First characterization of a nursery ground for the commercial sea cucumber *Cucumaria frondosa*

Jean-François Hamel [a], Rachel Morrison [b], Sara Jobson [b], Annie Mercier [b,*]

[a] *Society for the Exploration and Valuing of the Environment (SEVE), St. Philips, A1M 2B7, Newfoundland, Canada*
[b] *Department of Ocean Sciences, Memorial University, St. John's, Newfoundland, A1C 5S7, Canada*

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ABSTRACT

This study characterised the nursery ground of the cold-water sea cucumber *Cucumaria frondosa* for the first time. New recruits and early juveniles 0.9–40 mm in length were discovered at depths of 1.8–2.5 m in Qikiqtait (traditional name of the Belcher Islands, Nunavut, Canada) at a site with salinities ≥27 psu. They were primarily attached to live individuals and empty shells of the blue mussel *Mytilus edulis* and to stones. Based on laboratory rearing and known spawning times, the smallest individuals (0.9–1.4 mm) found in October 2021 and June 2022 were estimated to be 3–4 and 11–12 months old, respectively (year class 0-I). Other juveniles found at the same time were mostly ≤4-year-old, likely representing subsequent anual recruitment pulses. Densities of juveniles measuring 0.9–40 mm varied between 4 and 104 ind. m^{-2}. Recruits <2 mm occurred in complex substrata, mostly mussel byssal threads, while larger juveniles, especially those >9 mm, were on exposed surfaces of shells and stones. No adults occupied the shallow nursery site. This study draws attention to ontogenetic migration allowing the occurrence of cryptic nursery sites that may occur in shallower environments than the typical adult habitats, of particular significance for the management of commercial species.

1. Introduction

Knowledge of reproductive cycles and recruitment processes is foundational to the management of commercial marine species (Fodrie and Levin, 2008; Gillanders, 2002), including sea cucumbers (Rogers et al., 2021). The parameters can help build an understanding of population turnover rates, as well as identify areas that should be designated for marine protection (Caley et al., 1996; Slater et al., 2010). Moreover, understanding juvenile ecology and habitat preferences may help scientists determine the ultimate carrying capacity of a given marine region (Rogers et al., 2021).

Most of the existing knowledge on the spatial distribution of Holothuroidea relates to adults, and information on small individuals is often gathered within broad assessments of density, abundance, distribution and/or reproductive cycle of a species (e.g. Chao et al., 1994; Herrero-Pérezrul et al., 1999; Mercier et al., 2000; Shiell and Uthicke, 2006; Sloan and Von Bodungen, 1980). Adult stages of sea cucumbers are benthic; some species live on hard substrata while others live either on the surface or buried inside soft sediment (Mercier et al., 2023). Comparatively less work has been undertaken to document and assess nursery grounds of marine species (Miller and Christodoulou, 2014;

Olds et al., 2014; Roberts, 2000) defined as a subset of all habitats where juveniles occur (Beck et al., 2001).

Information regarding juveniles of wild sea cucumbers is consequently sparse for most species, including those of commercial interest. Shiell (2004) developed a list of 22 species in which juveniles were documented. More recently, Wolfe et al. (2023) updated the list to more than 80 species and 178 records of juvenile sightings worldwide from a variety of habitats, mostly tropical, including seagrass beds and reef flats, coral rubbles, coral reefs, stones, algae, sand and mud. The few studies dedicated to juveniles generally found them in localized areas and in low numbers (Shiell, 2004; Wolfe et al., 2023) without strong support for the existence of a delimited nursery habitat. In one of the first exhaustive studies on juvenile sea cucumbers, Mercier et al. (2000) described settled pentactulae and early juveniles (<9 mm) of *H. scabra* occurring in large numbers on the surface of seagrass leaves in Solomon Islands, close to the habitat where adults are abundant on sandy-muddy substratum. The investigators noted that the size, location, and abundance of juveniles were correlated with habitat characteristics such as depth, granulometry and organic richness of the substratum, and with the nearby presence of seagrass beds. In another detailed study conducted in New Zealand, juveniles of *Australostichopus mollis* 30–60 mm

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long were present (0.1–0.18 ind. m^{-2}) in areas with adult densities between 0.72 and 1.14 m^2 (Slater and Jeffs, 2010). This habitat was characterised by elevated nitrogen content, high ratios of phaeopigment:chlorophyll-*a*, small grain size and the presence of large shell fragments (~10 cm), proposed to provide a unique settlement microhabitat for competent larvae (Slater and Jeffs, 2010). High densities of juveniles of *Apostichopus japonicus* (6.7 ind. m^{-2}) were also reported in the intertidal zone in Japan, in association with large amounts of the macroalgae *Sargassum* spp. and *Ulva* spp., moderate eutrophication and protection from environmental fluctuation (desiccation and wave energy) during low tide (Yamana et al., 2006). Factors such as water movement, food availability and seagrass density were observed to affect the distribution of juveniles of *H. tubulosa* (Bulteel et al., 1992). Juveniles were found in habitats devoid of adults in the species *Acaudina molpadioides* (at low tide on muddy flats), *Actinopyga echinites* (unspecified habitat) and *Stichopus hermanni* (in algal beds) (Shiell, 2005). Young and Chia (1982) found that *Psolus chitonoides* preferred to settle on the adults and suggested that gregarious settlement could play an important role in the recruitment process. More recently in Belize, Rogers et al. (2021) found the oocytes as well as the developing embryos, larvae and early juveniles of *H. floridana* on the body wall of the adults as well as in the surrounding seagrass bed, confirming its role as a nursery for the species.

Despite the growing number of field reports mentioning sightings of juveniles from various species of holothuroids (Wolfe et al., 2023), very few studies have effectively identified new recruits (just settled individuals) and identified settlement/nursery grounds. Admittedly, it is not an easy task to detect small-sized individuals, let alone collect large quantities of them from the same area, which is required to confirm the occurrence of a nursery. A large enough surface area and a minimum number of individuals (including new recruits and subsequent generations) is crucial to validate the proposition. It is also not necessarily true that all species of holothuroids rely on nursery areas different from adult habitats; some species may be settling opportunistically or randomly in the native habitat without any specific requirements. Nevertheless, a growing number of sea cucumbers have been shown to have specific settlement and recruitment requirements, associated with sites that differ from the adult habitat, based on the field sampling of late larval stages or newly settled individuals (Mercier et al., 1999; Rogers et al., 2021; Wolfe et al., 2023).

