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Novel observations of capelin (*Mallotus villosus*) spawning directly on a brown algae species (*Desmarestia viridis*) in coastal Newfoundland, Canada

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Abstract

Capelin (*Mallotus villosus*) is a key forage fish species within its circumpolar range. This species' importance lies in its role in the typical marine 'wasp-waist' food web, where capelin acts as a conduit for energy flow from lower to higher trophic levels. Herein we describe a novel observation of capelin spawning subtidally on an annual brown algae species, *Desmarestia viridis*, during July–August 2019 in Placentia Bay, Newfoundland, Canada. Based on extensive video surveys of the seabed along with shoreline surveys and sediment sampling, we did not find other nearby sites with typical capelin subtidal and intertidal spawning habitat (*i.e.* medium sand to pebble gravel). Findings suggest that capelin spawned directly on this brown algae species, *D. viridis.* Eggs adhered to *D. viridis* developed normally and hatched successfully. As temperatures of intertidal areas are predicted to increase above temperatures suitable for capelin egg rearing (2–12°C) with climate change, *D. viridis* may become a high-quality subtidal spawning habitat for capelin and other fish species. In support, this algal species is adapted to colonize high disturbance areas, allowing protection from egg predators in a high flow environment while also being resistant to urchin grazing.

*Keywords***:** Capelin; spawning habitat; *Mallotus villosus*; Northwest Atlantic; Newfoundland; *Desmarestia viridis*

Introduction

Capelin *Mallotus villosus* (Müller, 1776) is an important forage fish species both commercially and ecologically in many northern marine ecosystems, whereby it plays a key role in funnelling energy from lower to higher trophic levels (Lavigne, 1996; Carscadden and Vilhjalmsson, 2002). In the Northwest Atlantic, the capelin population on the Newfoundland shelf collapsed in 1991 (Buren *et al.*, 2014) and has yet to recover (Buren *et al.*, 2014, 2019). The lack of recovery is thought to be related to bottom up processes, whereby changing seasonal sea ice dynamics and timing of spawning limit recruitment due to mismatches between larval emergence and favourable environmental conditions (*i.e.* low predator and high prey densities) for larval survival (Buren *et al.*, 2014; Mullowney *et al.*, 2016; Murphy *et al.*, 2018; Lewis *et al.*, 2019). Although the primary reproductive mode in coastal Newfoundland is thought to be intertidal ('beach') spawning (Nakashima and Wheeler, 2002), there are also historical reports of widespread and consistent subtidal spawning (Templeman 1948), which are further supported by more recent studies (Nakashima and Wheeler, 2002; Davoren *et al.*, 2006). As capelin eggs become sticky after fertilization (Davenport *et al.*, 1986), the spawning site becomes the egg-rearing site. Although larvae hatch in good condition from some subtidal sites (Penton and Davoren, 2008) but not others (Nakashima and Wheeler, 2002), incubation is often longer in subtidal habitat compared to beach habitat due to cooler water temperatures (Penton *et al.*, 2012), resulting in longer exposure to egg predators (Frank and Leggett, 1984), less growth/development time prior to winter, and potentially a higher probability of temporal mismatches with favorable environmental conditions. Overall, little information exists regarding the contribution of subtidal habitat to capelin recruitment (Davoren *et al.*, 2007).

Similar to intertidal spawning habitat, studies have linked subtidal capelin spawning locations primarily with a sediment size range (0.5–25mm; Templeman, 1948; Nakashima and Wheeler, 2002; Davoren *et al.*, 2007; Penton and Davoren, 2012, 2013) and secondarily with a temperature range (2–12°C; Carscadden *et al.*, 1989; Davoren, 2013; Crook *et al.*, 2017), with highest hatching success between 4–7°C (Penton and Davoren, 2013). For subtidal spawning, bathymetric features such as depressions (*i.e.*, trenches or 'holes') are also important, as they retain suitable spawning sediment in specific areas (Penton and Davoren, 2012). This sediment size range is key for proper oxygenation and waste removal (Penton *et al.*, 2012) and temperature range is vital to reduce the rate of abnormal egg development (Shadrin *et al.*, 2020). As fertilized capelin eggs adhere to all nearby structures, eggs have been anecdotally observed and reported adhered to algae by local fishers, along with other structures (*e.g.*, traps, trawls, other fishing nets and anchors) from 5–45m depth (Templemen, 1948). Adherence to algae and these other structures, however, is thought to occur incidentally, whereby eggs drift from nearby sediment-based spawning sites.

