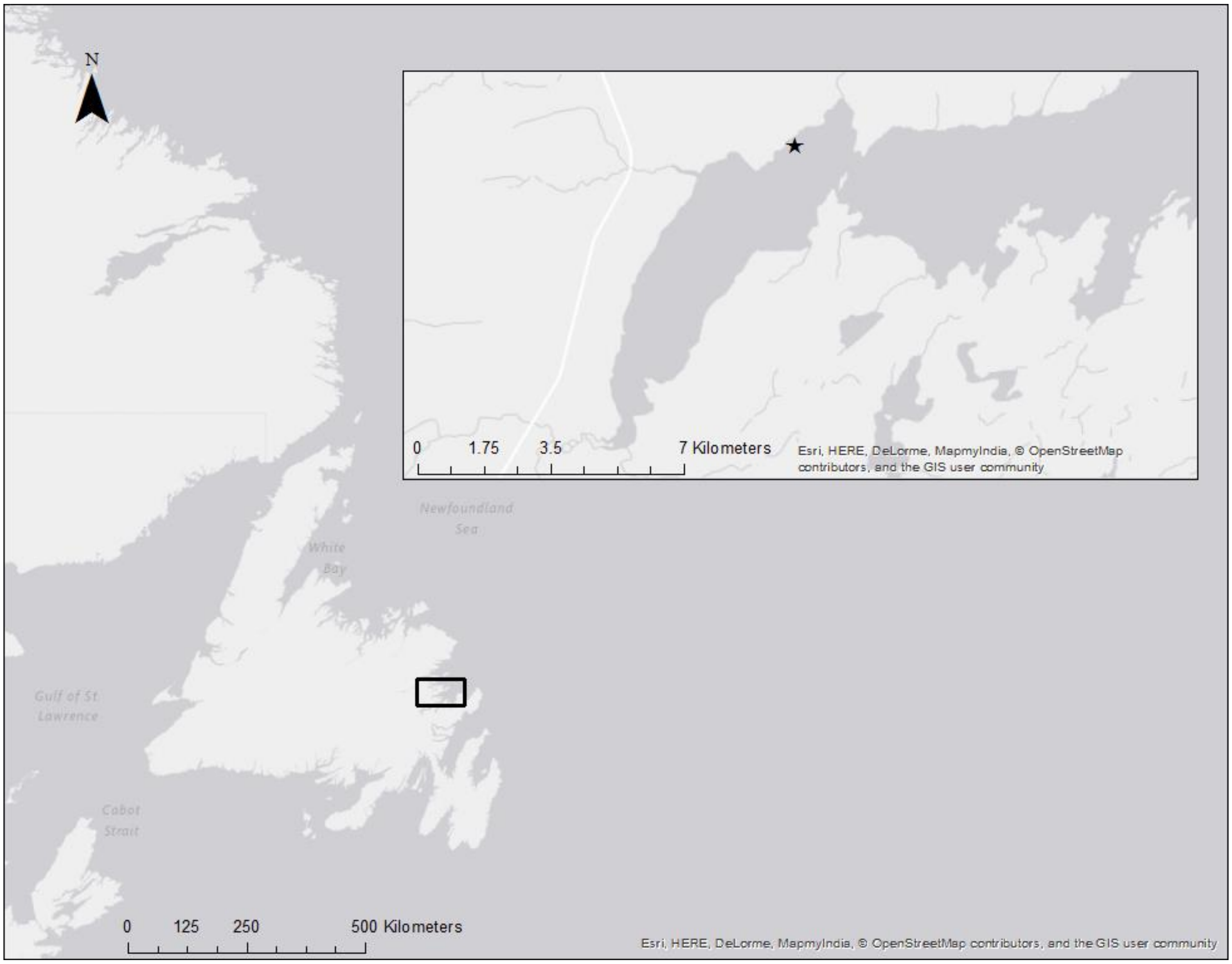

Figure 2.1: The study site, Newbridge Cove (star) is located within Newman Sound (inset), Bonavista Bay, on the east coast of Newfoundland, Canada.

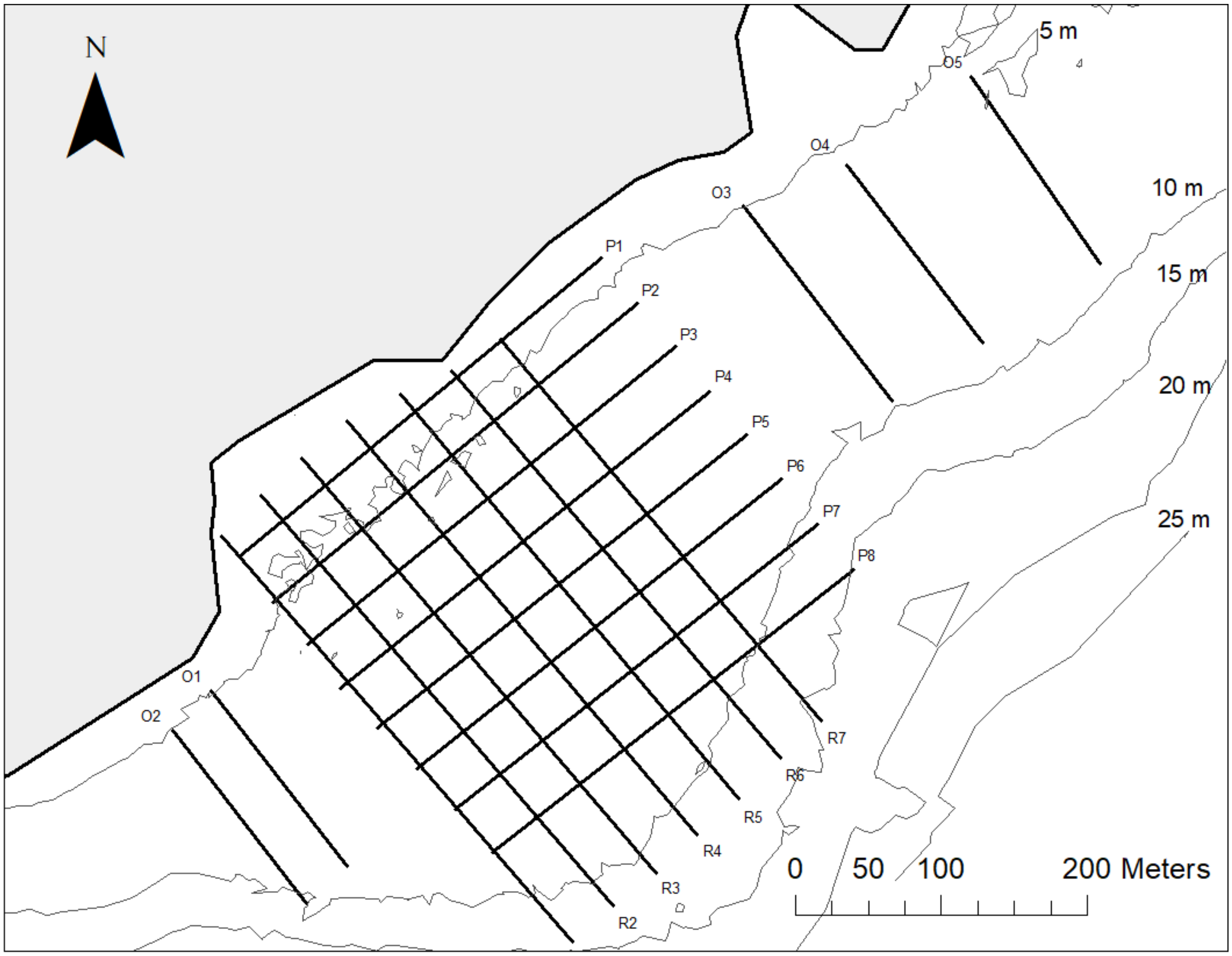

Figure 2.2: Locations of 20 video transects (black lines) – 8 parallel to beach (P), 7 perpendicular to beach (R), and 5 outside immediate beach area (O) – in Newbridge Cove, Newman Sound, Newfoundland (star in Figure 2.1). Parallel and perpendicular transects were conducted three times (August, September, October) and outside transects were completed twice (September, October) in 2016. Isobaths are 5 m depth intervals (grey lines).

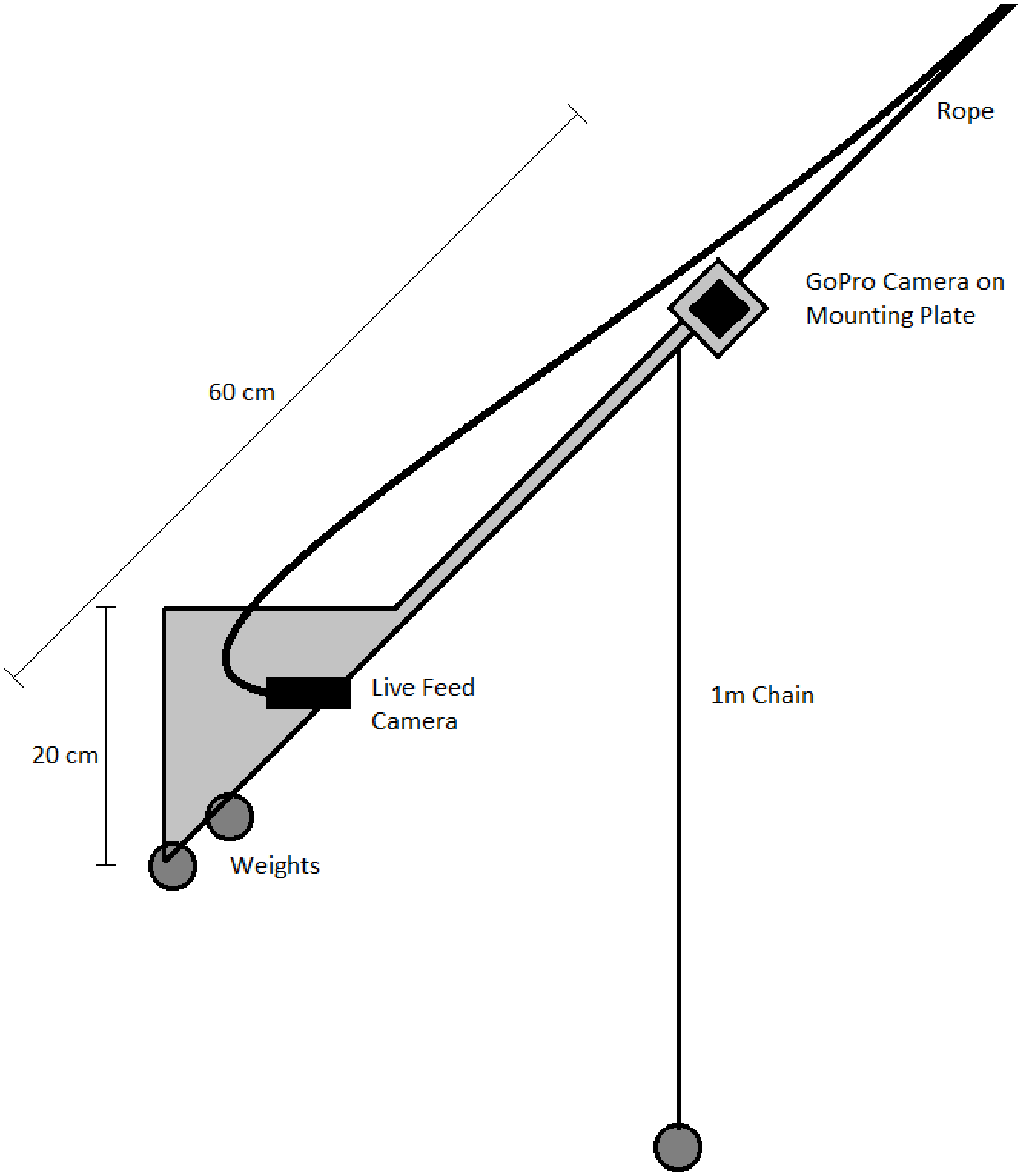

Figure 2.3: Schematic diagram of the camera deployment frame used to collect 1080p HD video with a GoPro camera (Hero 3+ or 4) and a live-feed video camera to observe transects in real time in order to avoid obstacles (e.g., boulders). Zip ties secured the waterproof GoPro casing to the mounting plate, which allowed me to swap out the GoPro between transects to recharge batteries. The live feed cable was secured to the tow rope with tape. Three zinc weights (totaling 3.6 kg) provided ballast.

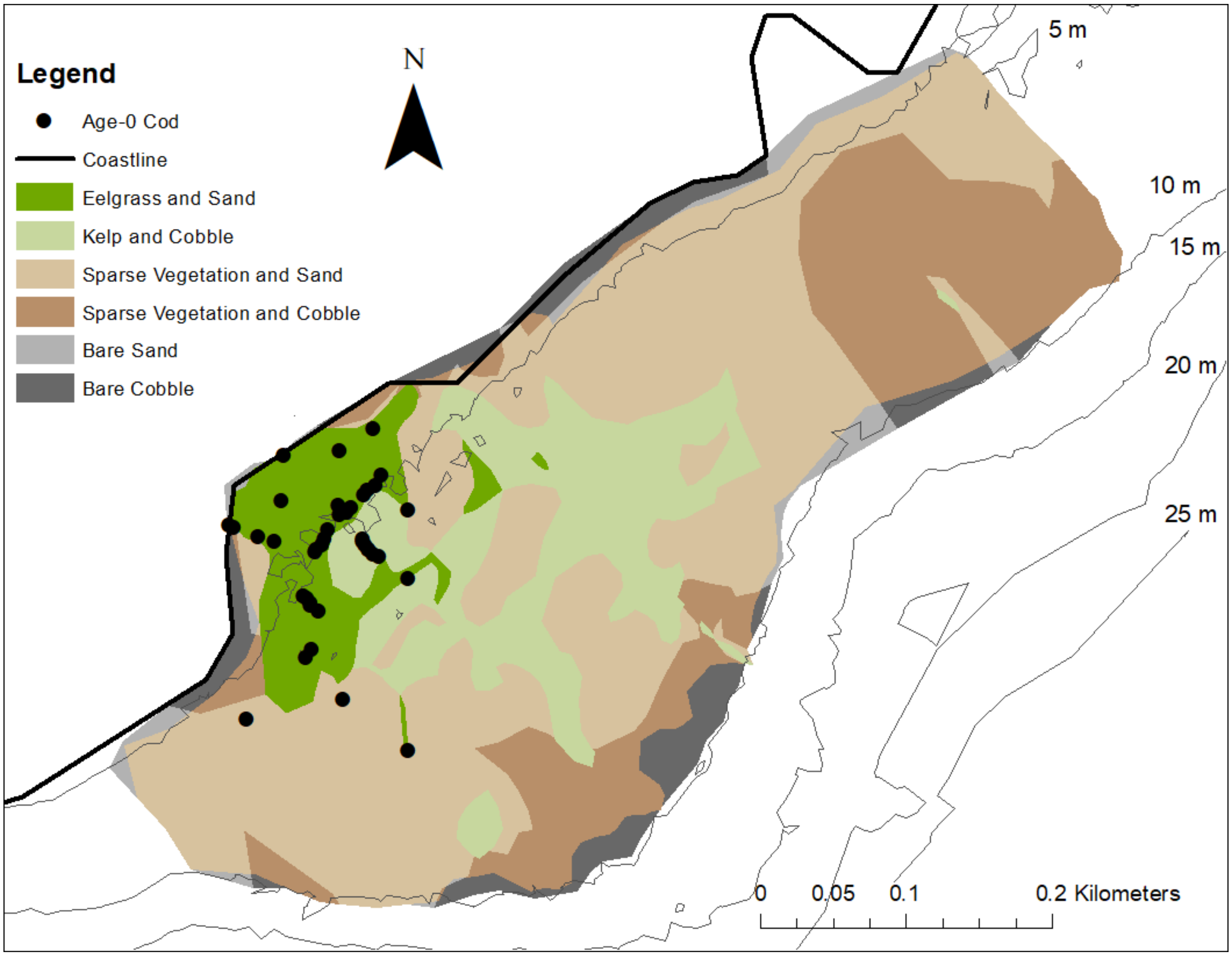

Figure 2.4: Habitat map of Newbridge Cove (star in Figure 2.1) with 5 m bathymetry contours (grey lines) and locations of observed age-0 Atlantic (*Gadus morhua*) and Greenland (*G. macrocephalus ogac*) cod (black dots). Habitat classifications were determined from video transects, where I recorded the edges of habitat patches.