The dendrochirotid sea cucumber *Cucumaria frondosa* has a broad distribution in the North Atlantic and Arctic oceans; it is a suspension-feeding species exhibiting annual spawning and pelagic lecithotrophic development that is being commercially exploited in North America and Europe (see comprehensive review by Gianasi et al., 2021). Stock assessments in the eastern provinces of Canada and in north-eastern USA have described populations composed either of adults ($\geq$120–250 mm long) or sub-adults down to ~20–50 mm long (Gianasi et al., 2021; Hamel and Mercier, 1996a; Medeiros-Bergen and Miles, 1997). Smaller juveniles 15–30 mm long were documented to occur underneath shallow-water pebbles and cobbles (Hamel and Mercier, 1996a) and some as small as ~2 mm long were reported from coralline algae, mussel shells and kelp holdfasts (Medeiros-Bergen and Miles, 1997); however yearly recruits <1 mm have never been reported. Moreover, almost nothing is known of population dynamics of *C. frondosa* in the Arctic, except mentions of the presence of adults in numerous areas around the territory of Nunavut (Hamel and Mercier, 2023a), Iceland, Greenland and other Scandinavian locations (Gianasi et al., 2021). In the Arctic, *C. frondosa* is prey to walruses, seals and eider ducks, and part of the diet of certain Indigenous Inuit communities, making the species central both to local marine ecosystems and food security.

Based on field collections and video surveys gathered over three years (2019, 2021, 2022), the present study highlighted and assessed the abundance of various sizes (cohorts) of juveniles of the sea cucumber *C. frondosa* down to 0.9 mm long inside an insular channel at high latitudes. Findings inside the Hudson Bay, Canada, are consistent with the existence of annual recruitment pulses, and help define the first nursery ground for this important commercial species.

2. Methods

2.1. Study area

Qikiqtait (the traditional name of the Belcher Islands) occupies the southeast part of Hudson Bay around 56.2° N of latitude and 79.3° W of longitude in the Nunavut territory of northern Canada. The archipelago is composed of about 1500 islands spread over almost 3000 km^2 (Fig. 1a and b). The major long and narrow islands and peninsulas are separated by channels sprinkled with hundreds of smaller islands and outcrops. The study site (Kataapik), known by Inuit to host dense populations of sea cucumbers, is located north of the archipelago (Fig. 1b and c). It forms a channel ~100–200 m wide and 1400 m long characterised by strong tidal currents. We investigated the channel (see details below) from the shore to its maximum depth of ~5 m, as well the southern and northern coasts (56.6286; −79.2654), and both entrances (west and east; 56.6253; −79.2829; 56.6318; −79.2532, respectively) between 5 and 60 m depths (Fig. 1c). The study site is surrounded by barren land (tundra) with no freshwater input except from the melting of ice cover during the spring thaw (Fig. 2).

2.2. Long pole net collection

A traditional fishing tool was used to collect sea cucumbers in shallow water along the coast. Called a long pole net, it consists of a long wooden pole terminated by a round net with an opening of ~35 cm and mesh size of ~1–2 cm; it was manipulated by hand from small boats or through holes cut into the sea ice (Fig. 3a, b, c). Samples (n = 57) were collected between 1.8 and 2.5 m depths in the Kataapik channel (Figs. 1c and 2); including 7 samples in March 2019, 26 in October 2021 and 24 in June 2022. Each sample of the benthos (including mussels, stones, mud, various marine benthic species) was collected on an estimated surface of ~0.25 m^{-2} and a substratum depth of ~5–7 cm, enough to detach stones and mussels with everything attached to them. Bulk samples were sorted directly on the boat, shore, or ice shelf close to the hole, and the sea cucumbers were examined and counted (Fig. 4). Their locations, attached to live mussels or empty shells, entangled in the byssus threads, attached to stones of various sizes, were noted (Fig. 4). Photographs were taken with an underwater camera (Olympus Touch TG 6). Each sea cucumber was then isolated and preserved in ~80% ethanol before transport to the Department of Ocean Sciences (Memorial University, Newfoundland) for finer analysis. A two-way analysis of variance (ANOVA) on ranked data (due to non-normal distributions), followed by pairwise comparisons using Holm-Sidak's method, was used to test for differences in the mean size of juveniles occupying the various substratum types across the two years.