Here we describe a novel observation of capelin spawning subtidally on brown algae, *Desmarestia viridis,* during July–August 2019 (Fig. 1) in Placentia Bay, Newfoundland, Canada. *D. viridis* is a canopy-forming, annual brown algal species that is usually found in nearshore intertidal and subtidal areas (<12m) at higher latitudes, most often in Arctic or sub-Arctic regions (van Oppen *et al.*, 1993). We investigated whether capelin spawned directly on *D. viridis* or whether the capelin eggs adhered to this algal species incidentally. These observations were made while investigating the spatial extent of subtidal spawning of capelin within this Newfoundland bay.

Materials and Methods

Underwater camera surveys were conducted during July–August, 2019 on the east coast of Placentia Bay, Newfoundland, Canada (Fig. 2A) within 12 areas highlighted as being potentially important for subtidal capelin spawning during fisher interviews adapted from Sjare *et al.* (2003). To determine camera survey sites, a 4.6km by 2.3km rectangle was drawn around the center of each of the 12 potential subtidal spawning areas identified by interviewees. Within each of these 12 rectangles, we used ArcMap 10.3.1 to generate 10 random sites at least 500m apart, which was based on the size of the chartered fishing

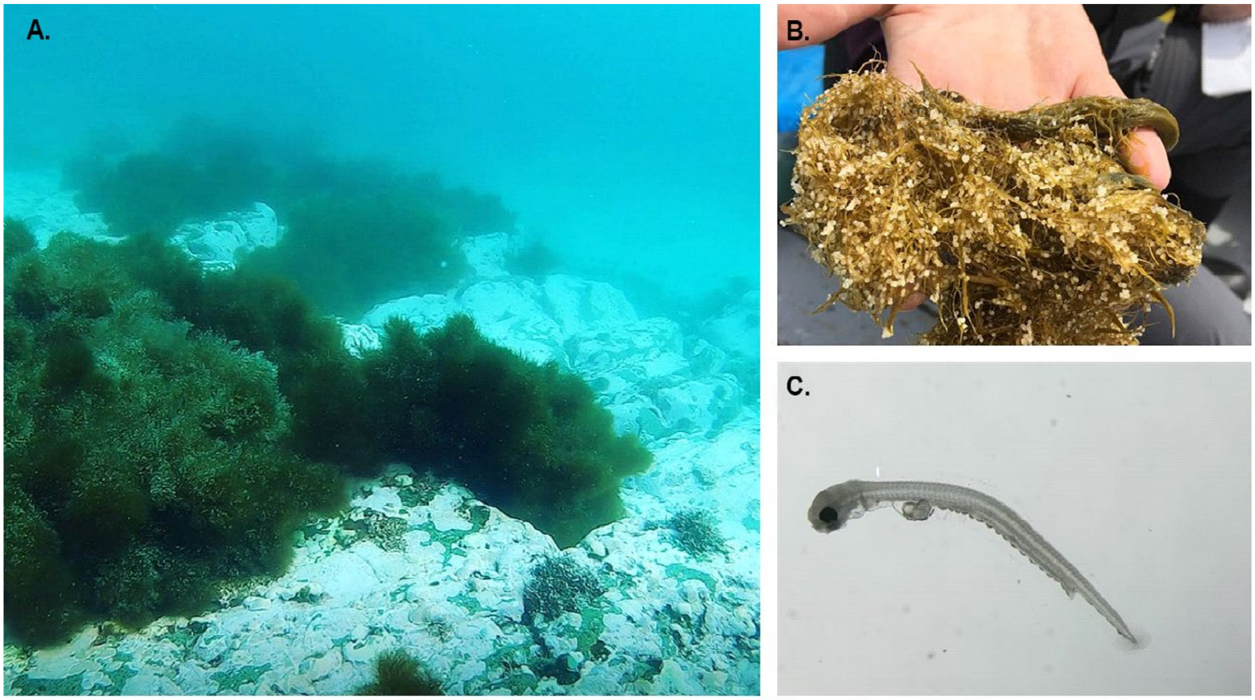

Fig. 1. Screenshot from camera surveys conducted on 20 July 2019 showing *Desmarestia viridis* covered in adherent capelin (*Mallotus villosus*) eggs (**A**). Photograph of a sample of *D. viridis* covered in yellow capelin eggs collected on 20 July 2019 (**B**). A microscope (Olympus SZX7, 25X magnification) photograph of the capelin larvae that hatched from laboratory-raised eggs found on *D. viridis* (**C**).