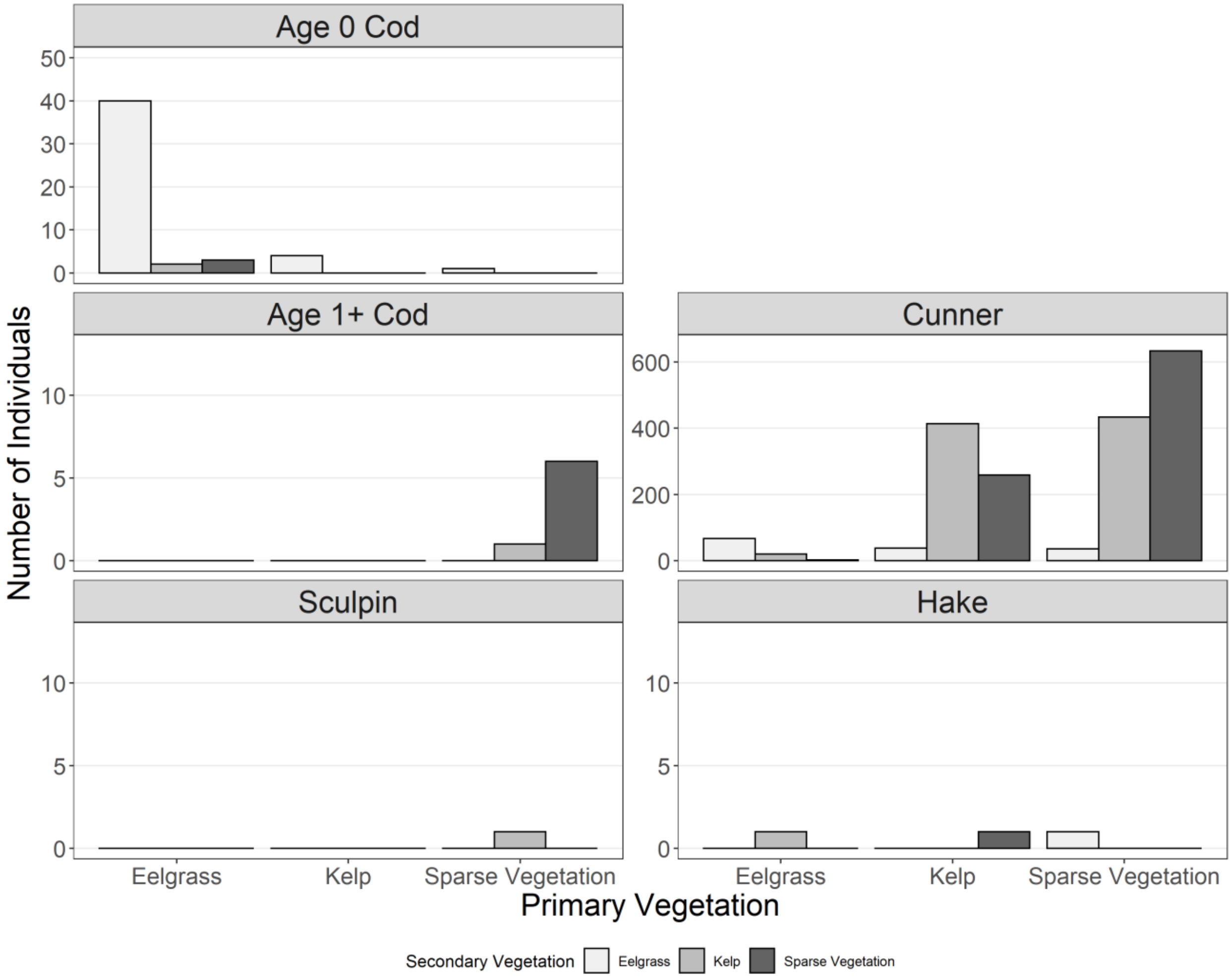

Figure 2.5: Total age-0 cod (Atlantic *Gadus morhua* and Greenland *G. macrocephalus ogac*) cod and their fish predators (sculpin *Myoxocephalus scorpius*, cunner *Tautogolabrus adspersus*, age-1+ conspecifics, hake *Urophycis tenuis*) observed in each vegetative habitat (primary and secondary combination), from towed video camera imagery in Newbridge Cove, Newman Sound, Newfoundland, August to October 2016. Primary vegetation, presented on the x-axis, is the vegetation that covered more that 50% of the video frame. Secondary vegetation, indicated by fill colour, is the vegetation that covered less than 50% of the video frame. Y-axis scales are independent for each species.

Co-Authorship Statement

The research described in Chapter 3 was designed by Evelyn MacRobert, in collaboration with Dr. Bob Gregory and Dr. Paul Snelgrove. Evelyn MacRobert collected and analysed the data, and prepared the manuscript. Dr. Bob Gregory and Dr. Paul Snelgrove contributed ideas and advised on data processing. Evelyn MacRobert will be lead author on any manuscripts arising from this thesis, and will include those collaborators who have contributed significantly to the manuscripts as co-authors.

Chapter 3 : Habitat risk associated with presence of predators

Abstract

Piscivorous fishes can exert substantial predation pressure on small-bodied fishes. However, habitat can mediate predation effects by physically barring movement and visually obscuring prey. As such, piscivorous fishes may occupy habitat that differs from their prey. In Newfoundland, predators of age-0 Atlantic (*Gadus morhua*) and Greenland (*G. macrocephalus ogac*) cod include older conspecifics, as well as cunner (*Tautogolabrus adspersus*) and shorthorn sculpin (*Myoxocephalus scorpius*). To determine habitat selection of these piscivores, I used acoustic telemetry to assess habitat use of 37 individuals in Newman Sound, Bonavista Bay, Newfoundland. Fish were tagged with unique acoustic transmitters in the spring (May – July), 2016 in Newbridge Cove, a site consisting of multiple discrete habitat types – eelgrass, kelp, sparse vegetation, and bare substrate. I detected unique signals from these tags using 23 acoustic receivers that recorded data through the summer and fall. I mapped positional data for individual fish detections over habitat polygons pre-determined at this site in order to assess habitat use among seasons (spring, summer, fall) and diel periods (dawn, day, dusk, night). Habitat use differed significantly among species. Season significantly affected habitat use for Greenland cod, cunner, and sculpin. Greenland cod and cunner selected eelgrass in the spring, then transitioned to deeper water habitats (kelp, sparse vegetation, and bare substrates) during summer and fall. Sculpin selected sparse vegetation in spring and fall, and kelp and bare sand in summer. I detected no Atlantic cod in the fall; however, they selected sparse vegetation and bare sand in spring and summer. Only cunner exhibited significant diel variation in habitat use, a pattern consistent with the quiescent behaviour typical of this species during non-daylight hours, with detections resuming within 2 hours of sunrise. The tagged piscivores in my study primarily

occupied deeper water habitats, outside eelgrass beds, that are not frequented by age-0 cod. These spatial and temporal patterns in habitat use suggest segregation of piscivorous fishes from their prey.

Introduction

High mortality characterizes the early life history stages of fishes (Pauly 1980; Houde 1987; Chen and Watanabe 1989), with piscivorous fishes exerting substantial predation pressure on small-bodied fishes. However, habitat can mediate predation effects by physically barring movement and visually obscuring prey (Gotceitas and Colgan 1989; Lindholm *et al.* 1999). In Newman Sound, Newfoundland, age 1-2 Atlantic (*Gadus morhua*) and Greenland (*Gadus macrocephalus ogac*) cod, shorthorn sculpin (*Myoxocephalus scorpius*), cunner (*Tautogolabrus adspersus*), and white hake (*Urophycis tenuis*) represent major predators of age-0 Atlantic and Greenland cod (Linehan *et al.* 2001). Although previous studies consider older conspecifics and hake as the dominant predators of age-0 cod (Linehan *et al.* 2001; Laurel *et al.* 2003a), their findings suggest that cunner may account for over half of predator attacks on age-0 cod in shallow (< 3 m) water. Because Atlantic cod settle in multiple pulses throughout the summer and fall (Methven and Bajdik 1994; Grant and Brown 1998; Ings *et al.* 2008), even age-0 cod may cannibalize smaller individuals from their own year class, noting their capability of consuming other fish up to half their length (Bogstad *et al.* 1994). Therefore, age-0 Atlantic cod individuals in later settlement pulses are more vulnerable to predation later in the season compared to early settlers, due to size-based predation risk from other piscivorous fish species, older conspecifics, and early settlers of the same age class.

Previous work in Newman Sound reported greater predator attacks on age-0 cod in deeper water than in shallow water (Linehan *et al.* 2001). Predation was also greater in non-vegetated habitat than in eelgrass beds (Linehan et al. 2001). Because structural complexity can reduce visibility of prey (Lindholm *et al.* 1999), reduced predation rates on age-0 cod occur over structurally complex habitats, such as eelgrass, cobble, and rock reefs (Gotceitas *et al.* 1997;

Lindholm *et al.* 1999; Linehan *et al.* 2001). Increased visibility in low relief areas, such as bare sand, extends the range over which piscivores may detect their prey (Lindholm *et al.* 1999). This increased visibility coincides with increased preference for barren substrates by piscivorous fishes (e.g., cunner: Pottle and Green 1979a; Atlantic cod: Gregory and Anderson 1997). Additionally, predation increases with depth outside eelgrass beds (Linehan *et al.* 2001), where older and larger juvenile cod (age-1+) occur during the day (Methven and Bajdik 1994). Avoidance of shallow-water habitats during the day by piscivores may provide a means for these larger fish to avoid their own avian and terrestrial predators (Crowder *et al.* 1997; Cote *et al.* 2008a, 2008b). Piscivorous 1-2 year old cod often move into shallow waters at night (Keats 1990; Linehan 2001) where they may forage (Pihl 1982). Sculpin also forage more at night (Landry *et al.* 2019) than during other diel periods, contrasting the absence of activity by cunner, which are quiescence at night (Pottle and Green 1979b).

Purpose and Hypotheses

In Chapter 2, I used video transects to document the distribution of individual age-0 cod and their predators among habitats in Newman Sound, and examined habitat associations. In this chapter, I quantify the frequency of habitat use of fishes known to prey on age-0 cod in Newman Sound. I tracked their movements using acoustic telemetry to determine habitat use across diel and seasonal time scales. Given that predators of age-0 cod must also maximize their own survival by accessing prey and avoiding their own predators, I predicted that during the day piscivores would prefer habitats in deeper water, such as kelp and cobble in contrast to shallower habitats, such as eelgrass, which are occupied by age 0 cod and easily accessible by terrestrial predators. In contrast, I predicted that piscivores would utilize shallow water habitats at night.

Methods

Study Site

The study site, Newbridge Cove (48.5838° N, 53.9269° W), is located along the northern shore of the inner basin of Newman Sound (Figure 3.1). This site is bounded by bare rocky and cobble habitats inhabited by predators of juvenile cod – older juvenile Atlantic and Greenland cod, sculpin, and cunner. See Chapter 2 for a full description of the site.

Acoustic Tagging

I tagged 37 individual piscivorous fish from four species in order to determine their movements within my site – 10 each of Atlantic cod (16.5 ± 1.3 cm, mean SL [Standard Length] ± standard deviation (s.d.)), Greenland cod (16.5 ± 3.1 cm) and cunner (18.2 ± 2.2 cm), and 7 sculpin (27.3 ± 5.4 cm). Trained Fisheries and Oceans Canada technicians surgically implanted the acoustic tags (Vemco^{TM} V7-4L, 22.5 mm long, 7 mm diameter, 1.8 g weight in air, power output of 136 dB re 1 μPa at 1 m, transmission interval of 240 ± 70 seconds, expected tag life ~415-450 days) in each predator under approved Animal Care Protocol Number NAFC 2016-03. Tags were inserted through a ~2 cm incision made off centre of the ventral mid-line between the pelvic girdle and anus. Following insertion, the incision was closed with two sutures. Atlantic and Greenland cod were tagged on May 19, 2016, and most sculpin on June 13, with one tagged on July 5, 2016. Of the 10 cunner, five were tagged on July 5, 2016, and five on July 19, 2016. At the time of tagging, white hake were less than the 14 cm SL body length required to surgically implant tags under the protocol. Predators were captured at the study site by SCUBA divers (sculpin only), beach seines, or angling. I used beach seines to capture both cod species and cunner within 50 m of shore, and I captured cunner and sculpin by angling and SCUBA diving and dip netting within 150-200 m of the shoreline, near my study site.

To detect the acoustic tags, nine Vemco^{TM} (VR2W, 69 kHz receiving frequency) acoustic receivers were deployed (eight with accompanying stationary reference transmitters, called sync tags, to correct internal clock drift of the acoustic receivers) on May 18, 2016 along a 1 km stretch of shoreline centered on Newbridge Cove (Figure 3.2). Receivers were suspended 1 m off the bottom to reduce interference from substrate and vegetation, and placed about 300 – 400 m apart to ensure the detection radii (~400 m, assessed by field tests in Newman Sound) of each receiver overlapped with a minimum of two other receivers to allow for triangulation of detections.

In addition to the receivers deployed at Newbridge Cove, I used detection data collected from acoustic receivers deployed in areas outside the immediate study site within Newman Sound (Figure 3.7, see Appendix 1) to determine broader-scale seasonal movements. Because these receivers were not placed with overlapping radii, they only gave relative positions of fish around Newman Sound. I grouped detections by individual fish, and determined the number of individuals visiting each station in each season.

Telemetry Analysis

Following retrieval and data download of acoustic receivers on November 15, 2016, Vemco Ltd.^{TM} processed raw detection data using proprietary software to generate position estimates using hyperbolic positioning (Smith 2013). In brief, hyperbolic positioning uses the time-difference-of-arrival to estimate an equal distance curve from which a tag's acoustic signal originated. When detected by a third receiver, a second curve is estimated, and the location of the tag is taken as the intersection of these two curves.

I filtered raw position data using calculated horizontal positioning error (HPE, a unitless estimate of error sensitivity) to minimize measurable positioning error (HPEm, the difference in known and calculated positions for sync tags, in meters) while balancing data loss (Coates *et al.* 2013; Smith 2013). Following visual examination of the relationship between HPE and HPEm (Figures 3.4 and 3.5), I selected a limit of 12 HPE in order to minimize data loss, while balancing data accuracy, and removed positions above this value. Filtering resulted in a median and 90th percentile HPEm of 0.9 m and 2.9 m, respectively, for the remaining data (Figure 3.4), and 94% retention of predator position data (Figure 3.5). The filtered positions were grouped by season and diel period, defining the 2016 seasons – spring, summer and fall – based on mean daily water temperature, with "spring" defined by a steady rise in temperature from May 18 to July 14, "summer" by trendless but variable high temperature from July 15 to September 14, and "fall" by a consistent decline in temperature from September 15 to November 15 (Figure 3.6). I used "sun angles" (i.e., azimuth) obtained from the National Research Council Canada (https://www.nrc-cnrc.gc.ca/eng/services/sunrise/advanced.html) to group the data into the following diel periods (Thorsen 2013):

- Dawn, the time between the start of nautical twilight and sunrise;
- Day, the time between sunrise and sunset;
- Dusk, the time between sunset and the end of nautical twilight; and
- Night, the time between the end of nautical twilight (dusk) and the start of nautical twilight (dawn).

I mapped position data as points onto the habitat map layer generated from Chapter 2 (Figure 3.3) and assigned each position to a habitat, removing only 90 (of >89,000) positions I could not assign to any single habitat. For each day of my study period, I calculated habitat use for each combination of season and diel period as the percent of detections located within each habitat polygon, such that proportions summed to 100% for each combination, to account for the different lengths of each diel period. I then standardized the data by percent area of available habitat.

Statistics

Fine-scale telemetry data is, by nature, serially autocorrelated. To account for this concern, I examined habitat selection using proportion of detections per diel period. I tested for differences in proportional habitat use by season and diel period using a Type III Permutational Multivariate Analysis of Variance (PERMANOVA; Anderson 2001) carried out in PRIMER (v.6.1.11) software installed with the PERMANOVA+ (v.1.0.1) add-on. My two-way design treated season (spring, summer, and fall) and diel period (dawn, day, dusk, and night) as fixed factors, and I determined differences between factor levels using pair-wise PERMANOVA contrasts. All tests used 999 permutations of residuals under a reduced model. Proportional habitat use greater than percent habitat availability was interpreted as selection for that habitat, while I Interpreted proportional habitat use less than percent habitat availability as underutilization of a habitat.

Results

Data Filtering/Retention

Over the course of my study, my 37 tagged predators yielded a total of 1,162,691 individual acoustic detections. These detections resulted in 142,692 raw positions for the four species (Table 3.1a). After filtering position by HPE < 12 and removing rarely detected individuals (i.e., < 10 positions; 2 Atlantic cod, 1 Greenland cod, 1 sculpin) or presumed dead (1 Atlantic Cod), a total of 134,710 positions remained (94%). Of these, 45,230 positions occurred outside habitat polygons (Table 3.1b), and I subsequently omitted them from my analysis as proportional habitat use could not be determined for these positions. I discarded an additional 90 positions because they occurred on the edges between habitat polygons and I could not assign them to a single habitat. The remaining 89,390 (66%) positions were used to calculate proportional habitat use for each individual per day for each diel period, and this proportional habitat use was used in my PERMANOVA analysis (Table 3.1a).

Habitat Preference Within Newbridge Cove

The greatest number of detections occurred in sparse vegetation, followed by kelp, which were the habitats most represented at the study site by area. Proportional habitat use by predators differed among species and seasons, with a significant species*season interaction (two-way PERMANOVA, Pseudo-$F = 7.6$, df = 5, P(perm) = 0.001, Table 3.3). Therefore, I re-examined habitat use for each predator species separately.

Atlantic Cod Habitat Preference

Atlantic cod showed no significant differences in habitat use among seasons or diel periods (two-way PERMANOVA, P(perm) > 0.05, Table 3.4), with only a small proportion of the variance (5.8%) explained by season and diel period. Atlantic cod selected sparse vegetation in spring, and increased use for bare sand in summer. Kelp was underutilized in summer, and eelgrass was underutilized in all seasons (Figure 3.8). Although Atlantic cod were more frequently detected outside the habitat polygons (Table 3.1b), I rarely detected Atlantic cod in the habitat polygons in fall, and high error values (HPE > 12) characterized all my detections in that season. Therefore, I could not determine habitat selected during the fall, although the overall lack of detections (Table 3.1b) indicates that the tagged individuals had left the immediate detection area within my receiver array.

Greenland Cod Habitat Preference

Habitat use for Greenland cod differed significantly among season (two-way PERMANOVA, Pseudo-F = 3.3, df = 2, P(perm) = 0.010, Table 3.5a), with a small proportion of the variance (8.7%) explained by season and diel period. Habitat use differed significantly between spring and summer (pair-wise PERMANOVA, t = 2.5, p = 0.001), but not in the fall (p > 0.05, Table 3.5b). Greenland cod selected eelgrass and kelp in the spring, but underutilized eelgrass in summer and fall. They underutilized bare substrates (sand and rock) in all seasons (Figure 3.9). Greenland cod were detected more frequently outside the habitat polygons in summer and fall (Table 3.1b). Detections of Greenland cod in the habitat polygons in fall were few and occurred almost exclusively at night, indicating that tagged Greenland cod had left the detection area during the day.

Cunner Habitat Preference

PERMANOVA results for cunner indicated a significant interaction between season and diel period (two-way PERMANOVA, Pseudo-F = 1.9, df = 4, P(perm) = 0.025, Table 3.6a).