2.3. Mini-trawl collection

A 45-cm wide metal trawl (Fig. 3d), with a net mesh size of ~5–6 cm, was used to collect deeper samples in October 2021 (Fig. 1). It was deployed from a small boat (6 m long) for a duration of 20–30 min at depths ranging from 5 to 60 m (n = 14) outside the Kataapik channel, mostly at both entrances (Figs. 1c and 2). Rocks and other hard substrata were examined before being discarded, and all collected sea cucumbers were sorted and measured aboard the boat. Most individuals harvested with this method were found unattached so that their original substratum was unknown. Information on substratum preference therefore mainly relied on video surveys (see below). Subsequently, all individuals were dissected in a temporary wet laboratory located in the nearby hamlet of Sanikiluaq. Whole wet weight, length and diameter were recorded as well as the eviscerated body wall weight. The gonad was removed and preserved in 100% ethanol for transport to the laboratory
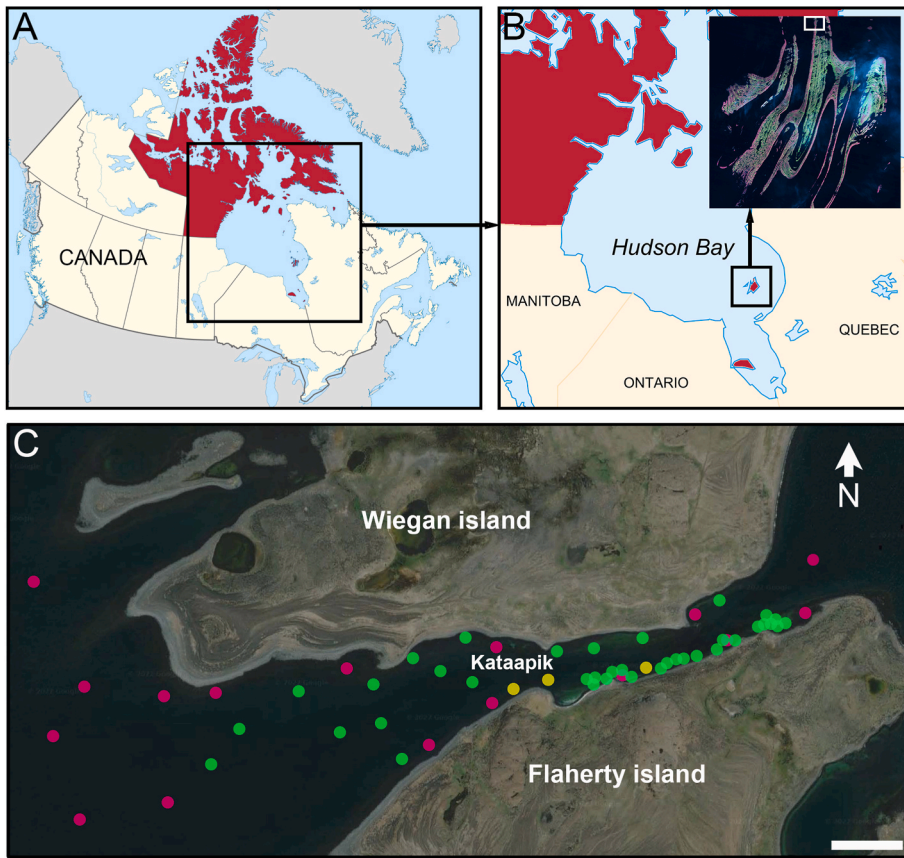
Fig. 1. (A) Map of Canada showing the territory of Nunavut (in red). (B) Enlargement of boxed area in A, illustrating the location of Qikiqtait inside Hudson Bay (box), with inset showing a satellite image of the archipelago and white box identifying the field site. (C) Field site (Kataapik) located between two islands in the northern part of the archipelago (enlargement of white box shown in B inset). Areas sampled in March 2019 (yellow), October 2021 (pink) and June 2022 (green) are shown. Scale bar in C represents ~100 m. Note that, at this scale, the same general area may encompass more than one sampling site. Basemaps in (A-B): MapGrid licensed under CC BY-SA 4.0. Basemap in (C): Map data ©2023 Imagery ©2023 CNES/Airbus, Maxar technologies. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)
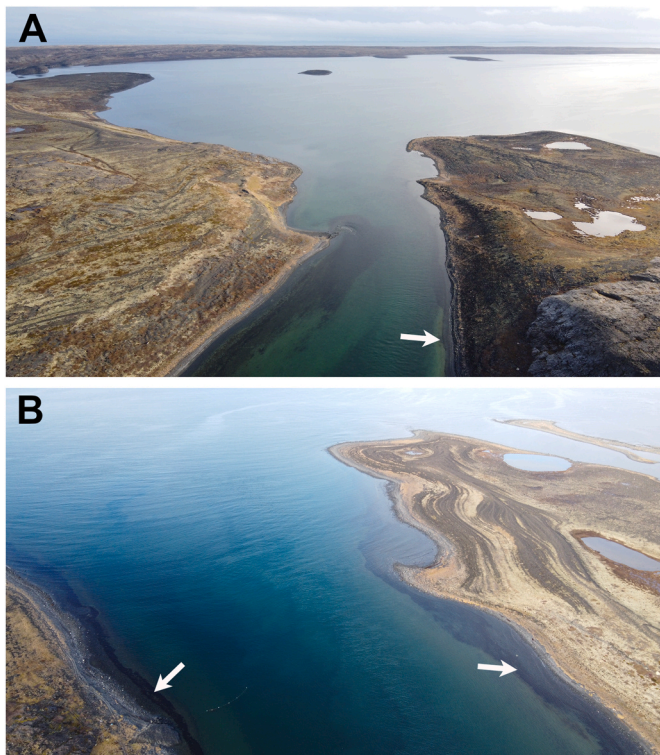

Fig. 2. Aerial drone view of the Kataapik channel in the northern section of Qikiqtait. (A) Eastern entrance. (B) Western entrance. The darker band along the coast (arrows), about 4–6 m wide and 1.8–2.5 m deep, constitutes the nursery habitat of *Cucumaria frondosa*.

(Department of Ocean Sciences, Memorial University). Once there, the wet weight was measured and the sex determined using a gonad smear examined under a Nikon Eclipse 80i light microscope.

2.4. Video surveys

Video surveys lasting 10–35 min were obtained from various sites (n = 17) using a remotely operated vehicle (ROV; Deep Trekker DGT3) deployed at depths between 3 and 60 m in June 2022. Surveys mainly covered the Kataapik channel and the water surrounding it at both ends (east and west, see above for details, Figs. 1c and 2). Records of seawater temperature were collected with the ROV sensors during the surveys. Salinity was opportunistically measured with a multiprobe (YSI PRO 1030). Video data were used to identify and characterize areas that harboured populations of *C. frondosa* and their geographic limits. Densities of *C. frondosa* were estimated per square meter from image analysis; size measurements were enabled by the underwater laser scaler. The substrata used by *C. frondosa* were also recorded, including mud, sand, pebbles, cobbles, boulders, live mussels (*Mytilus edulis*) and empty mussel shells.