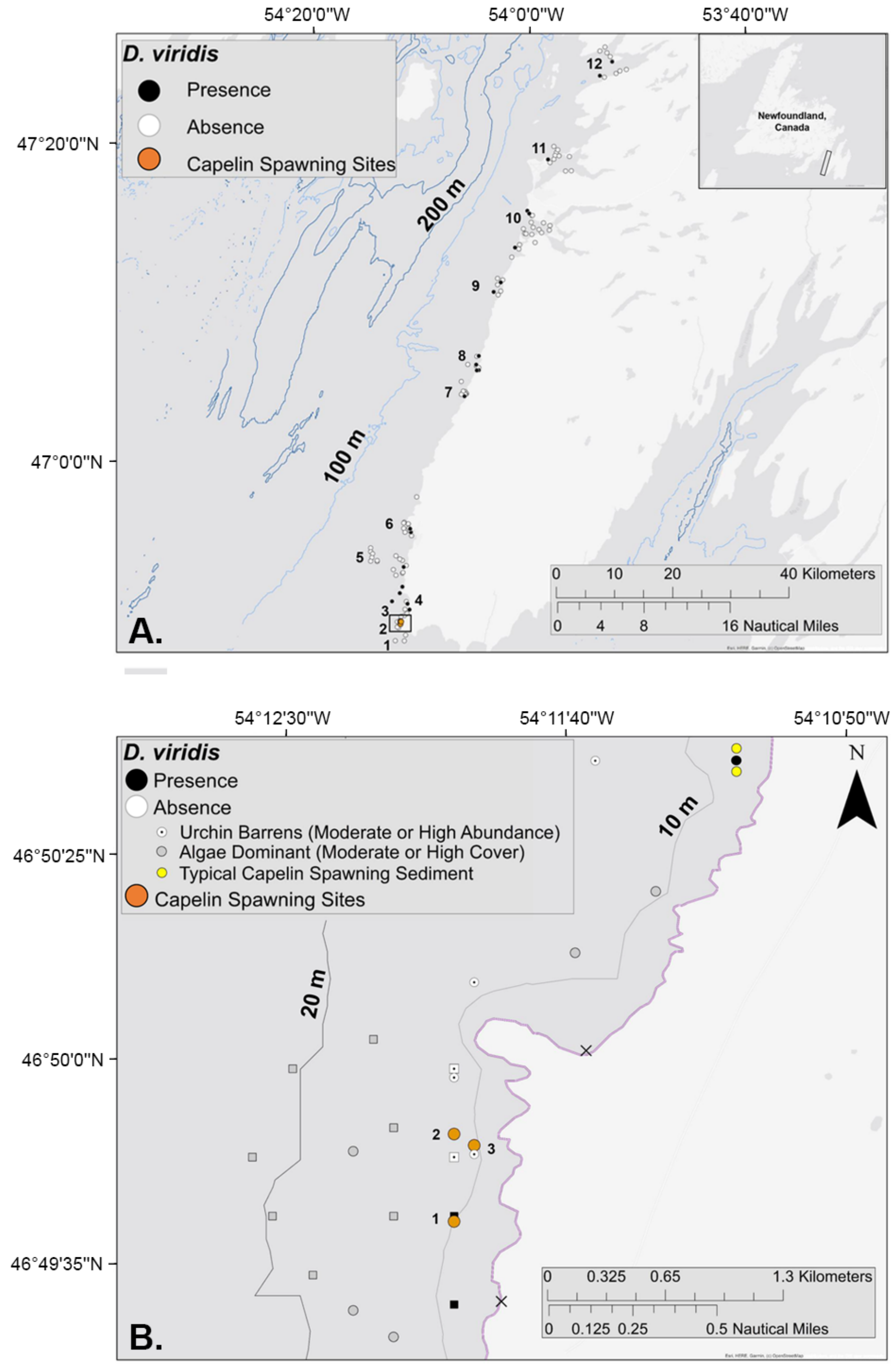

Fig. 2. The location of the east coast of Placentia Bay, Newfoundland, Canada (**A**, inset). (**A**) The distribution of *Desmarestia viridis* along the east coast of Placentia Bay based on the 136 sites surveyed during July–August, 2019 within the 12 areas highlighted as being potentially important for subtidal capelin (*Mallotus villosus*) spawning during fisher interviews. The sites where capelin eggs were adhered to *D. viridis* are indicated (capelin spawning sites) and the square indicates the region highlighted in **B**. (**B**) The fine-scale distribution of *D. viridis* with adherent capelin eggs (capelin spawning sites 1–3) and without capelin eggs, along with nearby sites that were both absent of *D. viridis* and one of the following: algal-dominated, urchin barrens, or typical capelin subtidal spawning sediment (medium sand to pebble gravel). Squares represent the 11 delineation sites, while circles represent the original randomly generated sites. The purple line along the coast indicates the area searched with binoculars for typical capelin intertidal spawning habitat and evidence of intertidal spawning, while the black Xs indicate beaches, which were comprised of large cobbles and boulders.

vessel (6m) and expected drift, to reduce the probability of covering the same area in separate surveys. In addition to these 120 random sites, other sites were added based on the previous fishing experience and knowledge of chartered fishers in the area, for a total of 136 sampling sites.

Prior to beginning camera surveys, we regularly contacted local fishers and monitored a citizen-science social media platform (www.ecapelin.ca) to ensure that boat-based surveys began after capelin had arrived in coastal regions and had begun spawning in the bay. We sequentially visited each site, during which we deployed a metal frame (meshless crab or lobster pot) with two underwater video cameras (GoPro Hero 7) attached along with a data logger (Star-Oddi DST) that measured temperature (°C) and salinity via conductivity (mS/cm) every 5 s. The metal frame was lowered to the seabed where it remained for 5 min to allow instrumentation to calibrate, and then was lifted ~ 1m off the seabed and allowed to drift for 4 min on average (± 6 s), or ~ 250–300m, to explore more of the seabed immediately adjacent to each site for the presence of capelin eggs.