However, only a very small proportion of the variance (2.8%) was explained by season and diel period. Separate analysis of seasons in pairwise PERMANOVA tests indicated significant differences in habitat use between all diel comparisons in summer and fall ($p < 0.05$, Tables 3.6c, d), but not spring ($p > 0.05$, Table 3.6b). Cunner were rarely detected outside my habitat polygons (Table 3.1b).

Cunner preferred eelgrass only during the spring (Figure 3.10), whereas kelp was selected in all three seasons. Cobble use was also greater than expected in summer. Cunner underutilized sparse vegetation and bare sand in all seasons.

Cunner were only detected during a portion of the diel period, starting two hours after sunrise and ending two hours after dusk. Cunner habitat use differed among diel periods with reduced use of eelgrass at dusk, except in spring (Figure 3.10). In spring and fall, kelp use was lowest during the day whereas cobble use was greater during the day than dusk or night.

Sculpin Habitat Preference

Sculpin habitat use differed significantly among seasons (two-way PERMANOVA, Pseudo-F = 32.7, df = 2, P(perm) = 0.001, Tables 3.7a), with a small proportion of the variance (6.8%) explained by season and diel period. Pairwise PERMANOVA tests indicated significant differences in habitat use between all season combinations ($p < 0.01$, Table 3.7b). Sculpin were rarely detected outside of the habitat polygons (Table 3.1b). Sculpin selected sparse vegetation in spring and fall, but selected kelp and bare sand in summer (Figure 3.11). Sculpin underutilized eelgrass in all seasons.

Fish Around the Sound

Data from receivers located outside the study area detected many of my tags during my study, indicating that predators moved beyond Newbridge Cove. I detected individual Atlantic cod throughout the Sound (Table 3.2, see Appendix 1), although they generally remained along its northern shore. I detected the majority of individuals in the spring, with declining numbers in summer and fall. Greenland cod exhibited a similar pattern to Atlantic cod. In contrast, few sculpin ventured outside Newbridge Cove; individuals remained in the inner sound, and did not move past the narrows. Dispersal of sculpin from Newbridge Cove did not differ by season. Cunner travelled the least distance from Newbridge Cove, generally traveling only as far as the next neighbouring site (Buckley’s Cove), (see Figure A1.3, Appendix 1). I detected more tagged cunner in Buckley’s Cove in summer and fall (4 and 5, respectively) than in spring (1).

Discussion

Seasonal Habitat Use

Tagged predators primarily occupied habitats outside of eelgrass beds, with proportionally higher usage of kelp and sparsely vegetated habitats. Predators were most frequently detected in sparse vegetation, however this was not always in proportion to the amount of habitat available, indicating variation in selection for this habitat among seasons and diel periods. Habitat use by predators differed among seasons, with the exception of 1-2 year old Atlantic cod. Atlantic cod were detected more frequently outside of the habitat map, often in depths greater than 10 m. Previous studies reported age-1 Atlantic cod in depths greater that 10 m (Gregory and Anderson 1997; Cote *et al*. 2001), suggesting that these depths are an important habitat for age-1 cod.

During spring, cunner and Greenland cod had a higher rate of occurrence in eelgrass and kelp, whereas sculpin slightly preferred kelp and sparse vegetation. This early preference for eelgrass by age-1+ Greenland cod and cunner may reflect reduced post-winter eelgrass biomass, either as a result of ice-scour (Robertson and Mann 1984) or lack of early-season growth (Lalumière *et al.* 1994). The data for my habitat map (Chapter 2) were collected from August through October, when leaf biomass had peaked (Lalumière *et al.* 1994). Therefore, the eelgrass use by cunner and Greenland cod in spring I report here may be over-represented, because eelgrass had not yet resumed growing post-winter.

Use of eelgrass habitat decreased for all species into the summer, where selection shifted to kelp and sparse vegetation for sculpin and Greenland cod, respectively. I expected this shift for Atlantic cod (Gotceitas *et al.* 1997), but not for sculpin, because sculpin have been reported to frequent both bare substrates and eelgrass (Linehan *et al.* 2001; Laurel *et al.* 2003a). Cunner have been reported to prefer rocky substrates, such as rock reefs, boulders, and exposed bedrock (Pottle and Green 1979a, 1979b; Tupper and Boutilier 1997). These substrates were largely absent from the study site, and in this study cunner were observed in kelp and cobble. In Chapter 2, I found that cunner associated with sand, but not boulders. Selection for these deeper water habitats may reflect temperature preferences (e.g. cod: Clark and Green 1991) or predator avoidance (Crowder *et al.* 1997; Cote *et al.* 2008a, 2008b). Additionally, the presence of tall eelgrass may restrict movements of these larger-bodied fishes (Savino and Stein 1982) within this habitat, and the lack of detections of predators in eelgrass may signify that the eelgrass has reached sufficient biomass and density to exclude predators from the nursery habitat, since eelgrass leaf biomass peaks in summer (Lalumière *et al*. 1994). This shift to deeper water habitats by piscivorous fish also coincides with the onset of settlement of age-0 cod into eelgrass nursery beds (Ings *et al*. 2008). This suggests that there is temporal segregation of predator from age-0 cod, with age-0 cod "trading places" with predators.

In the fall, habitat use resembled that of summer for Greenland cod and cunner, but not for Atlantic cod and sculpin. Sculpin selection shifted from kelp and bare sand in the summer to predominantly sparse vegetation in the fall. Age-1 Atlantic cod transition from nursery habitats to deeper water (Gregory and Anderson 1997), and begin moving toward the outer shelf at age 2 (Anderson and Gregory 2000). This transition to deeper water may explain the decrease in detections in fall for Atlantic cod, as individuals move out of range of the acoustic receivers. This absence further segregates age-0 cod from their older conspecifics, potentially mediating cannibalism (Bogstad *et al*. 1994), Greenland cod continued to select sparse vegetation in daylight hours, although there was a strong selection for kelp at night. In my study, kelp habitat was found in shallower water than sparse vegetation, and this shift to shallower habitat may indicate diel migrations by Greenland cod to forage, a behaviour seen in many piscivores (Pihl 1982; Linehan *et al.* 2001; Landry *et al.* 2019). Overall, predators remained spatially segregated from age-0 in fall.

Diel Habitat Use

In contrast to previous work, of the four species I studied, only cunner differed significantly in their use of the different habitats among diel periods. Previous studies reported increased presence of cod and sculpin in shallow water at night (Keats 1990; Linehan *et al.* 2001), with cod moving into shallower water at night to forage (Pihl 1982). Sculpin activity also reportedly increases at night (Ivanova *et al.* 2018). These studies examined either limited habitat choices (e.g., eelgrass vs non-eelgrass: Linehan *et al*. 2001) or limited diel periods (i.e., no twilight: Keats 1990; Pihl 1982). Acoustic telemetry enables monitoring of habitat selection by individual fish across a suite of habitat choices in multiple seasons and diel periods. However, in my study minimal detections of Atlantic cod, Greenland Cod, and sculpin in summer and fall at Newbridge Cove may have contributed to the absence of diel patterns in these species.

I never detected cunner during dawn. The night period detections all occurred within 2 hours of dusk, consistent with their quiescent behaviour (Pottle and Green 1979a), where cunner either camouflage against the substrate, or aggregate in rock crevices (Dew 1976). The cunner in my study likely used rock crevices, as these crevices would interfere with the acoustic signal from the tag resulting in a lack of detections. The cunner “re-emerged” during the day, with detections resuming within 2 hours after sunrise. The decrease in activity at night and dawn may reduce predation pressure from cunner on age-0 cod during these diel periods.

Movement Around the Sound

Both Atlantic and Greenland cod moved beyond Newbridge Cove, generally staying along the northern shore of Newman Sound. Tag detections in the spring exceeded those in summer and fall, indicating both species may have sought out deeper water beyond the range of the acoustic receivers. Selection for deeper water may reflect cod temperature preferences (Clark and Green 1991), or a means of predator avoidance (Linehan *et al.* 2001; Cote *et al.* 2008a, 2008b). The reduced presence of age-1+ cod in summer and fall may increase habitat segregation from age-0 cod, reducing the number of interactions between age-0 cod and older conspecifics.

Cunner and sculpin were both more localized than cod, remaining at the sites nearest Newbridge Cove (e.g., Buckley’s Cove). This pattern may reflect small territorial ranges in cunner (< 75 m^2; Pottle and Green 1979a). Sculpin traveled farther, and were more likely to cross the Sound than either cunner or cod. Previous studies suggest that sculpin may be territorial

(Landry *et al.* 2019), but with ranges of up to 0.8 hectares (Ivanova *et al.* 2018). Compared to age-1+ cod, the continued presence of cunner and sculpin in Newbridge Cove may mean that these species exert greater predation pressure on age-0 cod, as their presence increases opportunities for interactions.

Potential Impact of Piscivorous Fishes on Age-0 Cod Habitat Selection

All tagged predators generally occupied deeper water outside eelgrass beds, with proportionally higher usage of kelp and sparsely vegetated habitats. This behaviour among piscivores likely reduces predation from their own avian and terrestrial predators (Crowder *et al.* 1997; Cote *et al.* 2008a, 2008b). The general absence of piscivorous fishes from eelgrass habitat may indicate it is more suitable as a refuge for age-0 cod from piscivorous fishes occupying deeper waters – where my tagged individuals were located.

The structural complexity of eelgrass may restrict the movements of larger-bodied predators (Savino and Stein 1982), as well as reduce encounter rates (Lindholm *et al.* 1999), thus reducing capture success (Gotceitas and Colgan 1989; Gotceitas et al. 1997; Tupper and Boutilier 1997). However, elevated predation on age-0 cod occurs along edges of eelgrass patches (Gorman *et al.* 2009). This increase likely reflects access to the habitat, and greater rates of capture success, by piscivorous fishes. For example, as ambush predators, sculpin occupy eelgrass when prey are present (Laurel and Brown 2006). However, in the absence of prey, laboratory studies indicate that sculpin prefer sandy substrate (Laurel and Brown 2006). The presence of piscivores in habitats outside of eelgrass beds suggests that these habitats may carry a greater predation risk to age-0 cod.

Not only do age-0 cod and their piscivorous predators spatially segregate, but they temporally segregate as well. Whereas Greenland cod and cunner select eelgrass in spring, age-0 cod do not begin the settle into eelgrass beds until July or August (Laurel *et al.* 2003b; Ings *et al.* 2008). In my study, summer began in mid-July, and my telemetry data showed that the tagged piscivorous had moved out of eelgrass beds by that time. Therefore, age-0 cod would not occupy eelgrass beds at the same time as their predators. The spatial and temporal habitat segregation of piscivores from their prey mediates cannibalism in Atlantic cod (Gotceitas *et al.* 1997), reducing predation pressure on age-0 cod.

Conclusion

Habitat use of piscivorous Atlantic cod, Greenland cod, cunner, and shorthorn sculpin reveals that these species primarily occupied habitats in deeper water outside eelgrass beds. Habitat use differed among species, as well as among diel periods for cunner, and among seasons for piscivorous Greenland cod, cunner, and sculpin. Greenland cod and cunner used eelgrass habitat in the spring; in contrast, all piscivorous species preferred either kelp or sparse vegetation in summer and fall. This preference suggests spatial segregation of these piscivores from age-0 cod, likely limiting predator-prey interactions that may result in reduced risk to potential prey. The use of acoustic telemetry has provided additional understanding of spatial-temporal habitat use relative to net-based and visual surveys, by examining both season and diel variation predator habitat selection for a broad suite of habitat types.

References

Anderson, J. T., and Gregory, R. S. (2000). Factors regulating survival of northern cod (NAFO 2J3KL) during their first 3 years of life. ICES Journal of Marine Science 57, 349–359. doi:10.1006/jmsc.1999.0530

Anderson, M. J. (2001). Permutation tests for univariate or multivariate analysis of variance and regression. Canadian Journal of Fisheries and Aquatic Sciences 58, 626–639. doi:10.1139/cjfas-58-3-626

Bogstad, B., Lilly, G. R., Mehl, S., Pálsson, Ó. K., and Stefánsson, G. (1994). Cannibalism and year-class strength in Atlantic cod (*Gadus morhua* L.) in Arcto-boreal ecosystems (Barents Sea, Iceland, and eastern Newfoundland). ICES Marine Science Symposia 198, 576–599.

Chen, S., and Watanabe, S. (1989). Age dependence of natural mortality coefficient in fish population dynamics. Nippon Suisan Gakkaishi 55, 205–208. doi:10.2331/suisan.55.205

Clark, D. S., and Green, J. M. (1991). Seasonal variation in temperature preference of juvenile Atlantic cod (*Gadus morhua*), with evidence supporting an energetic basis for their diel vertical migration. Canadian Journal of Zoology 69, 1302–1307. doi:10.1139/z91-183

Coates, J. H., Hovel, K. A., Butler, J. L., Klimley, A. P., and Morgan, S. G. (2013). Movement and home range of pink abalone *Haliotis corrugata*: Implications for restoration and population recovery. Marine Ecology Progress Series 486, 189–201. doi:10.3354/meps10365

Cote, D., Gregory, R. S., and Stewart, H. M. J. (2008a). Size-selective predation by river otter (*Lontra canadensis*) improves refuge properties of shallow coastal marine nursery habitats. Canadian Journal of Zoology 86, 1324–1328. doi:10.1139/Z08-120

Cote, D., Stewart, H. M. J., Gregory, R. S., Gosse, J., Reynolds, J. J., Stenson, G. B., and Miller, E. H. (2008b). Prey selection by marine-coastal river otters (*Lontra canadensis*) in Newfoundland, Canada. Journal of Mammalogy 89, 1001–1011. doi:10.1644/07-MAMM-A-192.1

Crowder, L. B., Squires, D. D., and Rice, J. A. (1997). Nonadditive effects of terrestrial and aquatic predators on juvenile estuarine fish. Ecology 78, 1796–1804.

Dew, C. B. (1976). A contribution to the life history of the cunner *Tautogolabrus adspersus* , in Fishers Island, Connecticut. Chesapeake Science 17, 101–113.

Gorman, A. M., Gregory, R. S., and Schneider, D. C. (2009). Eelgrass patch size and proximity to the patch edge affect predation risk of recently settled age 0 cod (*Gadus*). Journal of Experimental Marine Biology and Ecology 371, 1–9. doi:10.1016/j.jembe.2008.12.008

Gotceitas, V., and Colgan, P. (1989). Predator foraging success and habitat complexity: quantitative test of the threshold hypothesis. Oecologia 80, 158–166. doi:10.1007/BF00380145

Gotceitas, V., Fraser, S., and Brown, J. A. (1997). Use of eelgrass beds (*Zostera marina*) by juvenile Atlantic cod (*Gadus morhua*). Canadian Journal of Fisheries and Aquatic Sciences 54, 1306–1319. doi:10.1139/f97-033

Grant, S. M., and Brown, J. A. (1998). Nearshore settlement and localized populations of age 0 Atlantic cod (*Gadus morhua*) in shallow coastal waters of Newfoundland. Canadian Journal of Fisheries and Aquatic Sciences 55, 1317–1327.

Gregory, R. S., and Anderson, J. T. (1997). Substrate selection and use of protective cover by juvenile Atlantic cod *Gadus morhua* in inshore waters of Newfoundland. Marine Ecology Progress Series 146, 9–20. doi:10.3354/meps146009

Houde, E. D. (1987). Fish early life dynamics and recruitment variability. American Fisheries Society Symposium 2, 17–29.

Ings, D. W., Gregory, R. S., and Schneider, D. C. (2008). Episodic downwelling predicts recruitment of Atlantic cod, Greenland cod and white hake to Newfoundland coastal waters. Journal of Marine Research 66, 529–561.

Ivanova, S. V., Kessel, S. T., Landry, J., O'Neill, C., McLean, M. F., Espinoza, M., Vagle, S., Hussey, N. E., and Fisk, A. T. (2018). Impact of vessel traffic on the home ranges and movement of shorthorn sculpin (*Myoxocephalus scorpius*) in the nearshore environment of the high Arctic. Canadian Journal of Fisheries and Aquatic Sciences 75, 2390–2400. doi:10.1139/cjfas-2017-0418

Keats, D. W. (1990). A nocturnal inshore movement of juvenile cod *Gadus morhua* L. in eastern Newfoundland. Journal of Experimental Marine Biology and Ecology 139, 167–173. doi:10.1016/0022-0981(90)90144-2

Lalumière, R., Messier, D., Fournier, J. J., and Peter McRoy, C. (1994). Eelgrass meadows in a low arctic environment, the northeast coast of James Bay, Québec. Aquatic Botany 47, 303–315. doi:10.1016/0304-3770(94)90060-4

Landry, J. J., Kessel, S. T., McLean, M. F., Ivanova, S. V., Hussey, N. E., O'Neill, C., Vagle, S., Dick, T. A., and Fisk, A. T. (2019). Movement types of an arctic benthic fish, shorthorn sculpin (*Myoxocephalus scorpius*), during open-water periods in response to biotic and abiotic factors1. Canadian Journal of Fisheries and Aquatic Sciences 76, 626–635. doi:10.1139/cjfas-2017-0389

Laurel, B. J., and Brown, J. A. F. (2006). Influence of cruising and ambush predators on 3-dimensional habitat use in age 0 juvenile Atlantic cod *Gadus morhua*. Journal of Experimental Marine Biology and Ecology 329, 34–46. doi:10.1016/j.jembe.2005.08.003

Laurel, B. J., Gregory, R. S., and Brown, J. A. (2003a). Predator distribution and habitat patch area determine predation rates on age-0 juvenile cod *Gadus* spp. Marine Ecology Progress Series 251, 245–254. doi:Doi 10.3354/Meps251245

Laurel, B. J., Gregory, R. S., and Brown, J. A. (2003b). Settlement and distribution of age-0 juvenile cod, *Gadus morhua* and *G. ogac*, following a large-scale habitat manipulation. Marine Ecology Progress Series 262, 241–252. doi:10.3354/meps262241

Lindholm, J. B., Auster, P. J., and Kaufman, L. S. (1999). Habitat-mediated survivorship of juvenile (0-year) Atlantic cod *Gadus morhua*. Marine Ecology Progress Series 180, 247–255. doi:10.3354/meps180247

Linehan, J. E., Gregory, R. S., and Schneider, D. C. (2001). Predation risk of age-0 cod (*Gadus*) relative to depth and substrate in coastal waters. Journal of Experimental Marine Biology and Ecology 263, 25–44. doi:10.1016/S0022-0981(01)00287-8

Methven, D. A., and Bajdik, C. (1994). Temporal variation in size and abundance of juvenile Atlantic cod (*Gadus morhua*) at an inshore site off eastern Newfoundland. Canadian Journal of Fisheries and Aquatic Sciences 51, 78–90.