2.5. Age class determination

The age class of individuals collected throughout the study was estimated by comparing their contracted length against published results of size studies in *C. frondosa* (Hamel and Mercier, 1996a; So et al., 2010). Cohorts of juveniles were determined based on growth rates measured in early juveniles under the coldest temperature (0–5 °C) tested by Hamel and Mercier (1996a), which are close to the present field conditions. Supplementary morphological characters including the presence of ossicles, the number of ambulacral podia and the tentacle ramifications were also used for aging, as per Gianasi et al. (2018).
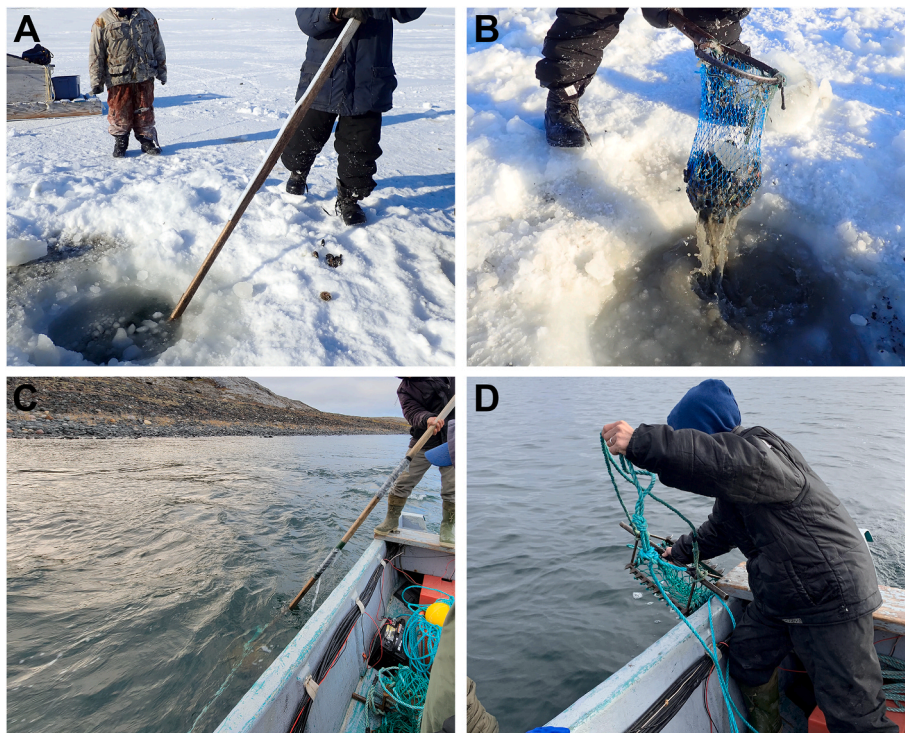
Fig. 3. Sample collection methods. (A-B) Long pole net used through an opening in the ice in winter. (C) Long pole net used from a small boat in the fall. (D) Small bottom trawl used from a boat in the spring or fall.
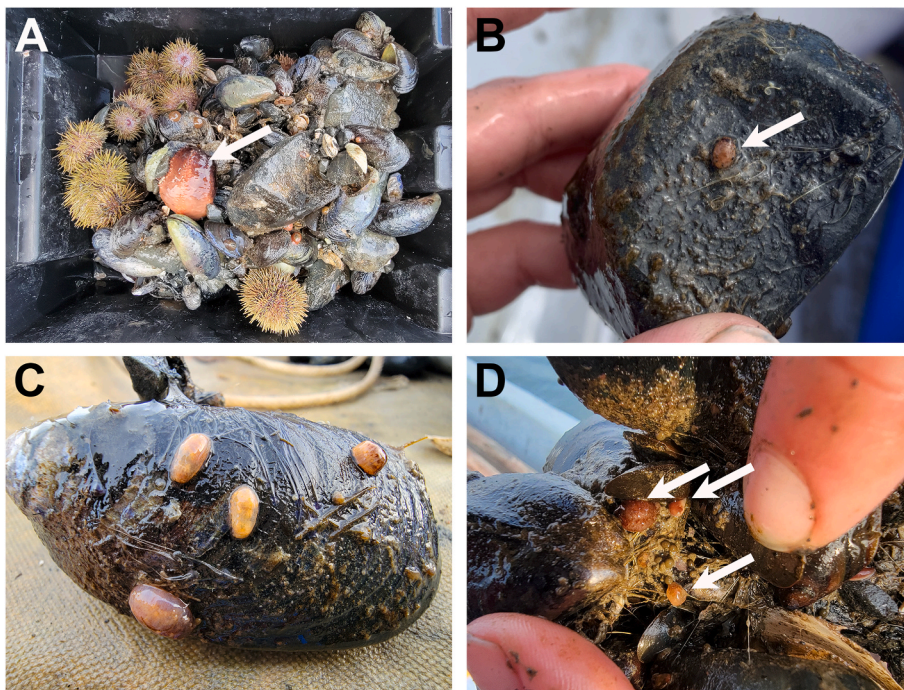

Fig. 4. Examples of samples obtained. (A) Bulk sample from ~2 m depth, showing a medium sized juvenile of *C. frondosa* (arrow), along with sea urchins *Strongylocentrotus droebachiensis*, blue mussel *Mytilus edulis* and stones of various sizes. (B) Early recruit of *C. frondosa* (~3 mm long; arrow) found on a stone. (C) Four juveniles ~10 mm long attached to the shell of a live mussel *Mytilus edulis*. (D) Smaller individuals (arrows) found entangled in mussel byssus. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

2.6. Size at sexual maturity and sex ratio

The size at sexual maturity was assessed using the individuals collected closest to the presumed spawning period in June 2022, when gonads would be most mature. A total of 37 individuals ≥80 mm in length were examined, among which 29 harboured a visible gonad. Each gonad was examined under a stereomicroscope (Leica M205) to establish the level of gonad maturity based on the gametogenic stages (tubule thickness, colour and diameter, as well as gamete sizes) described by Hamel and Mercier (1996b). The detection of mature gametes was used to identify the size at first sexual maturity. The state and ripeness of the whole gonad was also examined to determine whether individuals were just sexually mature or would likely be involved in the impending spawning. The ratio of males to females was established on all sexable individuals harvested in 2021 and 2022 during the determination of the size at sexual maturity.

2.7. Carrying capacity for juveniles around Qikiqtait

Based on the number of early juveniles per square meter in the study site between 1.8 and 2.5 m depths, the abundance of juveniles across the entire archipelago was estimated. Considering the nursery substrata determined for the new recruits and early juveniles and the reported length of coastline offering such substrata according to Inuit traditional knowledge (informal discussions) and satellite images (Google Map-Earth), the total abundance of juveniles between 0.9 and ~51 mm long was estimated for the whole archipelago.