After the camera surveys were completed at each site, mean depth, temperature and salinity were derived from the data logger. Videos for each survey site were analyzed to determine the dominant sediment type, occurrence of capelin eggs, along with a qualitative index (*i.e.*, high, moderate, low, and zero) of the percent cover of *D. viridis* and other algal species, and abundance of green urchins (*Strongylocentrotus droebachiensis*). For this paper, we focus on *D. viridis* because this was the only algal species on which adherent capelin eggs were found. We used the Wentworth Scale to qualitatively classify the dominant granulated sediment type on videos (Wentworth, 1922).

To determine if capelin eggs were present, sediment was sampled using a 15-cm^2 Ponar Grab system. Capelin eggs adhered to algae were also incidentally sampled when algae became tangled in our metal frame. Eggs were preserved in Stockard's (50 mL formaldehyde, 37% solution; 40mL glacial acetic acid; 60mL glycerin; 850mL sea water) and later examined under a dissecting microscope (Olympus SZX7) to determine species identity based on egg size and colour (Fridgeirsson, 1976), as well as comparison to reference capelin egg samples collected from active capelin spawning sites in other areas of Newfoundland. We also quantified the percentage of eggs in different developmental stages within at least one random sample of 50–100 eggs from each site. Following Frank and Leggett (1981), early developmental stages (Stages I–II) represented recent spawning, while later developmental stages (Stages III–VI) represented stages closer to hatching. Eggs adhered to algae were also lab-reared within a controlled environmental chamber at ~8°C until hatch to confirm species identity using morphological characteristics (Fahay, 2007).

Ethical Statement

The care and use of experimental animals complied with Canadian Council of Animal Care animal welfare laws, guidelines and policies as approved by Canadian Council of Animal Care (Protocol: F16-017/1/2/3).