Pauly, D. (1980). On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. ICES Journal of Marine Science 39, 175–192. doi:10.1093/icesjms/39.2.175

Pihl, L. (1982). Food intake of young cod and flounder in a shallow bay on the Swedish west coast. Netherlands Journal of Sea Research 15, 419–432. doi:10.1016/0077-7579(82)90068-0

Pottle, A., and Green, M. (1979a). Territorial behaviour of the north temperate labrid, *Tautogolabrus adspersus*. Canadian Journal of Zoology 57, 2337–2347.

Pottle, R. A., and Green, J. M. (1979b). Field observations on the reproductive behaviour of the cunner, *Tautogolabrus adspersus* (Walbaum), in Newfoundland. Canadian Journal of Zoology 57, 247–256.

Robertson, A. I., and Mann, K. H. (1984). Disturbance by ice and life-history adaptations of the seagrass *Zostera marina*. Marine Biology 80, 131–141. doi:10.1007/BF02180180

Savino, J. F., and Stein, R. A. (1982). Predator-prey interaction between largemouth bass and bluegills as influenced by simulated, submersed vegetation. Transactions of the American Fisheries Society 111, 255–266. doi:10.1577/1548-8659(1982)111<255

Smith, F. (2013). Understanding HPE in the VEMCO Positioning System (VPS). doi:VEMCO Document # Doc-005457-07

Tupper, M., and Boutilier, R. G. (1997). Effects of habitat on settlement, growth, predation risk and survival of a temperate reef fish. Marine Ecology Progress Series 151, 225–236. doi:10.3354/meps151225

Tables and Figures

Table 3.1a: The number of raw acoustic detections (“pings”), and calculated positions (both raw and filtered) used in the Permutational Multivariate Analysis of Variance (PERMANOVA) for Atlantic cod (*Gadus morhua)*, Greenland cod (*G. macrocephalus ogac*), cunner (*Tautogolabrus adspersus*), and shorthorn sculpin (*Myoxocephalus scorpius*).

		Predator Species			
	Total	Atlantic Cod	Greenland Cod	Cunner	Sculpin
Raw detections	1,162,691	330,536	145,107	404,044	283,004
Raw positions	142,692	57,929	7137	43,561	34,065
Filtered positions (HPE < 12)	13710	53,488	6679	41,355	33,188
# positions used in PERMANOVA	89,390	18,410	4312	36.608	30,060

Table 3.1b: The number of calculated positions located inside and outside the habitat map polygons for Atlantic cod (*Gadus morhua)*, Greenland cod (*G. macrocephalus ogac*), cunner (*Tautogolabrus adspersus*), and shorthorn sculpin (*Myoxocephalus scorpius*).

		Predator Species				
	Season	Total	Atlantic Cod	Greenland Cod	Cunner	Sculpin
Inside Habitat	Spring	32,207	17,873	4179	2029	8126
	Summer	27,116	535	64	21933	4584
	Fall	29,995	0	39	12620	17,336
Outside Habitat	Spring	21,804	20,459	1093	114	138
	Summer	15,478	10,142	944	2521	1871
	Fall	7950	4457	331	2088	1074

Table 3.2: Number of tagged predators (Atlantic cod *Gadus morhua*, Greenland cod *G. macrocephalus ogac*, cunner *Tautogolabrus adspersus*, and shorthorn sculpin *Myoxocephalus scorpius*) detected at receivers located throughout Newman Sound, Newfoundland. *** indicates the Newbridge study site. Receivers are ordered from farthest west to farthest east of Newbridge, with odd numbered receivers denoting those found on the northern shore of the Sound and even numbered receivers denoting those on the southern shore.

		Predator Species			
Receiver #	Distance from Newbridge (m)	Atlantic Cod	Greenland Cod	Cunner	Sculpin
1	4151	2	5	0	2
3	2439	4	7	0	1
2	2065	4	4	0	1
4	1467	4	1	0	2
5	735	7	7	1	2
***	0	10	10	10	7
7	1059	8	9	7	1
9	1531	7	5	1	0
6	2334	3	0	0	0
11	2749	4	5	1	0
13	4983	3	4	1	0
10	4192	2	0	0	0
8	4110	1	0	0	0
12	4763	1	0	0	0
14	5893	1	0	0	0

Table 3.3: Permutational analysis of variance (PERMANOVA) table for effects of species (*Gadus morhua, G. macrocephalus ogac*, *Tautogolabrus adspersus*, *Myoxocephalus scorpius*), diel period (dawn, day, dusk, night), and season (spring, summer, fall) on proportional habitat use. Proportional habitat use refers to the proportion of positions detected within a habitat polygon for a given combination of season and diel period (to account for length of diel period), standardized by the proportion of available habitat. Habitats analyzed include eelgrass, kelp, sparse vegetation, bare sand, and bare cobble. Bold font indicates a significant p-value.

Source	df	Sum of Squares	MS	Pseudo-*F*	P(perm)
Species	3	1.06 e5	35300	16.8	**0.001**
Season	2	21400	10700	5.10	**0.001**
Diel	3	4320	1440	0.69	0.702
Species * Season	5	79900	16000	7.61	**0.001**
Species * Diel	8	18400	2300	1.10	0.335
Season * Diel	6	13300	2210	1.05	0.396
Species * Season * Diel	10	26300	2630	1.25	0.171
Residual	4035	8.48 e6	2100		
Total	4072	9.43 e6			

Table 3.4: Permutational analysis of variance (PERMANOVA) table for effects of diel period (dawn, day, dusk, night), and season (spring, summer, fall) on proportional habitat use by Atlantic cod (*Gadus morhua*). Proportional habitat use refers to the proportion of positions detected within a habitat polygon for a given combination of season and diel period (to account for length of diel period), standardized by the proportion of available habitat. Habitats analyzed include eelgrass, kelp, sparse vegetation, bare sand, and bare cobble.

Source	df	Sum of Squares	MS	Pseudo-*F*	P(perm)
Season	1	4490	4490	2.48	0.072
Diel	3	5410	1800	1.00	0.440
Season * Diel	3	5610	1870	1.03	0.420
Residual	630	1.14 e6	1810		
Total	637	1.21 e6			

Table 3.5a: Permutational analysis of variance (PERMANOVA) table for effects of diel period (dawn, day, dusk, night), and season (spring, summer, fall) on proportional habitat use by Greenland cod (*Gadus macrocephalus ogac*). Proportional habitat use refers to the proportion of positions detected within a habitat polygon for a given combination of season and diel period (to account for length of diel period), standardized by the proportion of available habitat. Habitats analyzed include eelgrass, kelp, sparse vegetation, bare sand, and bare cobble. Bold font indicates a significant p-value.

Source	df	Sum of Squares	MS	Pseudo-*F*	P(perm)
Season	2	15400	7690	3.33	**0.010**
Diel	3	6580	2190	0.95	0.495
Season * Diel	3	5870	1960	0.85	0.555
Residual	154	3.56 e5	2310		
Total	162	3.90 e5			

Table 3.5b: Pair-wise tests for PERMANOVA of Greenland cod (*Gadus macrocephalus ogac*) habitat use (eelgrass, kelp, sparse vegetation, bare sand, bare cobble) by season (spring, summer, fall). Bold font indicates a significant p-value.

Groups	*t*	P(perm)
Spring, Summer	2.51	**0.001**
Spring, Fall	0.59	0.769
Summer, Fall	1.37	0.155

Table 3.6a: Permutational analysis of variance (PERMANOVA) table for effects of diel period (dawn, day, dusk, night), and season (spring, summer, fall) on proportional habitat use by cunner (*Tautogolabrus adspersus*). Proportional habitat use refers to the proportion of positions detected within a habitat polygon for a given combination of season and diel period (to account for length of diel period), standardized by the proportion of available habitat. Habitats analyzed include eelgrass, kelp, sparse vegetation, bare sand, and bare cobble. Bold font indicates a significant p-value.

Source	df	Sum of Squares	MS	Pseudo-*F*	P(perm)
Season	2	32100	16000	7.42	**0.001**
Diel	2	22900	11400	5.29	**0.001**
Season * Diel	4	16500	4130	1.91	**0.025**
Res	2078	4.49 e6	2160		
Total	2086	4.62 e6			

Table 3.6b: Pair-wise tests for PERMANOVA of cunner (*Tautogolabrus adspersus*) habitat use (eelgrass, kelp, sparse vegetation, bare sand, bare cobble) by season (spring, summer, fall) in spring. There was no positional data for cunner during the dawn period.

Groups	*t*	P(perm)
Day, Dusk	1.38	0.144
Day, Night	1.26	0.183
Dusk, Night	0.53	0.811

Table 3.6c: Pair-wise tests for PERMANOVA of cunner (*Tautogolabrus adspersus*) habitat use (eelgrass, kelp, sparse vegetation, bare sand, bare cobble) by season (spring, summer, fall) in summer. There was no positional data for cunner during the dawn period. Bold font indicates a significant p-value.

Groups	*t*	P(perm)
Day, Dusk	3.87	**0.001**
Day, Night	3.90	**0.001**
Dusk, Night	2.17	**0.003**

Table 3.6d: Pair-wise tests for PERMANOVA of cunner (*Tautogolabrus adspersus*) habitat use (eelgrass, kelp, sparse vegetation, bare sand, bare cobble) by season (spring, summer, fall).in fall. There was no positional data for cunner during the dawn period. Bold font indicates a significant p-value.

Groups	*t*	P(perm)
Day, Dusk	3.34	**0.001**
Day, Night	3.46	**0.001**
Dusk, Night	1.86	**0.018**

Table 3.7a: Permutational analysis of variance (PERMANOVA) table for effects of diel period (dawn, day, dusk, night), and season (spring, summer, fall) on proportional habitat use by shorthorn sculpin (*Myoxocephalus scorpius*). Proportional habitat use refers to the proportion of positions detected within a habitat polygon for a given combination of season and diel period (to account for length of diel period), standardized by the proportion of available habitat. Habitats analyzed include eelgrass, kelp, sparse vegetation, bare sand, and bare cobble. Bold font indicates a significant p-value.

Source	df	Sum of Squares	MS	Pseudo-*F*	P(perm)
Season	2	1.38 e5	69200	32.7	**0.001**
Diel	3	5780	1930	0.91	0.507
Season * Diel	6	11100	1860	0.88	0.585
Res	1173	2.48 e6	2120		
Total	1184	2.66 e6			

Table 3.7b: Pair-wise tests for PERMANOVA of shorthorn sculpin (*Myoxocephalus scorpius*) habitat use (eelgrass, kelp, sparse vegetation, bare sand, bare cobble) by season (spring, summer, fall). Bold font indicates a significant p-value.

Groups	*t*	P(perm)
Spring, Summer	5.79	**0.001**
Spring, Fall	2.41	**0.003**
Summer, Fall	7.31	**0.001**

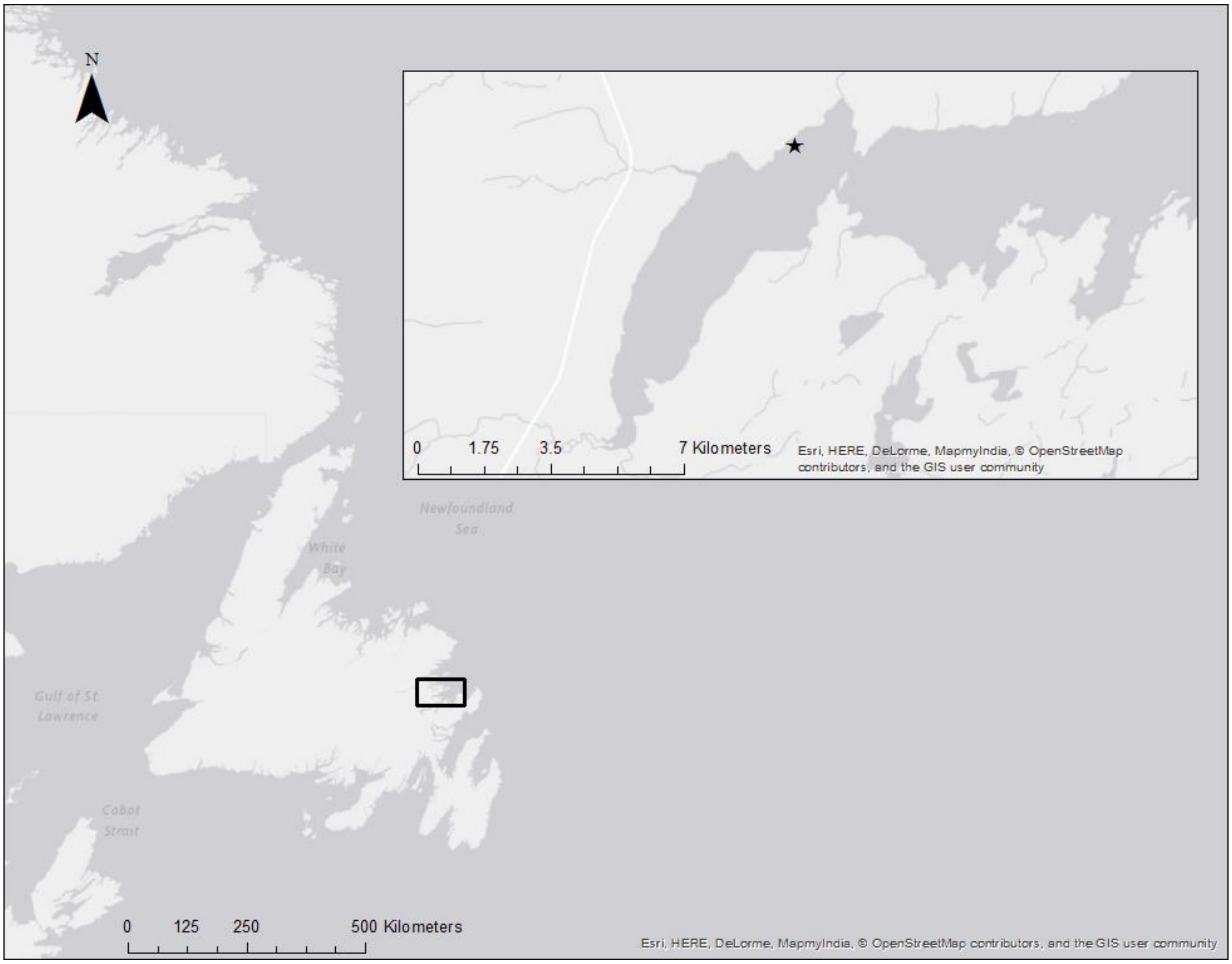

Figure 3.1: The study site, Newbridge Cove (star), located within Newman Sound (inset), Bonavista Bay, on the east coast of Newfoundland, Canada.

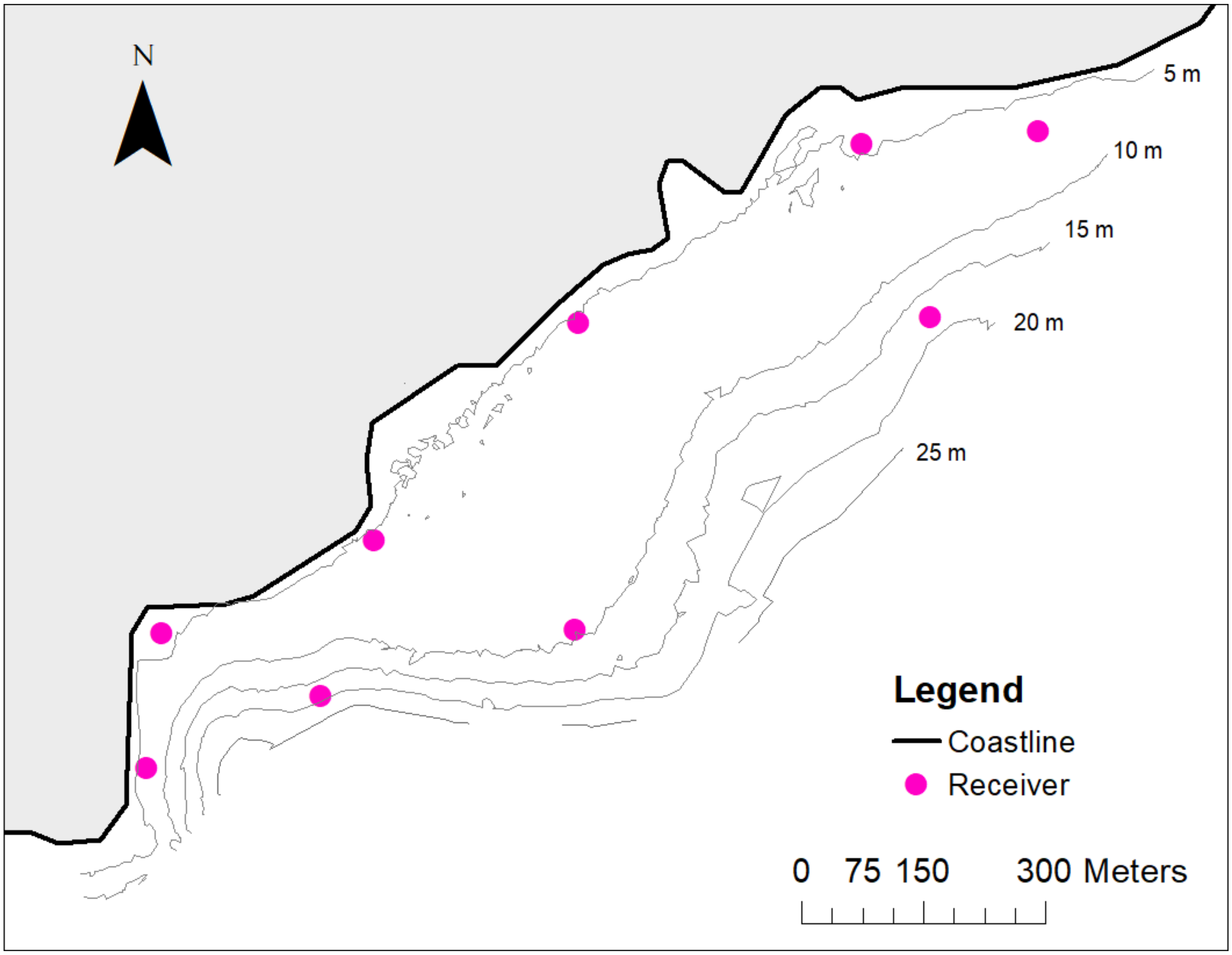

Figure 3.2: Locations of acoustic receivers (pink dots) around Newbridge Cove (indicated by the star in Figure 3.1) with 5 m bathymetry curves (grey lines).