3. Results and discussion

The present study revealed for the first time the occurrence of large quantities of early juvenile stages of the sea cucumber *Cucumaria frondosa*, in the shallow waters around Qikiqtait (Hudson Bay, Nunavut, Canada; Fig. 1). Sightings included suspected recruits in the 0-I year class, measuring 0.9–2.0 mm long, as well as successive annual cohorts of juveniles (Figs. 4 and 5); larger individuals were confined to adjacent deeper areas. This discovery likely represents the largest confirmed sea cucumber nursery ever described (see review by Wolfe et al., 2023). Although survey methods were not specifically adapted to the detection of the smallest juveniles, and samples types and sizes only allowed preliminary analyses to be conducted, this study provides convincing foundational evidence that should guide further investigations.

3.1. Environmental conditions in the nursery ground

Juveniles of *C. frondosa* were found between 1.8 and 2.5 m depths in Kataapik (northern Qikiqtait, Fig. 1) in an area that is covered by ice for up to 8 months every year, typically from late November until June (Eastwood, 2018; Hochheim and Barber, 2014), with a maximum ice thickness of 1.7 m (Landy et al., 2017). Salinities in this nursery area remained ≥27 psu, whereas the shallowest areas closest to the shore, directly influenced by melting ice during the spring (June 2022), did not harbour any sea cucumbers. Prevailing seawater temperatures ranged between −1.9 and 4 °C depending on the season, i.e., March 2019 (winter), October 2021 (fall), June 2022 (spring). Similar temperatures were previously described in other areas of the species distribution range, including southern Newfoundland and the St. Lawrence Estuary (Hamel and Mercier, 1996a; So et al., 2010). The main difference regards the longer winter (cold water conditions) and shorter summer (warm water conditions) in Qikiqtait. However, rearing temperatures around 0 °C are suitable for embryonic and larval development in *C. frondosa* (Hamel and Mercier, 1996a), indicating that this species is well adapted to Arctic conditions, as supported by its occurrence in northern Nunavut, Greenland and northern Scandinavia (Gianasi et al., 2021; Hamel and Mercier, 2023a). Finally, the nursery site is characterised by maximum tidal amplitudes of 1.2 m, and tidal currents of ~25–35 cm s^{-1} (Petrusevich et al., 2018; Ridenour et al., 2019; Stewart and Lockhart, 2005) in channel areas, which could give *C. frondosa* access to food and oxygen. In support of this, Sun et al. (2018) showed that flows between 21 and 40 cm s^{-1} were preferred by *C. frondosa*,
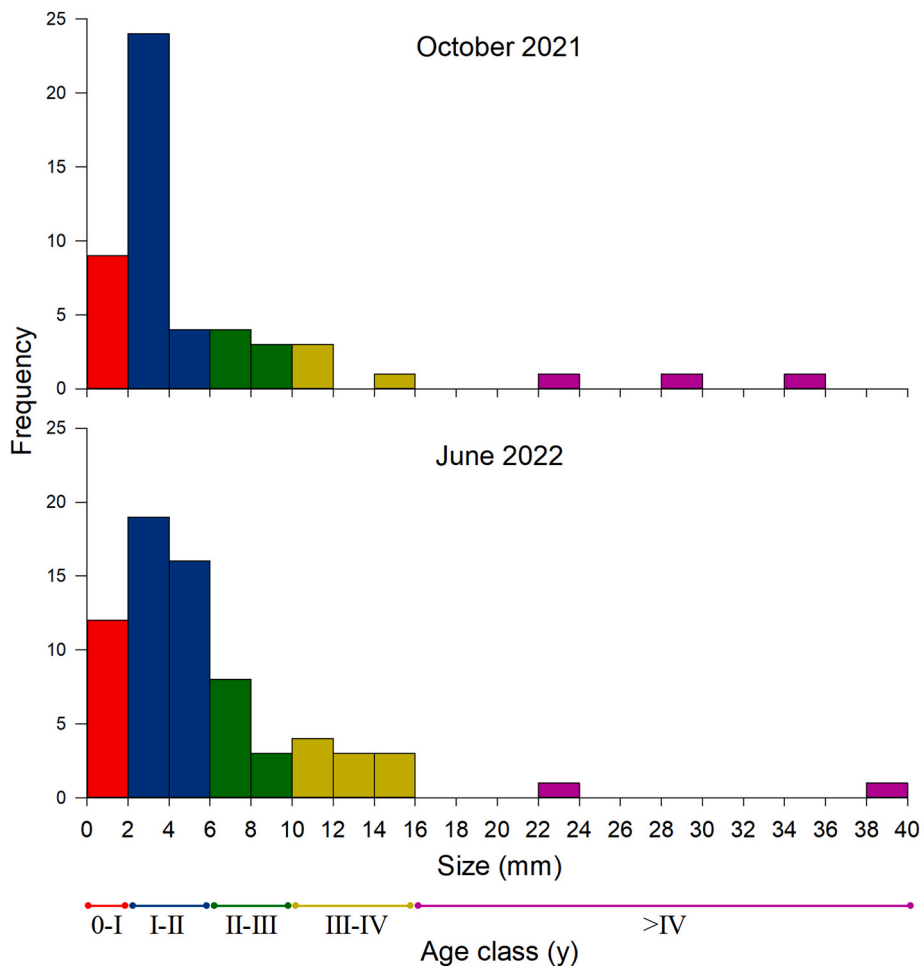

Fig. 5. Population size structure of *C. frondosa* at depths between 1.8 and 2.5 m in Kataapik (Qikiqtait) in October 2021 and June 2022. Size frequencies calculated on sampled area (0.25 m²) binned in 2-mm length intervals. Estimated age class of the various size classes (in years) are also shown.

providing an optimal balance between efficient food capture and energy expenditure for attachment to the bottom.