Results

During July–August 2019, we completed camera surveys at 136 unique sites within 12 potential subtidal capelin spawning areas in eastern Placentia Bay to determine the occurrence of capelin eggs (sampling dates: 16, 20, 21, 23, 25, 27 July and 6, 7, 9, 15 August). On 20 July 2019, we discovered eggs adhered to *D. viridis* during camera surveys at three sites within 128–483m of each other in one of the 12 potential areas (Fig. 2B). The seabed substrate was characterized as bedrock with no granulation at all three sites (Fig. 1A). While drifting away from each site, we did not find more typical capelin spawning sediment or capelin eggs adhered to any structures immediately adjacent to each site. We collected eggs from two of the three sites on the day of discovery (20 July), which were lab-raised to hatch and later identified as capelin larvae (Fig. 1B, 1C). Initial egg samples revealed 57% of capelin eggs at site 1 were in earlier stages of development (Stages I–II), while a lower percentage (17%) were in early stages at site 2 (Table 1). These three sites were revisited on August 1, 10 and 11, 2019. On 1 August, we only sampled eggs to monitor development (no camera surveys), but were unable to obtain a sample from sites 2 and 3 due to high tidal activity. Eggs sampled at site 1 on 1 August were all in later stages (III–VI), indicating no recent spawning. Note that abnormally developing, empty or dead eggs were not found in any sample. On 10 and/or 11 August, capelin eggs were no longer found adhered to algae at any of the three sites and the percent cover of *D. viridis* was lower relative to 20 July (Table 1). Temperature-based incubation duration was estimated for each site to be 16–21 d from 20 July, based on the equation in Frank and Leggett (1981), suggesting that the eggs had likely hatched by 10/11 August.

To determine if there was a nearby beach spawning site, we thoroughly surveyed the coastline from the boat (~ 500m offshore) using binoculars (purple line; Fig. 2B) within ~ 5km north and south of the three spawning sites during work at or nearby these sites (20–21, 23 July; 1, 10 –11 August). The general topography of the coastline was 120m cliffs, with two 2m wide beach sites. However,