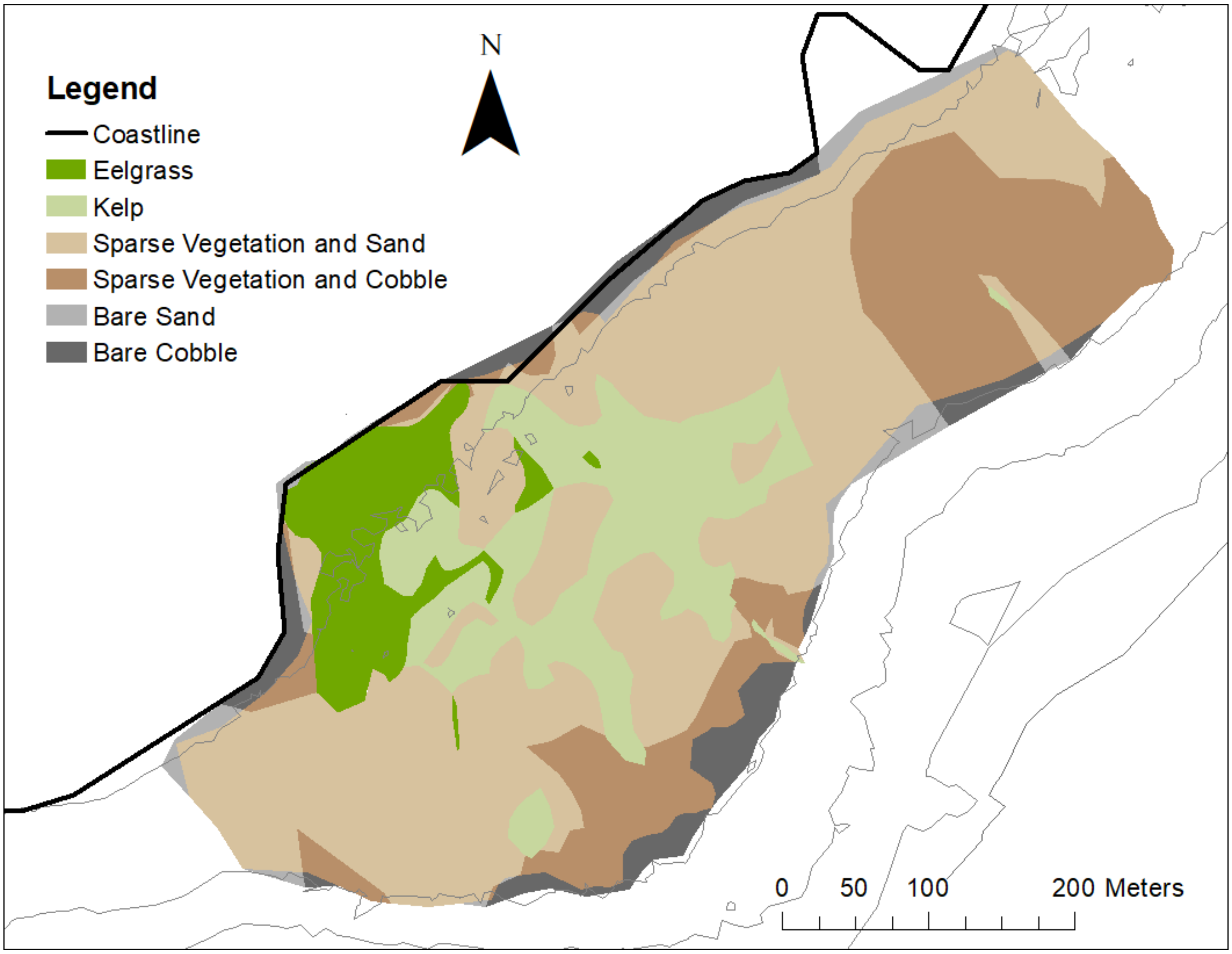

Figure 3.3: Habitat map of Newbridge Cove (indicated by the star in Figure 3.1) with 5 m bathymetry contours (grey lines). Habitat classifications were determined from video transects, where I recorded the edges of habitat patches. Classification of substrate type by size: cobble (25 cm – 1 m) and sand (< 5 mm). Vegetation included eelgrass (*Zostera marina*) and kelp (*Saccharina latissima*).

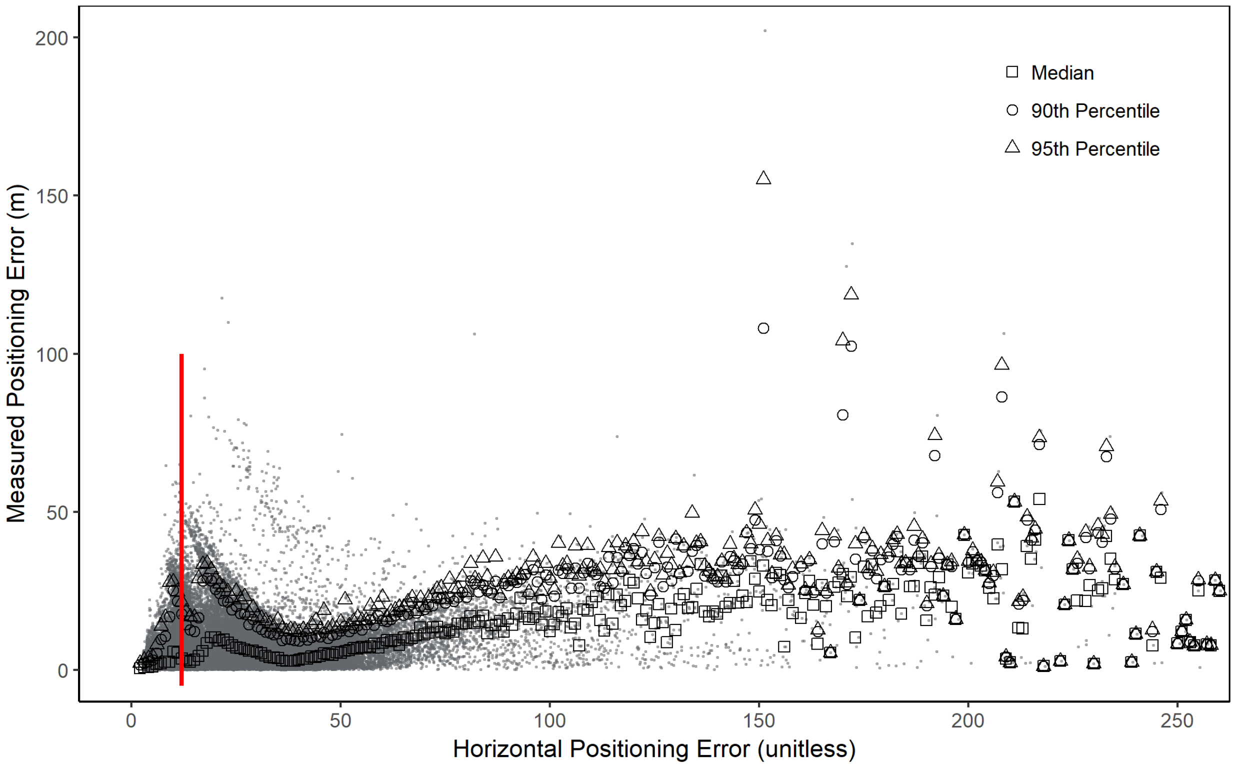

Figure 3.4: The measured positioning error (HPEm, in meters) for horizontal positioning error (HPE, unitless) values. Median (50th), 90th, and 95th percentiles for HPEm were calculated from 1 HPE bins for 161,581 detections from 8 sync tags for the duration of the study (May – November). For HPE values under 12, HPEm had 50th, 90th, and 95th percentiles of 0.9 m, 2.9 m, and 4.4 m respectively. HPE values greater than 12 (red line) were removed before analysis of telemetry data.

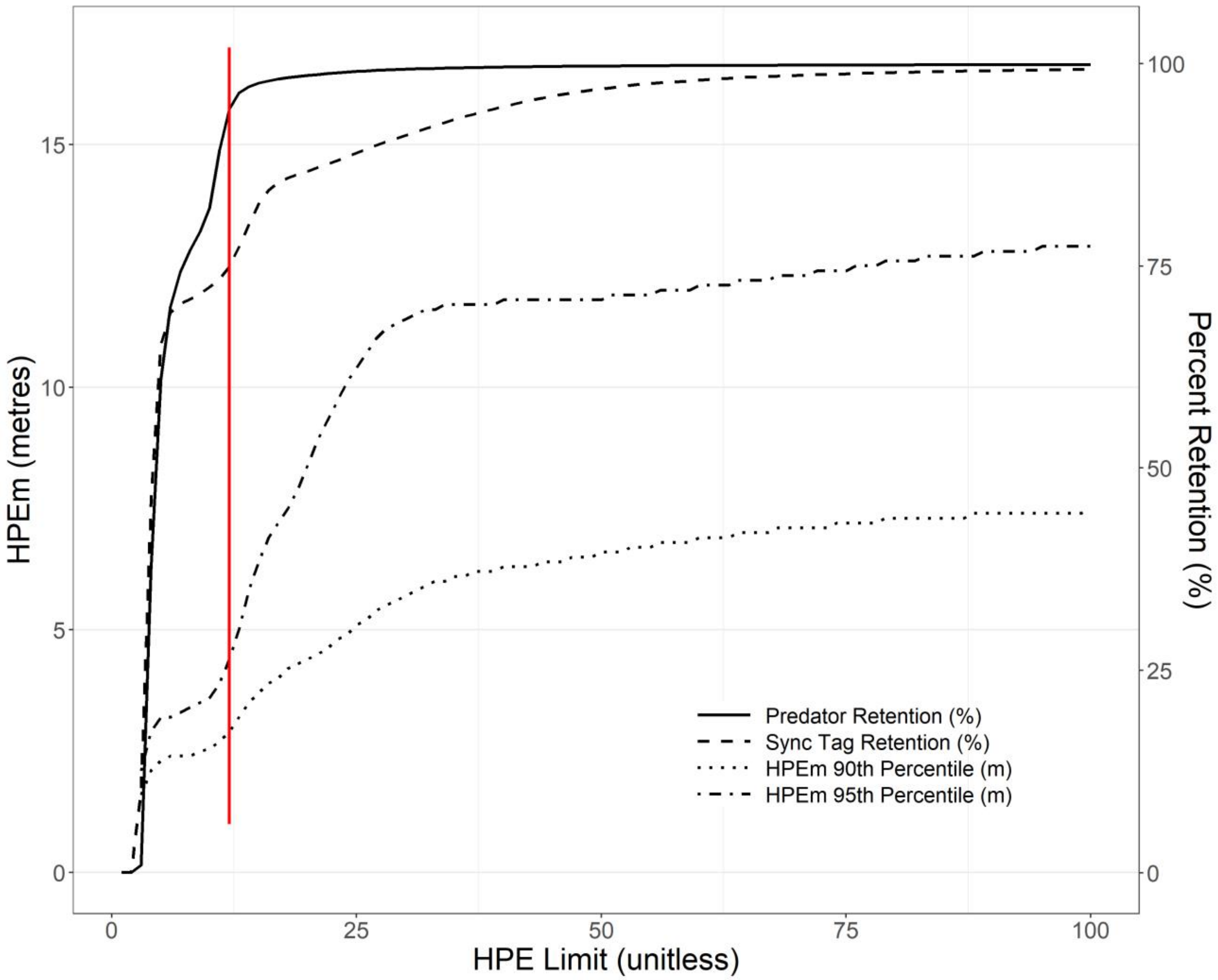

Figure 3.5: Data retention of predator position by horizontal positioning error (HPE, unitless) limit. The left axis indicates the 90th and 95th percentiles of the measured HPE (HPEm, in meters) for the remaining data at the given HPE limit (x-axis). The right axis indicates the percent data retention for the tagged predator data and the sync tag data. HPE values greater than 12 (red line) were removed before analysis of telemetry data.

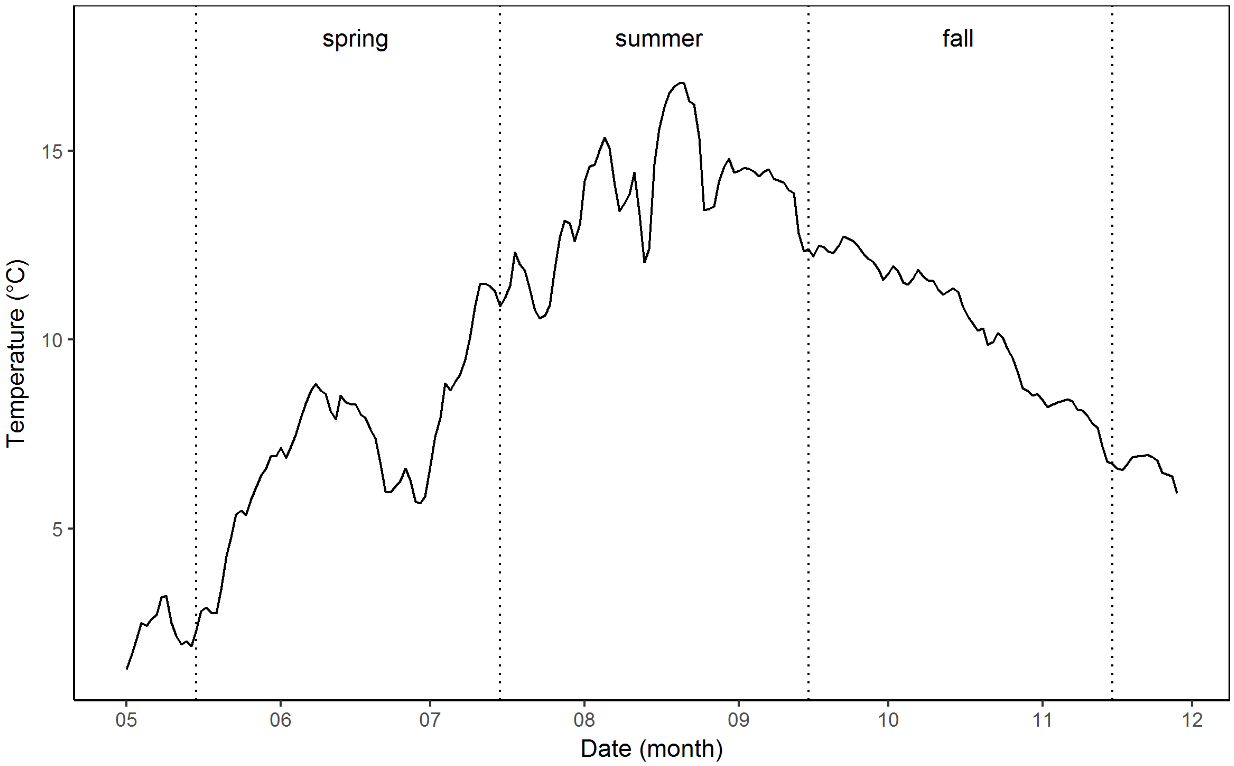

Figure 3.6: Mean daily water temperature in Newman Sound from May to December 2016. A rise in temperature characterized spring, in contrast to stable temperature in summer, and declining temperature in fall.