3.2. Densities and general population structure

The preliminary survey conducted in March 2019 had revealed the presence of individuals ~7–51 mm long, and later surveys conducted in 2021 and 2022 helped clarify the size structure (Fig. 5). The density of juveniles <40 mm in samples from Kataapik was between 4 and 104 ind. m^{-2} in October 2021 and 4–72 ind. m^{-2} in June 2022. Five of the pole net samples had no sea cucumbers in 2021 and six in 2022, representing ~25% of the sampling effort. In both years, no adults were seen in the shallow habitat (<2.5 m deep) of the juveniles. The difference in densities between October and June, with less individuals <6 mm long per meter square in June, could be explained by a collection before spawning in June (Figs. 4 and 5). Deeper areas (3–5 m) in the same general location (middle of the Kataapik channel; Fig. 2), characterised by sandy bottoms with scattered shells and stones, harboured mid-sized individuals (>90–160 mm length) attached to pebbles, cobbles or boulders at densities reaching 22 ind. m^{-2} (based on videos; Fig. 6a and b). The largest individuals (150–220 mm long) were found at the western entrance of the Kataapik channel attached to stones of different sizes at densities between 5 and 9 ind. m^{-2} (based on videos).

Beyond anecdotal reports, few studies have ever mentioned juveniles of *C. frondosa* <10 mm. Medeiros-Bergen and Miles (1997) reported the occurrence of juveniles of *C. frondosa* ~2–11 mm long among coralline algae, mussel beds and kelp holdfasts between 7.5 and 12.5 m depths along the coast of New England (USA) in 1993 and 1994. The authors estimated densities to be between 2 and 337 ind. m^{-2} in mussel beds, based on the number of individuals found on shells for which the surface area was determined, although this calculation disregards the fact that mussel beds represent a three-dimensional substratum with uneven distributions of juveniles. In general, the association with mussels and the lowest density estimates are consistent with the present results, whereas the depths of occurrence are different. Because no photographs were supplied and adults of *C. frondosa* were said to be absent from all the study sites, it cannot be excluded that some or all of the observed juveniles in that study were of different species.

3.3. Cohorts and age classes

Adult sea cucumbers examined in June 2022 displayed a gonad in the advanced growth stage, based on tubule diameter and scattered presence of mature (vitellogenic) oocytes, indicative of impending maturation. It was thus estimated that broadcast spawning would occur in early to mid-July in Qikiqtait. This is consistent with how local environmental factors are understood to influence gamete maturation and spawning in *C. frondosa* (Hamel and Mercier, 1996b). Settlement occurs at sizes between 550 and 950 μm total length, based on previous studies (Gianasi et al., 2019; Hamel and Mercier, 1996a; So et al., 2010). The growth rate is slow, with 1 year-old juveniles studied under mesocosm displaying a length ≤2–3 mm (Hamel and Mercier, 1996a; So et al., 2010). Therefore, the smallest individuals detected in October 2021 and June 2022 (<2 mm long) were assumed to be new recruits around 3–4 and 10-11 months-old, respectively (Fig. 5).

The overall size distributions of the juveniles were similar in 2021 and 2022, with four cohorts being detected based on extrapolation of size to year class (0-I, I-II, II-III, III-IV; Fig. 5). The latter estimates took into account growth rates, along with the development of the tentacles, tube feet and ossicles of this species under comparatively cold conditions (Hamel and Mercier, 1996a; So et al., 2010). The most abundant size class was composed of individuals between 2 and 6 mm in length, in both years, which may result from the combination of two recruitment pulses. On the other hand, Gianasi et al. (2018) highlighted large size differences among individuals of the same cohort due to genetic variation and allogenic fusion (formation of chimeras). Gradually, larger size classes, especially from ≥6 mm, showed decreased frequencies (Fig. 5). This dip in abundances could be the combined effect of mortality related to environmental disturbances and predation, including by sea urchins (Hamel and Mercier, 1996a), sea stars (So et al., 2010), worms (Medeiros-Bergen and Miles, 1997) and eider ducks feeding on the mussels (Jamieson et al., 2001; Merkel et al., 2007). Individuals larger than 12 mm were even less common, and gaps in size/year classes appeared between 16 mm and 40 mm (Fig. 5), consistent with suspected ontogenetic migration away from the nursery (see below).

3.4. Substrata occupancy

Clear trends were detected when analysing the sizes of the juvenile sea cucumbers relative to the substrata they occupied (Fig. 7). In both 2021 and 2022, the smallest juveniles were typically associated with the most complex substrata, i.e. entangled among byssus threads and wedged between live mussels. Slightly larger individuals more commonly occupied the surface of empty mussel shells and stones, the later substratum consistently harbouring the largest juveniles. A two-way ANOVA on ranks confirmed the marked influence of substratum type on the juvenile sizes ($F_{4,112}$ = 19.4, p<0.001) and did not highlight any clear effect of sampling year ($F_{1,112}$ = 3.9, p = 0.052), although
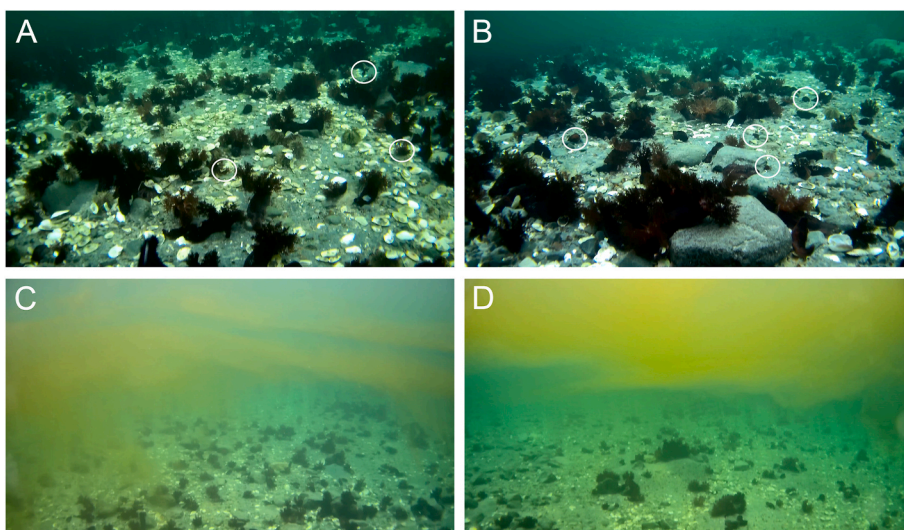