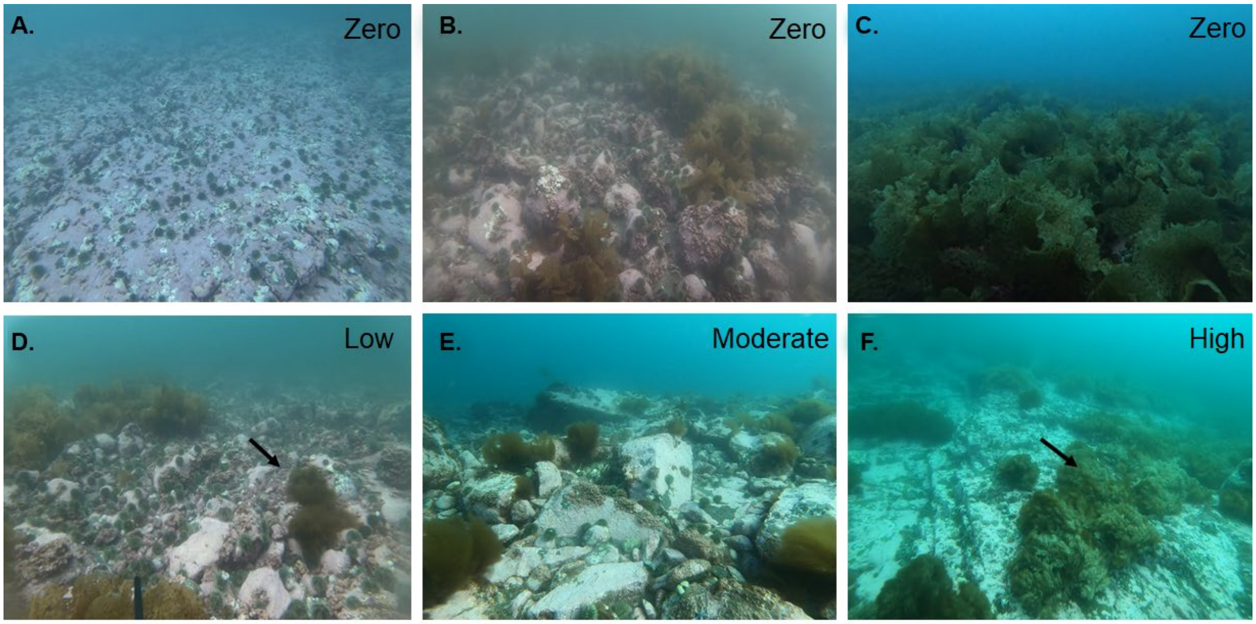

Fig. 3. Photographs from underwater video (GoPro Hero 7) during surveys for capelin (*Mallotus villosus*) subtidal spawning habitat in July–August, 2019 in Placentia Bay, Newfoundland, Canada. Examples of sites where *D. viridis* was absent (**A–C**) are shown, including low algal cover and a high density of green urchins *Strongylocentrotus droebachiensis* (**A**), moderate cover of *Agarum clathratum* (**B**), and high cover of *A. clathratum* (**C**). Examples of low, moderate, and high density of *D. viridis* (**D–F**) are also shown, including *A. clathratum* present with low *D. viridis* cover (**D**). Note the arrows indicate *D. viridis* (**D**) and yellow capelin eggs adhered to *D. viridis* (**F**).

these beaches were composed mostly of larger cobble and boulders fallen from the cliffside. The next nearest site with typical capelin subtidal spawning sediment (0.5–25mm) was 2.5km north of our sites (Fig. 2B, yellow circles), but eggs were not found adhered to the sediment when sampled on 21 and 23 July.

To determine if there was a subtidal spawning bed with more typical capelin spawning sediment size ranges from which fertilized eggs may have incidentally drifted to our three subtidal spawning sites, we conducted additional camera surveys on 10 August. To do this, we generated 11 more camera survey sites (‘delineation sites’) in a diamond-like shape around our three capelin spawning sites. Delineation sites were spaced ~500m apart to cover as much of the un-surveyed area near the three spawning sites while minimizing repeatedly covering the same areas (Fig. 2B, squares). Based on video analysis, all delineation sites were identified as bedrock with no granulation and *D. viridis* was only present at two of the shallowest sites (8–10m; Fig. 2B). The remaining nine delineation sites had either high densities of green urchins and very little to no algal species (*n* = 2 sites; Fig. 3A) or high percent cover of other algal species (*n* = 7 sites; Fig. 3B, 3c). Capelin eggs were not found adhered to *D. viridis*, other algal species or bedrock at or nearby any of the 11 delineation sites.

We revisited these sites during 2020 and 2021 to determine if *D. viridis* remained present and capelin eggs were consistently adhered. On 5 August 2020, we conducted camera surveys at all three spawning sites from 2019 and all 11 delineation sites. At the three sites where capelin eggs had been found adhered to *D. viridis*, capelin eggs were not present and *D. viridis* was absent at sites 1 and 2 (Table 1); however, *D. viridis* was present 100m inshore from the original location of site 1. Site 3 was the only site with *D. viridis* present but no capelin eggs were found. Of the 11 delineation sites, *D. viridis* was present again at the same two inshore sites (8–9m) from 2019, and the remaining nine sites continued to be characterized as bedrock with no granulation with either high densities of green urchins and little to no algal cover (*n* = 2 sites; Fig. 3A) or high percent cover of other algal species (*n* = 7 sites; Fig. 3B, 3C). During 2021, we revisited the three spawning sites from 2019 on 12–15 July and *D. viridis* was found with capelin eggs adhered on 15 July nearby site 1.

Discussion

During July 2019, we documented capelin spawning on the algal species *D. viridis.* After systemically surveying adjacent and nearby subtidal areas as well as intertidal areas along the coast (Fig. 2B), we were unable to find

Table 1. Depth, temperature, salinity and percent cover of *Desmarestia viridis* (*i.e.* high, moderate, low, zero) at each of the three sites at which capelin eggs were found adhered to *D. viridis* during July and August 2019, which were resurveyed during August 2020. Samples of capelin eggs were obtained on 20 July 2019 during underwater camera surveys and egg sampling was also attempted on 1 August 2019 without camera surveys. The percentage of eggs in early developmental stages (Stages I–II) and later stages (Stages III–VI) are indicated for each sample. All capelin eggs were absent by 10 and 11 August 2019 during camera surveys.