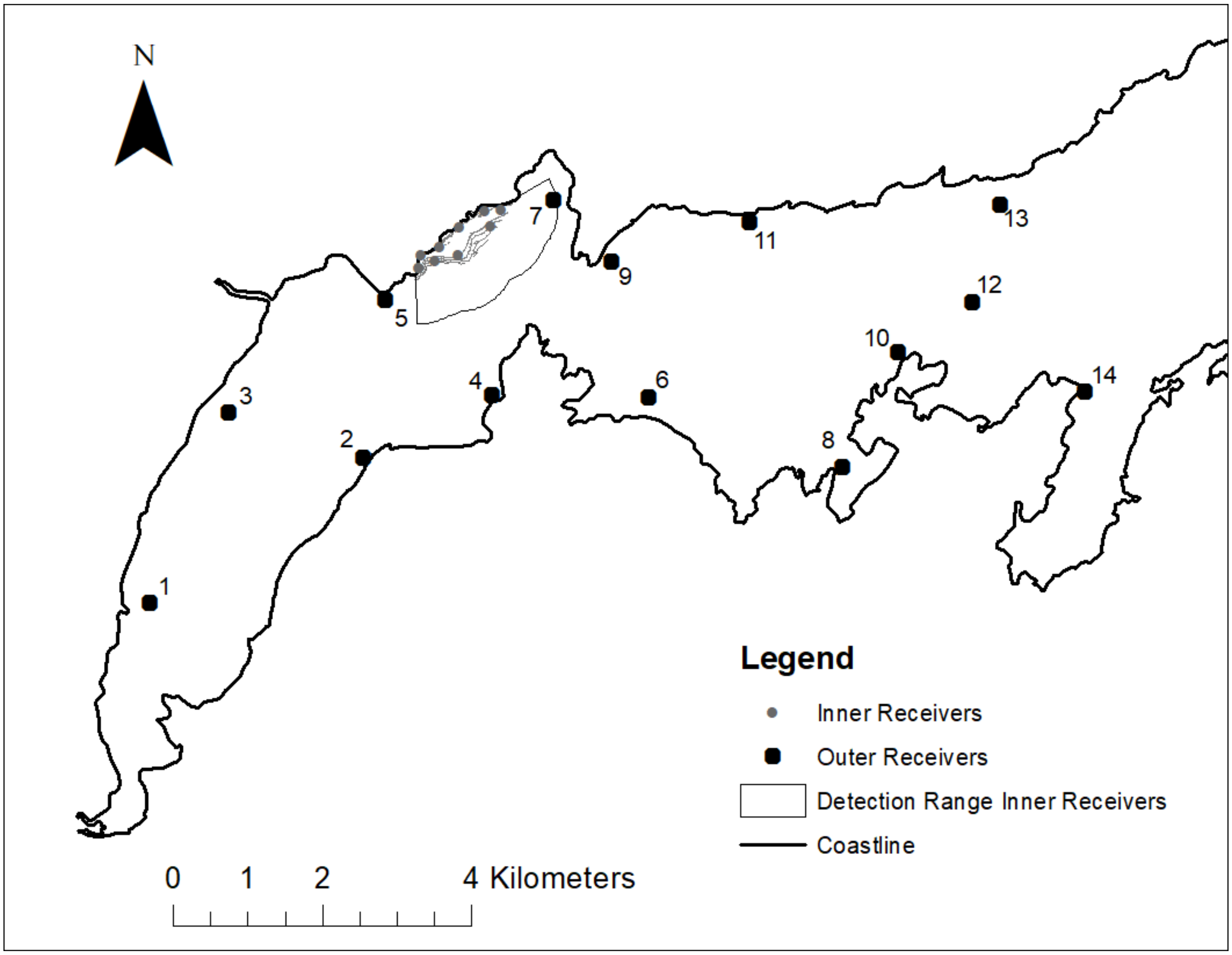

Figure 3.7: Location of acoustic receivers around Newman Sound. The area along the central northern shore, indicated by the polygon, shows the Newbridge Cove focal study location. The polygon indicates the detection range for the “inner receiver array”.

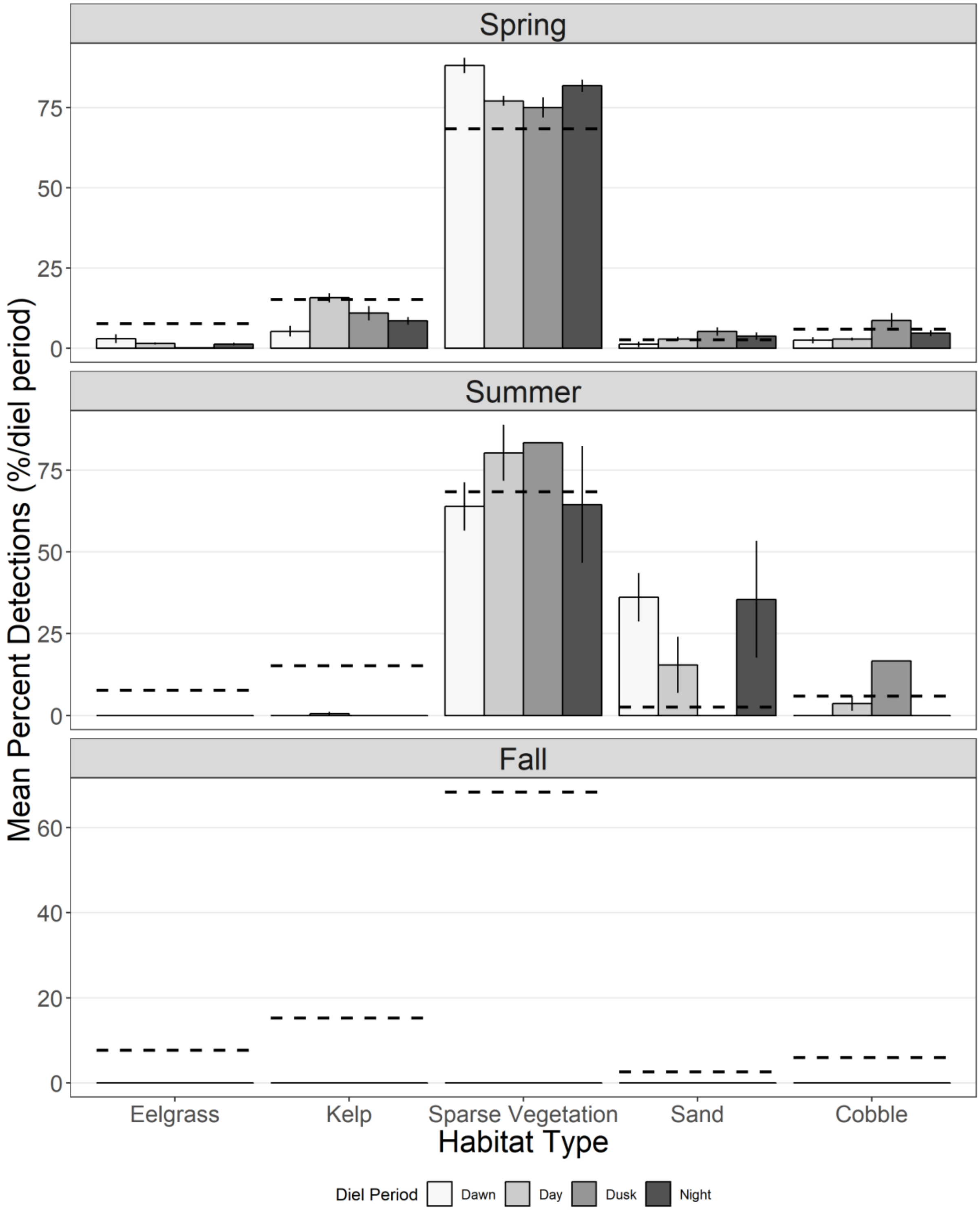

Figure 3.8: Habitat use by Atlantic cod (*Gadus morhua*) as the mean percent (± standard error) of positions occurring within a habitat per diel period. Dashed lines indicate the proportion of each habitat at the study site. Because of infrequent, poor quality detections of Atlantic cod during fall, I removed them from the analysis.

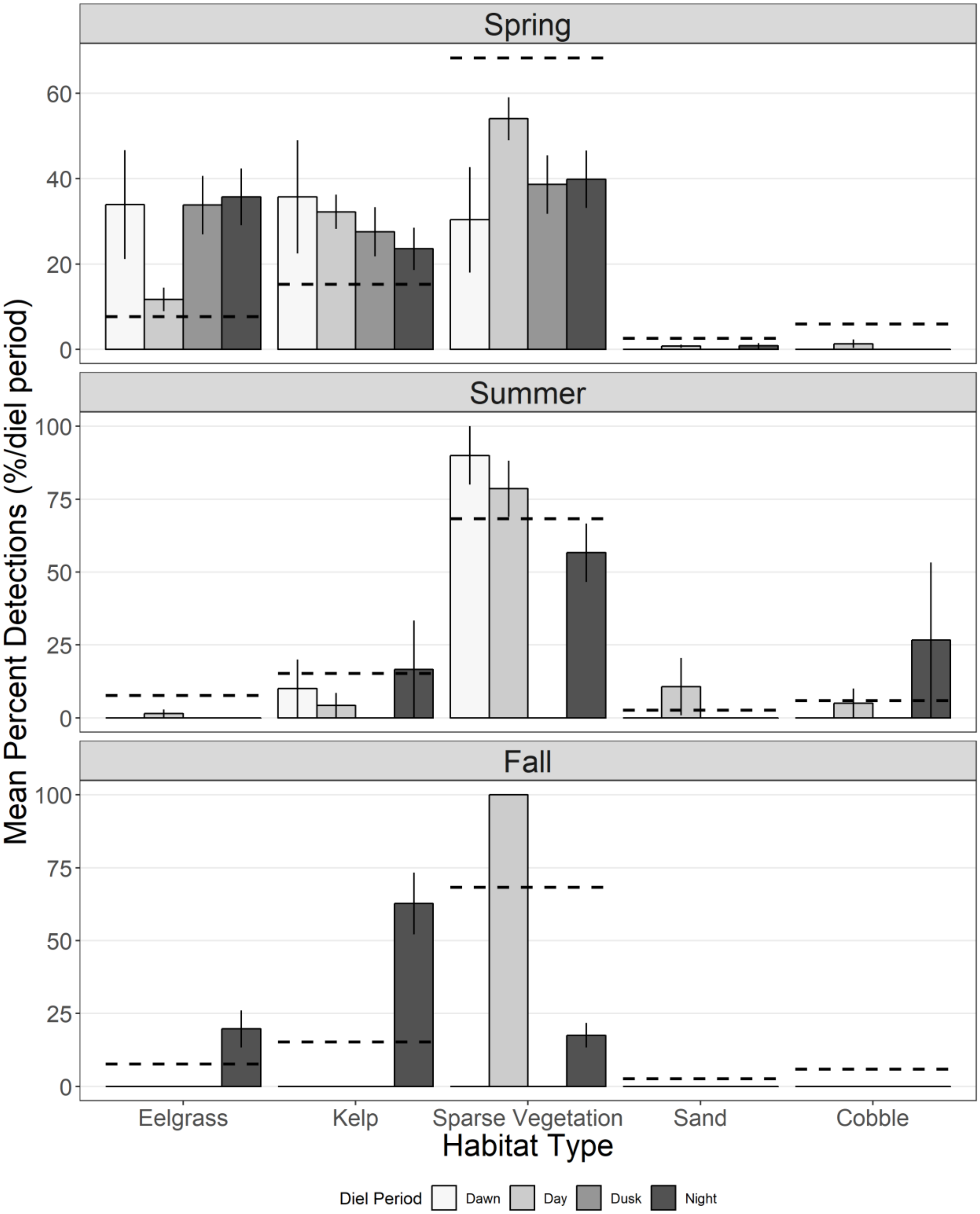

Figure 3.9: Habitat use by Greenland cod (*Gadus macrocephalus ogac*) as the mean percent (± standard error) of positions occurring within a habitat per diel period. Dashed lines indicate the proportion of each habitat at the study site. Greenland cod were detected infrequently during the fall.

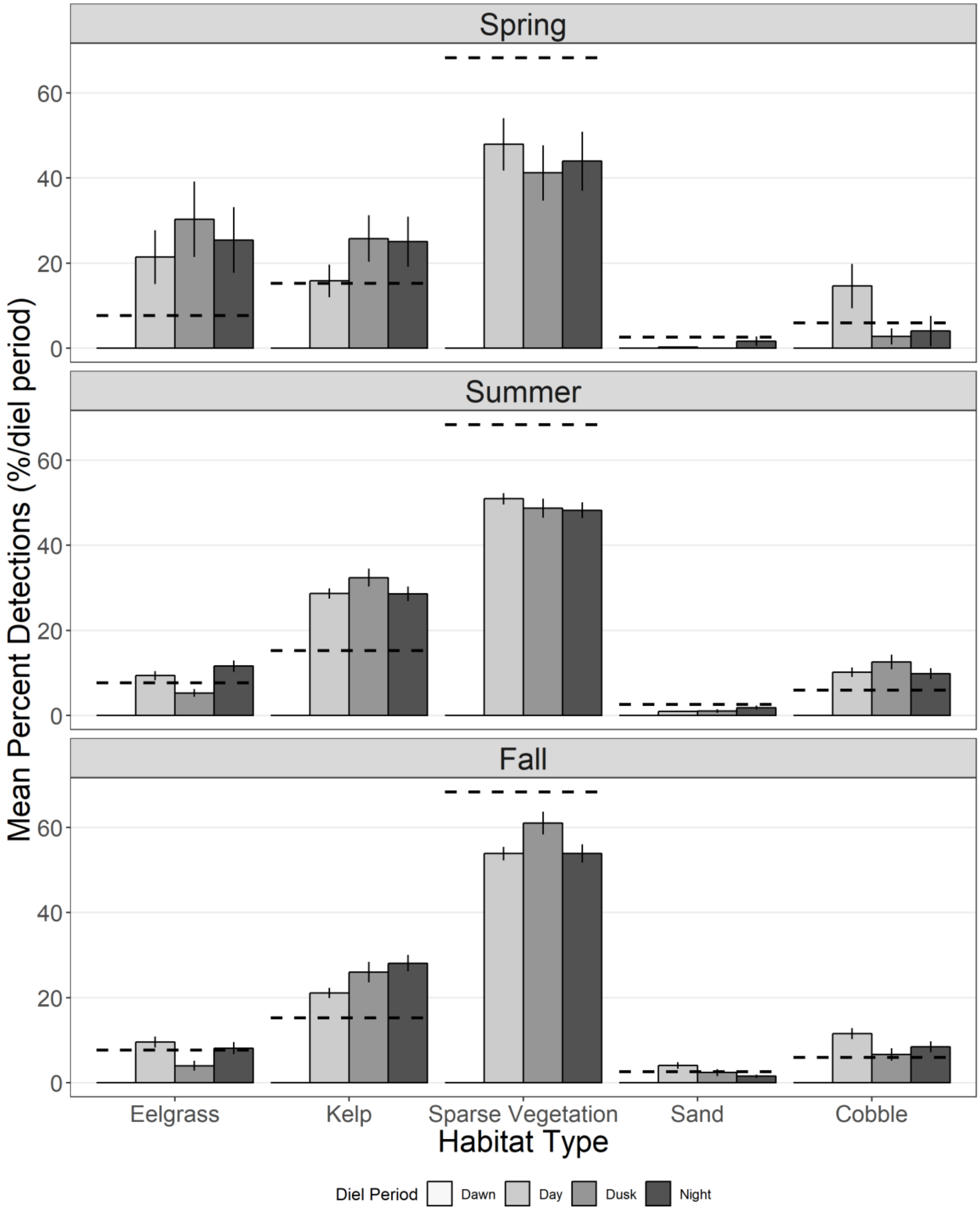

Figure 3.10: Habitat use by cunner (*Tautogolabrus adspersus*) as the mean percent (± standard error) of positions occurring within a habitat per diel period. Dashed lines indicate the proportion of each habitat at the study site. I never detected cunner during dawn, and all night detections occurred within 2 hours of the onset of that period. Detections resumed within 2 hours of sunrise.

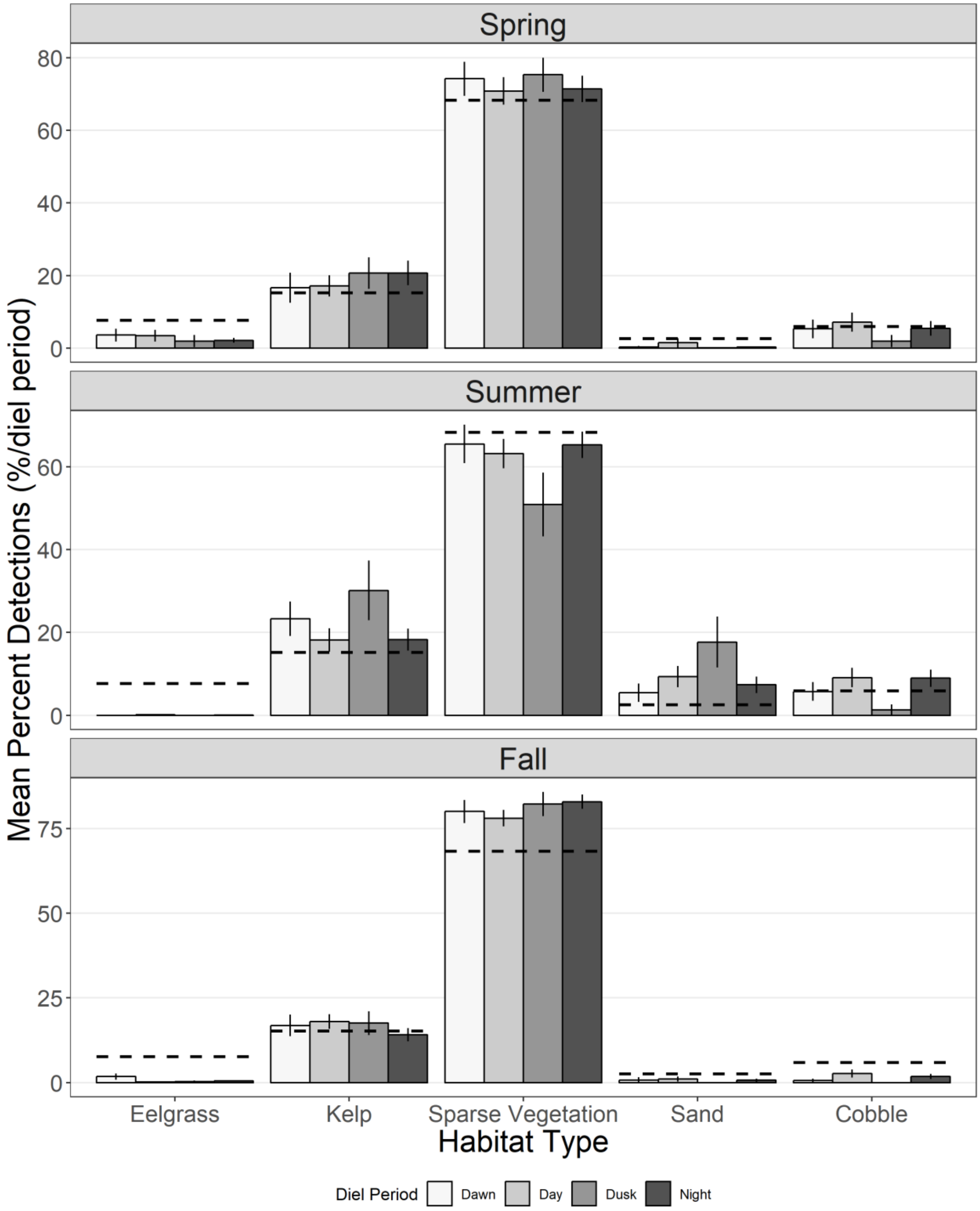

Figure 3.11: Habitat use by shorthorn sculpin cod (*Myoxocephalus scorpius*) as the mean percent (± standard error) of positions occurring within a habitat per diel period. Dashed lines indicate the proportion of each habitat at the study site.