Fig. 6. (A-B) Large juveniles or adults under 120 mm long (examples circled) among adults of *C. frondosa* (~150 mm long) at about 4–5 m depth in the Kataapik channel (water temperature: −1 °C). Note the deployment of oral tentacles consistent with feeding posture. (C-D) Visible algal bloom just under the ice cover and above the sea cucumbers. Note that this algal bloom also extended above the shallow subtidal area where the juveniles were observed. All photographs from June 2022.
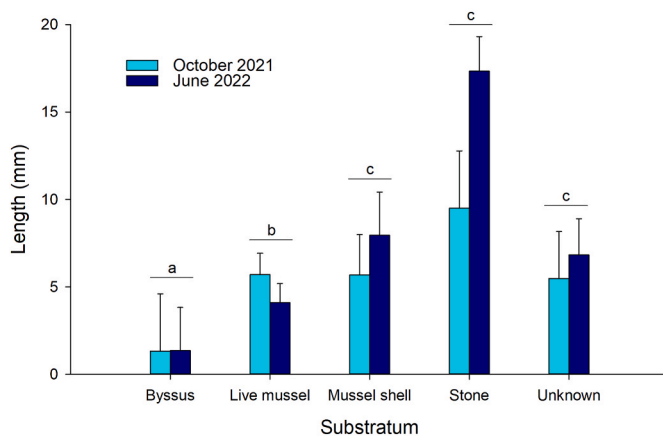
Fig. 7. Length distribution of individuals of *C. frondosa* collected on various substrata in Kataapik at depths between 1.8 and 2.5 m in October 2021 (left bars) and June 2022 (right bars). Data shown as mean ± standard error (n = 4–36). Different letters above the paired bars indicate differences in the sizes of juveniles among substrata, as shown by a two-way ANOVA on ranks (see text for details).

differences seemed more marked in June 2022 (Fig. 7). While caution must be applied to these preliminary results due to the unequal number of individuals found on the different substrata, the analysis concurred that the juveniles on byssus threads were the smallest (Holm-Sidak; p<0.001), followed by those on live mussels (p = 0.001–0.006).

The smallest size class of *C. frondosa* reported during a study in the St. Lawrence Estuary (QC, Canada) were 15–60 mm and they occurred on the under surfaces and sides of stones (Hamel and Mercier, 1996a), which is consistent with the present findings. In addition, Medeiros-Bergen and Miles (1997) reported young individuals of *C. frondosa* (down to 2 mm long) among mussels in Maine (USA), supporting the possible link between mussels and the recruitment of *C. frondosa*, not only in northern locations, but throughout its distribution range. The fact that the smallest recruits were also occasionally found on other substrata (e.g. stones) in the present study and reported from kelp holdfasts and coralline algae by Medeiros-Bergen and Miles (1997) suggests that settlement preferences are flexible or alternately that the cue from the mussels extends to surrounding substrata that serve as attachment for the mussels themselves.

In the present study, relatively small juveniles (~25–35 mm long) were also observed in deeper water (15–25 m deep) but in low numbers (David Deslauriers lab, personal communication), which may indicate that they settled there. The duration of pelagic development in *C. frondosa* is around 45 days (Hamel and Mercier, 1996a). If the preferred substrata are not available when larvae reach the pentactula stage and lose buoyancy, they might settle on non-optimal substrata in slightly deeper areas. Survival there might be lower due to greater environmental and predatory pressures on juveniles occupying less complex substrata. It is also possible that the sampling method underestimated the abundance of juveniles in deeper areas, even though efforts were made to detect them on the hard susbtrata collected. However, the occurrence of a shallow nursery remains the most likely scenario based on the evidence provided here and the limited reports of small-sized individuals at deeper depths in over 50 years of study.

3.5. Settlement and ontogenetic migration

The smallest sea cucumbers occurred in a shallow water column that would be only a few centimetres deep under the winter ice sheet at the main settlement site. Why are new recruits of a lower subtidal species like *C. frondosa* found nearshore where there is ice cover in winter and reduced salinities during the spring thaw? Phytoplankton is the main food source of *C. frondosa* from an early age (Gianasi et al., 2018; Hamel

and Mercier, 1998). It is possible that proximity to the under-ice allows the propagules to access larger quantities of suitable food. ROV images in spring 2022 showed what appeared to be blooms of sea-ice algae (possibly mixed with other phytoplankton) close to the water-ice interface (Fig. 6c and d). This represents large amounts of food for young suspension-feeding sea cucumbers, away from the competition of larger individuals and adults that occupy hard substrata in deeper water. The early life stages of *C. frondosa*, from the fertilized oocytes to the settled pentactulae showed faster development at the lowest salinity (24 psu) in experimental trials (Hamel and Mercier, 1996a). This haloplasticity of the early propagules may help them take advantage of a phytoplankton-rich stratum in which halotolerance limits the number of potential predators.

The concentration of larger juveniles in nearby but slightly deeper water allows us to suggest the occurrence of successive size/age-specific migrations in *C. frondosa*. This movement was first suspected in a previous study conducted many years ago in the St. Lawrence Estuary (QC, Canada) where increasingly larger individuals were found with increasing depth down to 40–60 m (Hamel and Mercier, 1996a). From the settlement location inside structurally complex substrata, including mussel shells/byssal threads, rock crevices and under surfaces, a first displacement apparently occurs as recruits reach a size that protects them against grazers. Sea cucumbers measuring ~10 mm were shown to be less vulnerable to the grazing activities of the sea urchin *Strongylocentrotus droebachiensis* (Hamel and Mercier, 1996a) and the predation of the sea star *Solaster endeca* (So et al., 2010). This first migration may only be over a few cm, without much of a depth component, also coinciding with a greater need to acquire food driving relocation to the upper surfaces of the substrata. This behaviour may be linked to a transition from deposit feeding to suspension feeding in the first months of growth (Gianasi et al., 2018) and the associated need to deploy the tentacles and expose them to nutrient rich water flows. Overall, juveniles >9–10 mm long were found to be less cryptic and more exposed than smaller conspecifics.