Sites with capelin eggs	Date	*D. viridis* cover	Depth (m)	Bottom Temperature (°C)	Salinity (mS/cm)	Eggs Present?	Stages I–II (%)	Stages III–VI (%)
Site 1 [46.828°N, 54.200°W]	20 Jul 2019	High	10	4.3	43.7	Yes	57	43
	1 Aug 2019	-	-	-	-	Yes	0	100
	10 Aug 2019	Low	10	7.6	46.4	No	-	-
	11 Aug 2019	Moderate	10	10.9	49.2	No	-	-
	5 Aug 2020	Zero	11	11.3	46.3	No	-	-
Site 2 [46.831°N, 54.199°W]	20 Jul 2019	Low	10	4.6	44.0	Yes	17	83
	1 Aug 2019	-	-	-	-	No	-	-
	10 Aug 2019	Zero	12	7.4	46.0	No	-	-
	5 Aug 2020	Zero	14	9.7	44.4	No	-	-
Site 3 [46.830°N, 54.199°W]	20 Jul 2019	Moderate	9	4.7	43.7	Yes	-	-
	11 Aug 2019	Zero	10	8.1	46.6	No	-	-
	5 Aug 2020	Low	11	8.2	43.7	No	-	-

subtidal or intertidal capelin spawning sites on typical sediment (*i.e.* medium sand to pebble gravel; Nakashima and Wheeler, 2002; Penton and Davoren, 2012). Although we cannot rule out that capelin spawned on small patches of undetected intertidal or subtidal sediment nearby our three algal capelin spawning sites, it is unlikely that eggs drifted from these sites and adhered only to *D. viridis* in the high densities observed despite the concurrent presence of other algal species. Overall, this evidence suggests that capelin spawned directly on *D. viridis*.

As the capelin eggs likely hatched successfully from *D. viridis* in the field, this algal species may represent a favourable capelin spawning habitat. Indeed, *D. viridis* may provide protection for developing eggs from predators, by providing a refuge for eggs away from benthic-feeding predators, such as flounder (Frank and Leggett, 1984), crabs (Mikkelsen and Pedersen, 2017), and amphipods (DeBlois and Leggett, 1993). Additionally, the sweeping motion of the algal branches deters urchin predation, allowing *D. viridis* to form high-density algal beds in regions with high wave action (Konar, 2000; Gagnon *et al.*, 2006) and providing further protection from pelagic fish egg predators (Gagnon *et al.*, 2006; Blain, 2013). Therefore, depositing eggs on *D. viridis* in areas of high wave action may provide a fixed incubation habitat with low predation for capelin eggs. The sweeping motion also likely results in regular oxygen replenishment and waste removal from the water surrounding eggs. Although the high acidity (H_2SO_4) of *D. viridis* might be considered an unsuitable, or even detrimental, incubation habitat for capelin eggs, sulphuric acid is only released at senescence, which is initiated >12°C (Blain and Gagnon, 2013; Gagnon *et al.*, 2013). Indeed, although *D. viridis* can survive short periods of average ocean temperatures up to 23°C (Breeman, 1988), it undergoes a rapid die-off when average temperatures are >12°C for extended periods (*e.g.* ~ 1 month; Gagnon *et al.,* 2013) and reproduction is inhibited at 10°C (Breeman, 1988). The higher temperatures during 2020 (8.2–11.3°C; Table 1), therefore, might explain the lower presence and density of *D. viridis* at the same inshore sites relative to 2019. Overall, if the conditions are favorable (*i.e.* high wave action and ≤12°C), *D. viridis* may be a high-quality incubation habitat for capelin eggs. In support, we found many sites with high algal cover in our study area, but never found capelin eggs attached to algal species other than *D. viridis*. Previous studies also reported that *D. viridis* is a preferred algal species for fish egg deposition in coastal Newfoundland relative to other algal species (*e.g.*, *Desmarestia aculeata*, *Agarum clathratum*; Blain, 2013).