Chapter 4 : Summary

I conducted two field studies to examine habitat segregation of age-0 cod from their predators. By using complimentary methods, I was able to assess habitat use for both small bodied age-0 cod, and larger, more mobile piscivores. In Chapter 2, I generated a habitat map and examined habitat associations of age-0 cod (*Gadus morhua* and *G. macrocephalus ogac*) in Newman Sound, Newfoundland using underwater video. The study site included eelgrass (*Zostera marina*), kelp (*Saccharina latissima*), sparse vegetation, and bare substrate habitats. Eelgrass occurred near shore in depths less than 7 m, whereas kelp occurred adjacent to eelgrass in water depths up to 9 m. Sparse vegetation and bare substrate neighboured eelgrass and kelp patches. Age-0 cod strongly associated with uniform eelgrass and sand habitat, with all individuals observed within 1 m of eelgrass. Larger piscivorous fishes (older conspecifics, shorthorn sculpin (*Myoxocephalus scorpius*), cunner (*Tautogolabrus adspersus*), and hake (*Urophycis tenuis*)) were predominantly observed outside of eelgrass beds, with cunner significantly associating with both uniform and mixed kelp and sand habitat. These findings suggest that age-0 spatially segregate from their predators.

In Chapter 3, I tested the patterns documented with video analysis by using acoustic telemetry to track the movements of 37 individual from four piscivorous fish species: age-1 and -2 Atlantic and Greenland cod, shorthorn sculpin, and cunner. From these data, I used frequency of detections over time as a proxy for habitat selection, and examined the selection of each species among season and diel period. Habitat use differed significantly by predator species. Greenland cod and cunner selected eelgrass in the spring, then transitioned to deeper water habitats (kelp, sparse vegetation, and bare substrates) during summer and fall. Sculpin selected sparse vegetation in spring and fall, and kelp and bare sand in the summer. Atlantic cod were not detected in the fall, but detections in spring and summer indicated that they selected sparse vegetation and bare sand during those seasons. Diel period significantly influenced habitat selection for cunner as a result of their quiescent behaviour during night and dawn. Overall, piscivores primarily occupied deeper water habitats outside eelgrass beds.

When considered together, these data suggest that age-0 cod are spatially and temporally segregated from their predators. When choosing habitat, potential 'prey' must consider trade-offs between energy resources and predation risk to maximize growth while minimizing mortality (Werner and Gilliam 1984), because the most productive habitats may also be the riskiest (Lima and Dill 1990; Hugie and Dill 1994). Individuals may be able to assess their predation risk in terms of encounter rates, escape rates, and time of vulnerability, and alter their behaviour in response to the perceived risk (Lima and Dill 1990). These decisions reflect resource availability, condition (starvation level), and risk level (Lima and Dill 1990; Hugie and Dill 1994), and risk levels may change based on foraging strategies of both predator and prey (Werner and Gilliam 1984). Fish alter their behaviour in response to predator species (Savino and Stein 1989; Laurel and Brown 2006) or predator behaviour (Gotceitas *et al.* 1995). Age-0 cod lower themselves into eelgrass in response to a cruising predator, such as older conspecifics, but remain above eelgrass in response to an ambush predator such as sculpin (Laurel and Brown 2006).

Building upon John Maynard Smith's (1982) 'Evolutionary Game Theory' (an equilibrium in behavioural strategies that can persist in a population), Hugie and Dill (1994) consider the "Game" in terms of habitat selection between predators and prey, proposing that individuals base habitat selection exclusively on habitat riskiness. In their model, prey select productive habitat in the absence of predators, but select less productive habitat that offers more protection in the presence of a predator than one that offers no such advantages (Hugie and Dill

1994). Interference effects, such as cover or light (Hugie and Dill 1994), modify this habitat selection strategy. The structure of vegetation interferes with predator mobility (Gotceitas and Colgan 1989) and reduces visibility of prey (Lindholm *et al.* 1999), and eelgrass could provide a suitable refuge for age-0 cod depending on plant stem densities within eelgrass patches (Gotceitas *et al.* 1997). Hugie and Dill's (1994) model also suggests that increased numbers of predators would be a characteristic of 'risky' habitats. Predation rates on age-0 cod outside of eelgrass beds exceed that inside eelgrass beds (Linehan *et al.* 2001) and, in both of my field experiments, piscivores associated with habitats outside of eelgrass, suggesting that these non-eelgrass habitats carry a higher 'riskiness'. By restricting their distributions to eelgrass habitats, age-0 cod spatially segregate themselves from their predators.

This "Game" extends beyond juvenile fish and their predators, and also applies to piscivorous fishes and their predators. Predators of piscivorous fishes, such as avian or terrestrial predators, may restrict piscivorous fishes to deeper water (Power *et al.* 1989; Harvey and Stewart 1991; Crowder *et al.* 1997; Cote *et al.* 2008), further reinforcing the habitat segregation of predators and prey. Eelgrass therefore may not offer suitable habitat for piscivorous fishes, given that, in addition to inhibiting mobility (Gotceitas and Colgan 1989), eelgrass patches occur primarily in shallow coastal water. Habitat segregation also mediates cannibalism in Atlantic cod, with age-0s primarily occupying eelgrass and older juveniles occurring on coarse substrates with macroalgae (Gotceitas *et al.* 1997). Although age-0 cod avoid substrates used by older conspecifics, age-1+ do not alter their substrate use in response to age-0s (Fraser *et al.* 1996).

Because I conducted the video transects during daylight hours, the habitat associations I report in Chapter 2 may not apply to all diel periods. Age-0 Atlantic cod alter their behaviour and habitat use among diel periods, often aggregating during the day (Laurel *et al.* 2004). In contrast, they aggregate less and occur higher in the water column at night – above their demersal predators (Anderson *et al.* 2007). They may also become less active and cease to feed at night in order to avoid older conspecifics (Grant and Brown 1998b). Previous studies showed that many larger piscivorous fish species move into shallow water at night (Keats 1990; Linehan *et al.* 2001; Shoji *et al.* 2017; Tanaka *et al.* 2018) presumably to feed (Linehan *et al.* 2001). As such, spatial segregation of age-0 cod from their predators may cease at this time.

I collected my video transects during the summer, and the habitat map constructed in Chapter 2 represents eelgrass at peak biomass (Lalumière *et al.* 1994). During spring, ice scour reduces post-winter eelgrass biomass (Robertson and Mann 1984), compounded by lack of early-season growth (Lalumière *et al.* 1994). Therefore, my analysis may over-represent eelgrass use by cunner and Greenland cod in spring, when eelgrass has not yet resumed growing post-winter. Regardless of whether eelgrass is present or not at this time, age-0 cod are not. Age-0 cod do not begin to settle into eelgrass beds until July (Ings *et al.* 1997, 2008; Grant and Brown 1998a; Laurel *et al.* 2003), by which time piscivores have generally moved into deeper water habitats. Such results indicate temporal segregation between predators and prey, further protecting juvenile cod from their predators. In Chapter 3, acoustically tagged piscivorous fishes did not return to the study site until late fall. At this time, age-0 Greenland cod and early pulses of Atlantic cod would have grown while living within the nursery eelgrass habitat, possibly to a sufficient size to minimize predation risk. Use of eelgrass habitat enhances growth of juvenile cod (Tupper and Boutilier 1995; Renkawitz *et al.* 2011), allowing juvenile cod the opportunity to attain size refugia from gape-limited predators (Sogard 1997).

In this thesis, I demonstrated spatial and temporal segregation of age-0 cod from their predators, which may reduce predation and cannibalism. In Chapter 2, I demonstrated that age-0 cod strongly associate with eelgrass habitat, where I rarely observed their predators, whereas in Chapter 3 tagged piscivores primarily occupied deeper water habitats (kelp, sparse vegetation, bare substrate) in summer and fall. This pattern suggests that habitat adjacent to eelgrass carries greater risk of predation mortality. Age-0 cod temporally segregate from their predators before they arrive in nursery eelgrass beds in spring. My study did not examine whether juvenile cod respond to the predation pressure of a single piscivorous fish species or the cumulative sum of predation pressures. Predation risk in the presence of multiple predators may not be additive, and indirect effects (interference, altered behaviour) may increase prey survival in the presence of multiple predator species (Crowder *et al.* 1997; Strand *et al.* 2020). However, avoidance of a single predator may leave prey vulnerable to another predator, resulting in decreased survival (Strand *et al*. 2020). Predation pressure on age-0 cod by piscivores always occurs, albeit caused by different species at different times. In my study, all tagged piscivorous fish species were present during the day, exerting some predation risk on age-0 cod. However, no predation pressure from cunner occurs during night and twilight periods because, in contrast to other piscivorous fish species in Newman Sound, cunner are quiescent at night (Pottle and Green 1979a), either camouflaging against substrate or aggregating in rock crevices (Dew 1976). Research examining this relationship would help in understanding the overall impact of predation on juvenile cod behaviour and habitat selection.

My thesis research highlights the importance of eelgrass for age-0 cod. It also emphasizes that threats to eelgrass also threaten juvenile cod. Habitat destruction through nearshore development (Short *et al.* 2011) and invasive species (e.g. green crab *Carcinus maenas*: Matheson *et al.* 2016) have contributed to global declines in eelgrass habitats. Habitat declines put juvenile cod at risk of increased predation mortality at a sensitive life-stage, with anticipated impacts on populations.

References

Anderson, J. L., Laurel, B. J., and Brown, J. A. (2007). Diel changes in behaviour and habitat use by age-0 Atlantic cod (*Gadus morhua* L.) in the laboratory and field. Journal of Experimental Marine Biology and Ecology 351, 267–275. doi:10.1016/j.jembe.2007.07.001

Cote, D., Gregory, R. S., and Stewart, H. M. J. (2008). Size-selective predation by river otter (*Lontra canadensis*) improves refuge properties of shallow coastal marine nursery habitats. Canadian Journal of Zoology 86, 1324–1328. doi:10.1139/Z08-120

Crowder, L. B., Squires, D. D., and Rice, J. A. (1997). Nonadditive effects of terrestrial and aquatic predators on juvenile estuarine fish. Ecology 78, 1796–1804.

Dew, C. B. (1976). A contribution to the life history of the cunner *Tautogolabrus adspersus*, in Fishers Island, Connecticut. Chesapeake Science 17, 101–113.

Fraser, S., Gotceitas, V., and Brown, J. A. (1996). Interactions between age-classes of Atlantic cod and their distribution among bottom substrates. Canadian Journal of Fisheries and Aquatic Sciences 53, 305–314. doi:10.1139/f95-183

Gotceitas, V., and Colgan, P. (1989). Predator foraging success and habitat complexity: quantitative test of the threshold hypothesis. Oecologia 80, 158–166. doi:10.1007/BF00380145

Gotceitas, V., Fraser, S., and Brown, J. A. (1995). Habitat use by juvenile Atlantic cod (*Gadus morhua*) in the presence of an actively foraging and non-foraging predator. Marine Biology 123, 421–430. doi:10.1007/BF00349220

Gotceitas, V., Fraser, S., and Brown, J. A. (1997). Use of eelgrass beds (*Zostera marina*) by juvenile Atlantic cod (*Gadus morhua*). Canadian Journal of Fisheries and Aquatic Sciences 54, 1306–1319. doi:10.1139/f97-033

Grant, S. M., and Brown, J. a. (1998a). Diel foraging cycles and interactions among juvenile Atlantic cod (*Gadus morhua*) at a nearshore site in Newfoundland. Canadian Journal of Fisheries and Aquatic Sciences 55, 1307–1316. doi:10.1139/cjfas-55-6-1307

Grant, S. M., and Brown, J. A. (1998b). Nearshore settlement and localized populations of age 0 Atlantic cod (*Gadus morhua*) in shallow coastal waters of Newfoundland. Canadian Journal of Fisheries and Aquatic Sciences 55, 1317–1327.

Harvey, B. C., and Stewart, A. J. (1991). Fish size and habitat depth relationships in headwater streams. Oecologia 87, 336–342.

Hugie, D. M., and Dill, L. M. (1994). Fish and game: a game theoretic approach to habitat selection by predators and prey. Journal of Fish Biology 45, 151–169.

Ings, D. W., Gregory, R. S., and Schneider, D. C. (2008). Episodic downwelling predicts recruitment of Atlantic cod, Greenland cod and white hake to Newfoundland coastal waters. Journal of Marine Research 66, 529–561.

Ings, D. W., Schneider, D. C., and Methven, D. a. (1997). Detection of a recruitment signal in juvenile Atlantic cod (*Gadus morhua*) in coastal nursery areas. Canadian Journal of Fisheries and Aquatic Sciences 54, 25–29. doi:10.1139/cjfas-54-S1-25

Keats, D. W. (1990). A nocturnal inshore movement of juvenile cod *Gadus morhua* L. in eastern Newfoundland. Journal of Experimental Marine Biology and Ecology 139, 167–173. doi:10.1016/0022-0981(90)90144-2

Lalumière, R., Messier, D., Fournier, J. J., and Peter McRoy, C. (1994). Eelgrass meadows in a low arctic environment, the northeast coast of James Bay, Québec. Aquatic Botany 47, 303–315. doi:10.1016/0304-3770(94)90060-4

Laurel, B. J., and Brown, J. A. F. (2006). Influence of cruising and ambush predators on 3-dimensional habitat use in age 0 juvenile Atlantic cod *Gadus morhua*. 329, 34–46. doi:10.1016/j.jembe.2005.08.003

Laurel, B. J., Gregory, R. S., and Brown, J. A. (2003). Settlement and distribution of cod, *Gadus morhua* and *G. ogac*, following a large-scale habitat manipulation. Marine Ecology Progress Series 262, 241–252. doi:10.3354/meps262241

Laurel, B. J., Gregory, R. S., Brown, J. A., Hancock, J. K., and Schneider, D. C. (2004). Behavioural consequences of density-dependent habitat use in juvenile cod *Gadus morhua* and *G. ogac*: the role of movement and aggregation. Marine Ecology Progress Series 272, 257–270. doi:10.3354/meps272257

Lima, S. L., and Dill, L. M. (1990). Behavioral decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology 68, 619–640. doi:10.1139/z90-092

Lindholm, J. B., Auster, P. J., and Kaufman, L. S. (1999). Habitat-mediated survivorship of juvenile (0-year) Atlantic cod *Gadus morhua*. Marine Ecology Progress Series 180, 247–255. doi:10.3354/meps180247

Linehan, J. E., Gregory, R. S., and Schneider, D. C. (2001). Predation risk of age-0 cod (*Gadus*) relative to depth and substrate in coastal waters. Journal of Experimental Marine Biology and Ecology 263, 25–44. doi:10.1016/S0022-0981(01)00287-8

Matheson, K., McKenzie, C. H., Gregory, R. S., Robichaud, D. A., Bradbury, I. R., Snelgrove, P. V. R., and Rose, G. A. (2016). Linking eelgrass decline and impacts on associated fish communities to European green crab *Carcinus maenas* invasion. Marine Ecology Progress Series 548, 31–45. doi:10.3354/meps11674

Maynard Smith, J. (1982). 'Evolution and the Theory of Games'. (Cambridge University Press: Cambridge.)

Pottle, A., and Green, M. (1979). Territorial behaviour of the north temperate labrid, *Tautogolabrus adspersus*. Canadian Journal of Zoology 57, 2337–2347.

Power, M. E., Dudley, T. L., and Cooper, S. D. (1989). Grazing catfish, fishing birds, and attached algae in a Panamanian stream. Environmental Biology of Fishes 26, 285–294. doi:10.1007/BF00002465

Renkawitz, M. D., Gregory, R. S., and Schneider, D. C. (2011). Habitat dependant growth of three species of bottom settling fish in a coastal fjord. Journal of Experimental Marine Biology and Ecology 409, 79–88. doi:10.1016/j.jembe.2011.08.004

Robertson, A. I., and Mann, K. H. (1984). Disturbance by ice and life-history adaptations of the seagrass *Zostera marina*. Marine Biology 80, 131–141. doi:10.1007/BF02180180

Savino, J. F., and Stein, R. A. (1989). Behavioural interactions between fish predators and their prey: effects of plant density. Animal Behaviour 37, 311–321. doi:10.1016/0003-3472(89)90120-6

Shoji, J., Mitamura, H., Ichikawa, K., Kinoshita, H., and Arai, N. (2017). Increase in predation risk and trophic level induced by nocturnal visits of piscivorous fishes in a temperate seagrass bed. Scientific Reports 7, 1–10. doi:10.1038/s41598-017-04217-3

Short, F. T., Polidoro, B., Livingstone, S. R., Carpenter, K. E., Bandeira, S., Bujang, J. S., Calumpong, H. P., Carruthers, T. J. B., Coles, R. G., Dennison, W. C., Erftemeijer, P. L. A., Fortes, M. D., Freeman, A. S., Jagtap, T. G., Kamal, A. H. M., Kendrick, G. A., Kenworthy, W. J., La Nafie, Y. A., Nasution, I. M., Orth, R. J., Prathep, A., Sanciangco, J. C., van Tussenbroek, B., Vergara, S. G., Waycott, M., and Zieman, J. C. (2011). Extinction risk assessment of the world’s seagrass species. Biological Conservation 144, 1961–1971. doi:10.1016/j.biocon.2011.04.010

Sogard, S. M. (1997). Size-selective mortality in the juvenile stage of teleost fishes: a review. Bulletin of Marine Science 60, 1129–1157.