The reason for the subsequent vertical migration of juveniles >15–20 mm may result from a combination of factors acting independently or synergistically. Upper water layers are subjected to steeper salinity fluctuations that may exceed the tolerance of larger juveniles and adults, which may at the same time become more susceptible to drag forces. Hamel and Mercier (1996a) and So et al. (2010) showed that there was a threshold salinity of about 26 psu below which the survival of the juveniles and adults of *C. frondosa* was negatively affected. Moreover, a salinity of 26 psu was shown by Hamel et al. (2019) to induce quick detachment of the ambulacral podia from the substratum and uptake of seawater. This reaction culminated with bloated individuals completely detaching from the substratum and becoming neutrally buoyant, so that a slight water movement was enough to carry them away passively (Hamel et al., 2019). Thus, low salinity may trigger an active or semi-passive migration from the initial shallow habitat through active buoyancy adjustment (ABA), resulting in a greater abundance of the larger size classes in the middle of the channel and at both eastern and western entrances of Kataapik (Figs. 1c and 2). Less commonly (n = 3 from 2 collections), larger individuals between 30 and 51 mm long were observed among the smaller recruits in the shallows, suggesting that not all sea cucumbers are following the same migration patterns. It is also possible that larger sea cucumbers occasionally get transported back to the shallows through ABA processes also suspected to be at the origin of strandings, e.g. following hyposaline or turbidity currents generated by storms (Hamel and Mercier, 2023b).

3.6. Size at sexual maturity and sex ratio

Individuals up to 100–120 mm long that were found in deeper water strata between 4 and 6 m were still characterised as juveniles based on their immature gonad devoid of mature oocytes/spermatozoa in June 2022. Individuals ≥130 mm long were determined to be sexually

mature, given the presence of some mature oocytes (400–550 μm in diameter) similar to those observed before spawning in conspecific sea cucumbers from other locations (Gianasi et al., 2021). This finding corresponds to a larger size at sexual maturity than that (120 mm) established for the same species in the St. Lawrence Estuary, eastern Québec (Hamel and Mercier, 1996a). Furthermore, the condition of the whole gonad in these sexually mature individuals was not consistent with readiness to spawn. In turn, individuals ≥160 mm long showed uniform gonad maturity across the larger gonad tubules consistent with readiness to spawn, meaning they would likely be involved in the impending spawning event.

The sex ratio estimated from individuals with a sexable gonad (possessing clear male or female characters) across all samplings made in Kataapik was 1.1 female for 0.9 male. This value is comparable to a ratio of 1 female for 1 male described in previously published worked from other locations along its geographic distribution (Gianasi et al., 2021; Hamel and Mercier, 1996a, 1996b).

3.7. Estimation of recruitment across Qikiqtait

The shallow subtidal band of rocky substrata (bedrock, stones, pebbles) and blue mussel beds occupied by recruits of *C. frondosa* (visible on Fig. 2a and b) was estimated to be between 4 and 6 m wide in the study areas and nearby locations along the coast. Shallow areas in the Qikiqtait archipelago where salinity is ≥27 psu and substrata can provide suitable habitat to just settled and early juveniles of *C. frondosa* spread on ~4,000 km out of the ~5000 km of coastline (https://www.qia.ca/nauttiqsuqtiit-inuit-stewards-program-expands-to-sanikiluaq/). Based on those criteria, the colonizable surface area for the early life stages was estimated between ~16,000 and 24,000 km^2 across the entire islands. Using the average densities determined during the present study for individuals 0.9–40 mm long, which were 22.3 and 18.5 ind. m^{-2} in 2021 and 2022, respectively, we estimated that between ~296 and 357 billion juvenile sea cucumbers could be found at any given time in the whole archipelago. As small sized sea cucumbers (30–100 mm) were also found occasionally in deeper water during trawl surveys, it is not impossible that this may be an underestimation. Inversely, because some coastal areas with suitable nursery habitat may not hold juvenile sea cucumbers due to other environmental factors, these numbers may represent an overestimation of the reality.

4. Conclusion

Considering the abundance of juvenile of all sizes and the number of adults detected in Qikiqtait, it seems that Arctic conditions are not limiting for *C. frondosa*. On the contrary, video transects show that waters around the islands may host one of the densest ever described populations of *C. frondosa* and preliminary estimates suggest that the fringing coastal zones could constitute the most extensive nursery ever found for a sea cucumber, especially if we consider that the sampling methods might not have captured all the juveniles present at the study sites. Further studies should endeavor to gather data over longer time series to confirm ontogenetic migration patterns, and across broader spatial scales to validate the presence of juveniles in coastal regions that contain similar habitats and environmental conditions.

Despite the abundance of individuals across the full breath of life stages, and what appears to be annual pulses of recruitment, populations likely took a long time to get established. *Cucumaria frondosa* is slow growing based on studies conducted in more southern regions (Hamel and Mercier, 1996a). Representatives in the Arctic may grow even slower and may thus require more than 12–15 years to reach full adult-commercial size, suggesting that a rigorous management plan should be developed to protect this resource over the long term.

Knowing and understanding the behaviour, habitat and ecology of *C. frondosa* in Arctic and subarctic environments is important to the sustainable development of subsistence and commercial fisheries in the

northern Canadian territories. Despite the prisitne habitats of Qikiqtait, with human population densities under 0.03 ind. km^{-2}, the development of the hydroelectric installations in the lower Hudson Bay (James Bay) has modified and continues to influence the prevailing oceanographic conditions. As the new recruits and early juveniles of *C. frondosa* appear to thrive in shallow channel environments (to 2.5 m) and to occur close to the ice cover (<5–10 cm under it), interannual changes in runoff patterns that alter salinity could cause mass mortalities and thereby jeopardize population turnovers around Qikiqtait and other areas of south-eastern Hudson Bay.

In Nunavut, *C. frondosa* is part of the diet of walruses, bearded seals, and eider ducks, thus representing a very important foundational taxon that fills key ecosystem functions as a suspension feeder and prey species. In addition, sea cucumbers are part of the traditional diet of the Inuit in the community of Sanikiluaq, and consequently represent a major pillar of their food security that should be managed sustainably. The Kataapik area also holds great cultural significance. The community recently proposed and received funding to develop an Indigenous Protected and Conserved Areas of 33,000 km^2 (Qikiqtait Protected Area project, an Inuit-led conservation program), which would fortuitously encompass the sea cucumber nursery characterised in the present study.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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