Strand, H. K., Pedersen, T., Christie, H., and Moy, F. (2020). Synergism between cruising cod and ambush sculpin predators on 0-group gadoids in modified by laylight cycle and presence of aggressive wolffish. Journal of Experimental Marine Biology and Ecology 526, 151356. https://doi.org/10.1016/j.jembe.2020.151356

Tanaka, H., Chiba, S., Yusa, T., and Shoji, J. (2018). Day–night change in fish community structure in a seagrass bed in subarctic waters. Fisheries Science 84, 275–281. doi:10.1007/s12562-017-1172-3

Tupper, M., and Boutilier, R. G. (1995). Effects of habitat on settlement, growth, and postsettlement survival of Atlantic cod (*Gadus morhua*). Canadian Journal of Fisheries and Aquatic Sciences 52, 1834–1841. doi:10.1139/f95-176

Werner, E. E., and Gilliam, J. F. (1984). The ontogenetic niche and species interactions in size-structures populations. Annual Review of Ecology, Evolution and Systems 15, 393–425.

Appendix 1 – Detections of tagged piscivorous fishes around Newman Sound

To determine broader movement pattern of tagged piscivorous fishes around Newman Sound, 14 acoustic receivers were deployed around Newman Sound (Figure 3.6) in addition to the nine acoustic receivers deployed in Newbridge Cove. These receivers were placed within 500 m of the shoreline in both the inner and outer basins of Newman Sound. Data from these receivers do not give exact positions, but a general location (+/- 500 m).

Data from these receivers indicated that predators were not localized to Newbridge Cove (Table 3.2). I detected the majority of individuals in the spring, with reduced numbers in summer and fall. Both Atlantic and Greenland cod ventured beyond my immediate study site, but generally stayed along the northern shore of Newman Sound (Figures A1.1, A1.2). Numbers of detections in the spring were greater than in the summer and fall, indicating they may have sought out deeper water beyond the range of the acoustic receivers.

Cunner and sculpin were both more localized than cod, remaining at the sites nearest Newbridge Cove (e.g., Buckley’s Cove). Few sculpin ventured outside my study site; individuals remained in the inner Sound, and did not venture out past the narrows (Figure A1.4). Movement patterns did not differ by season. Cunner were more localized than sculpin, traveling only as far as the next neighbouring site (Buckley’s Cove), except one individual that traveled easterly along the northern coast (~ 6 km; Figure A1.3). More individuals were detected at Buckley’s Cove in summer and fall than in spring.

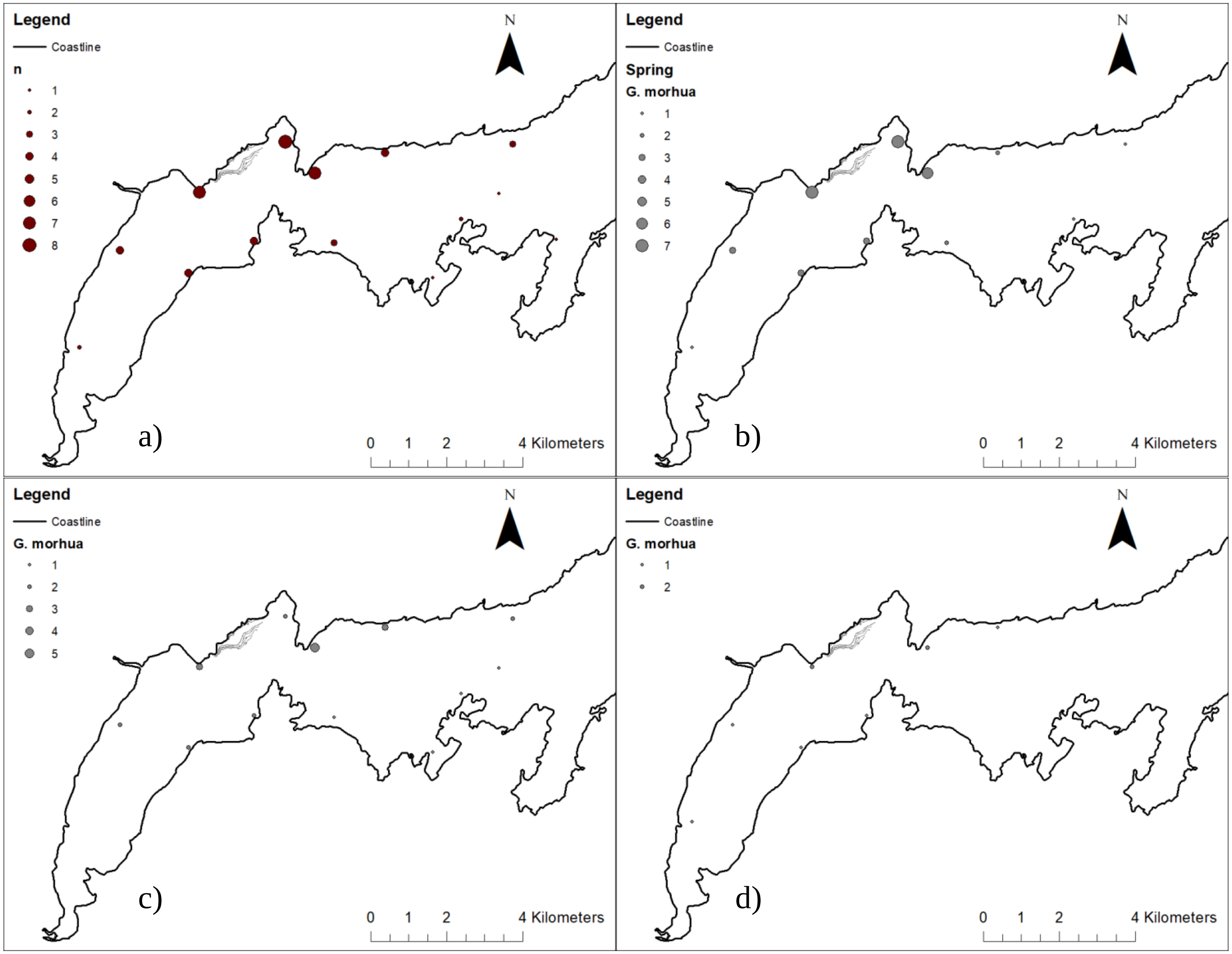

Figure A1.1: Detections of Atlantic cod (*Gadus morhua)* around Newman Sound for a) the full season, b) spring, c) summer, and d) fall.

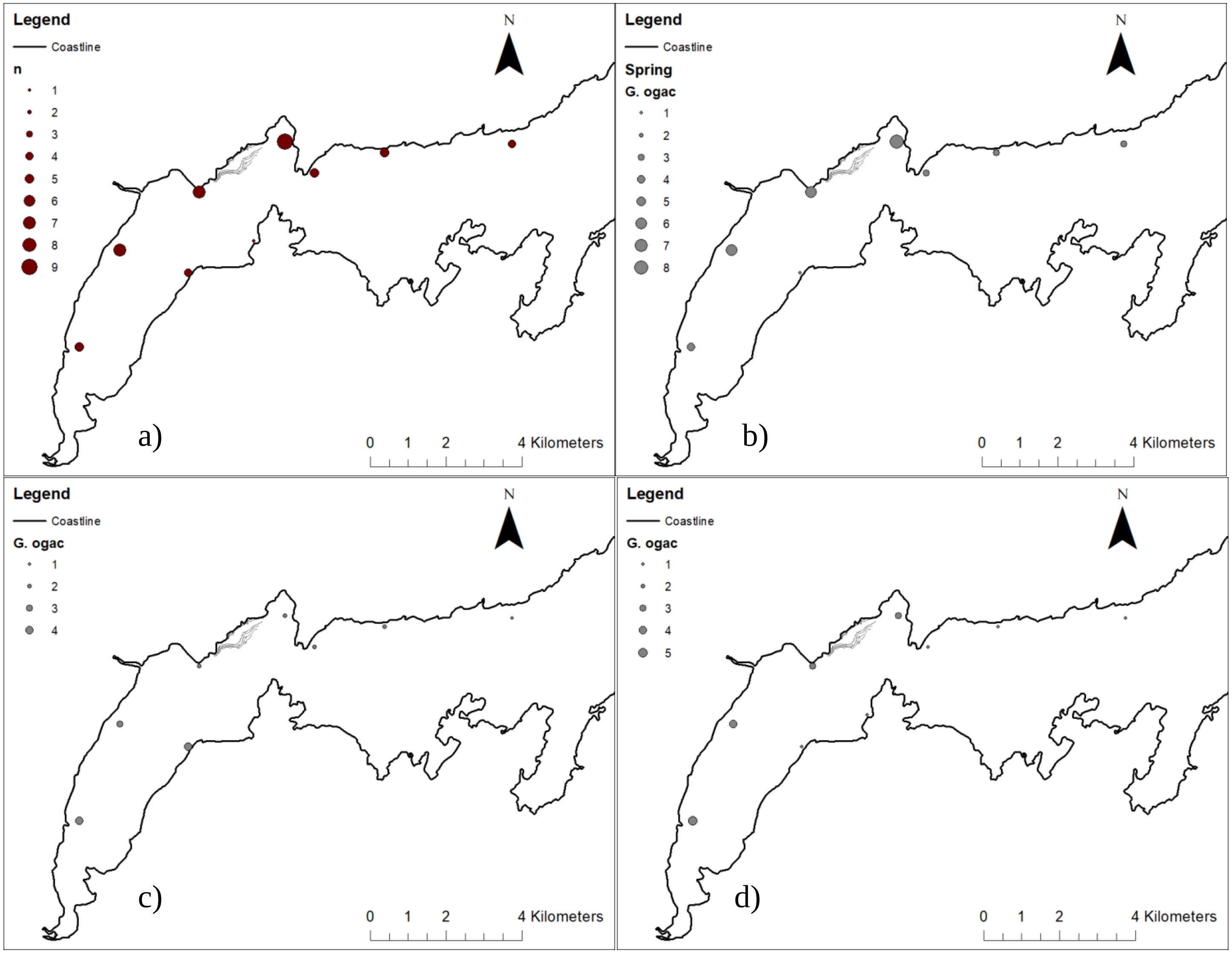

Figure A1.2: Detections of Greenland cod (*Gadus macrocephalus ogac*) around Newman Sound for a) the full season, b) spring, c) summer, and d) fall.

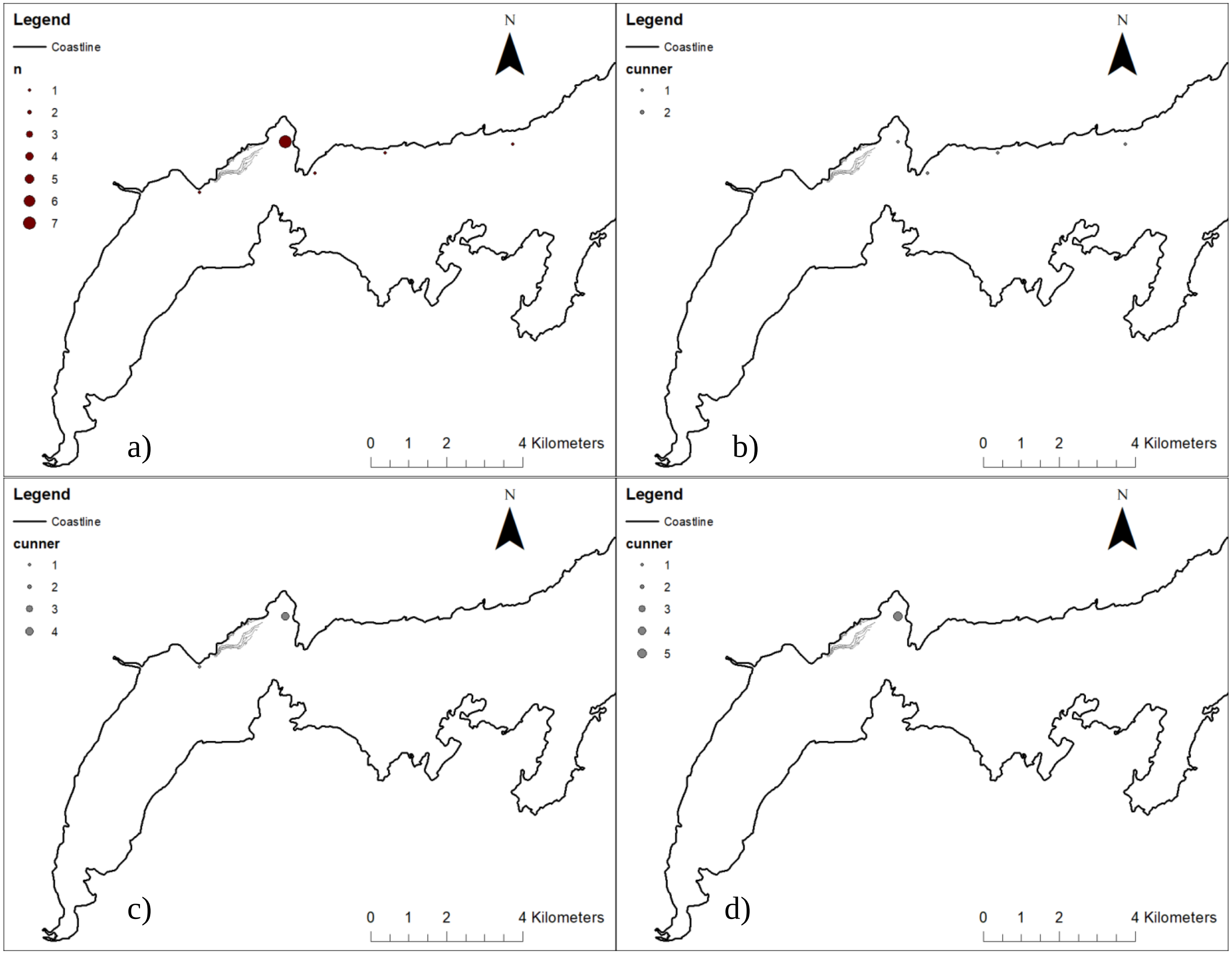

Figure A1.3: Detections of cunner (*Tautogolabrus adspersus*) around Newman Sound for a) the full season, b) spring, c) summer, and d) fall.

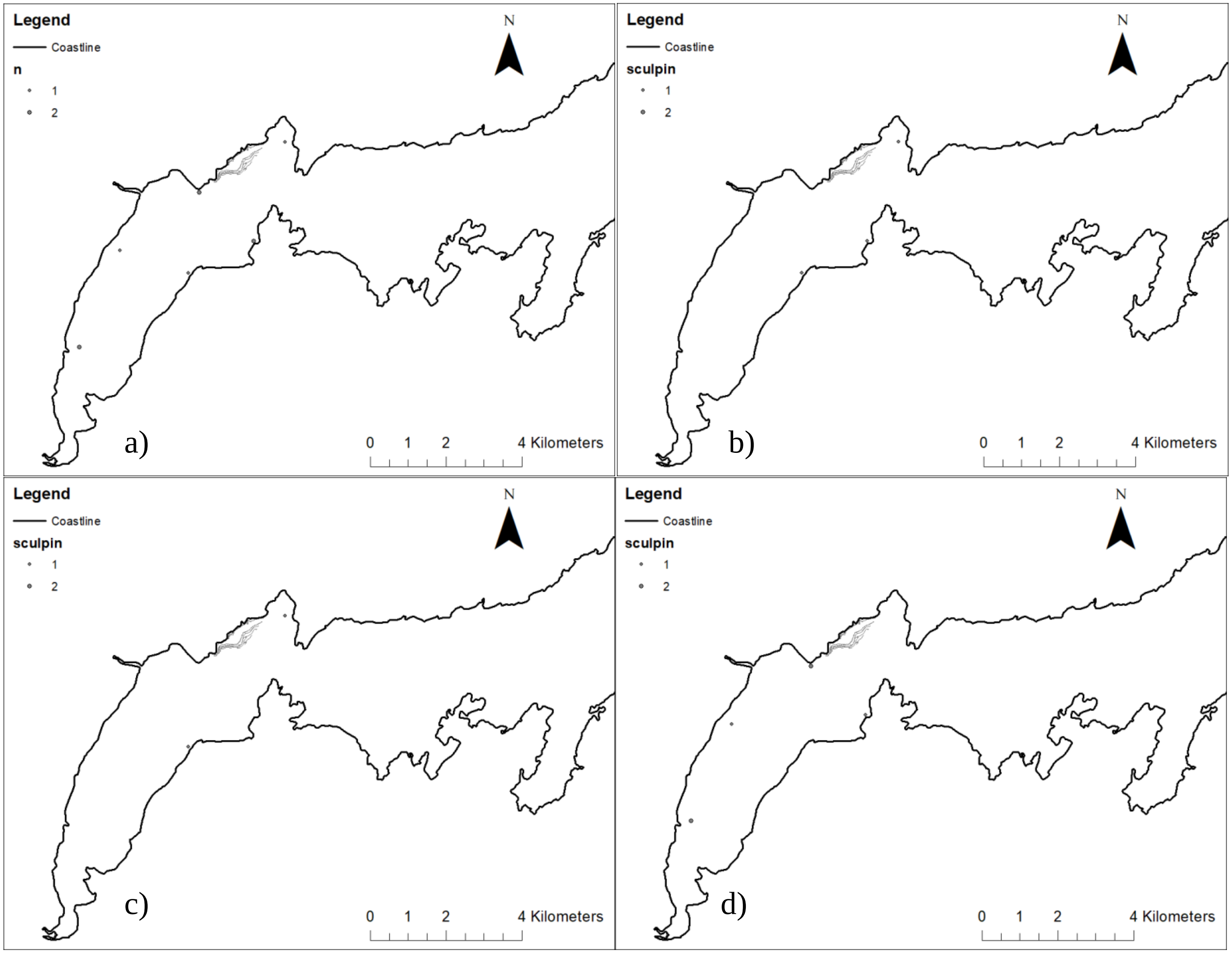

Figure A1.4: Detections of shorthorn sculpin (*Myoxocephalus scorpius*) around Newman Sound for a) the full season, b) spring, c) summer, and d) fall.