As *D. viridis* is resistant to urchin predation in areas of high wave action, it is highly successful at colonizing these areas (Konar, 2000; Gagnon *et al.*, 2006). This might explain the high densities of *D. viridis* observed (Fig. 3D–F) in inshore, shallow areas (2019: 10 ± 4m; 2020: 13 ± 4m), which are known to be high disturbance areas due to wave action. Other nearby sites, however, also had high densities of green urchins (Fig. 3A), which matched the description of green urchin barrens, previously defined as areas where algae is absent with high sea urchin densities (Konar, 2000). Previous studies in coastal Newfoundland have identified *D. viridis* as a first successional stage in the recolonization of urchin barrens, allowing the colonization of other algal species, such as the perennial *Agarum cribrosum* (*e.g.*, Fig. 3B, 3C, and 3D) and *Alaria esculenta* (Gagnon *et al.*, 2003; Molis *et al.*, 2009). This might explain the deeper sites farther offshore being dominated by these other algal species (Fig. 3B–C) in our study area. As algal beds are important for a variety of ecosystem functions (*e.g.,* fixed carbon source/primary productivity, habitat/shelter), shifts from algal-dominated to urchin-dominated alternative stable states (Folke *et al.*, 2004; Stewart and Konar, 2012; Filbee-Dexter and Scheibling, 2014) can be considered a collapse of the algal bed ecosystem (Chapman, 1981; Chapman and Johnson, 1990; Filbee-Dexter and Scheibling, 2014; Graham, 2004). Indeed, the lack of algal beds results in the reduction in fixed carbon and shelter availability which cascades up the food web negatively affecting higher trophic levels (Gaines and Roughgarden, 1987; Duggins *et al.*, 1989).

Although capelin eggs were only found adhered to *D. viridis* at three of the 25 sites this algal species was observed during 2019, citizen science reports of capelin beach spawning (www.ecapelin.ca) suggested that capelin likely did not move further north of our three spawning sites into Placentia Bay during this year. Additionally, although capelin eggs were only found adhered to *D. viridis* at these three sites during two out of three years, citizen science reports (www.ecapelin.ca) suggested lower spawning capelin biomass during the year when capelin spawn was not found adhered to this algal species (2020) relative to the two years when capelin eggs were found adhered (2019, 2021). These observations suggest that *D. viridis* may be used as an alternate subtidal spawning habitat when spawning capelin and this algal species co-occur and are both at least moderately abundant. The extent and consistency *D. viridis* is used as a spawning habitat by capelin is an important avenue for future research.

The high overlap between favourable habitat characteristics of incubating capelin eggs and *D. viridis* in coastal Newfoundland, including temperature (2–12°C; Penton and Davoren, 2012; Davoren, 2013; Crook *et al.*, 2017) and depth (< 40m; Penton and Davoren, 2012), suggest that the distribution of subtidal capelin spawning sites and that of *D. viridis* are similar. Current climate change models for Newfoundland predict that by 2063 bottom temperature will increase up to 0.4–2.1°C along the coast (Loder *et al*., 2013). Although capelin may be more likely to shift their range in response to this predicted change in ocean climate over the long-term (Rose, 2005), short-term responses may be habitat shifts within their current range. With continued increases in temperature and temperature variability at intertidal capelin spawning sites, capelin may initially occupy cooler subtidal habitat more relative to warm, beach spawning habitat to ensure offspring survival (Nakashima and Wheeler, 2002; Davoren, 2013; Penton and Davoren, 2013; Crook *et al.*, 2017). If spawning habitat is limited, as suggested by ongoing beach spawning habitat restoration work, this shift may lead to lower availability of favourable spawning habitat resulting in a recruitment bottleneck. The widespread distribution of *D. viridis* in nearshore regions (25 out of 136 sites; Fig. 2A), however, may reduce the chances of a climate change-induced bottleneck if subtidal beds of *D. viridis* are commonly used as spawning habitat by capelin. Alternately, as *D. viridis* is an annual species and is sensitive to variation in temperature (Blain and Gagnon, 2013; Gagnon *et al.*, 2013), the occurrence of this algal species may also decrease within their current range in the future. Nonetheless, as *D. viridis* is resistant to urchin grazing in areas with high wave action, this species may be able to colonize newly or highly disturbed areas with suitable temperature, thereby dynamically establishing favourable annual subtidal spawning habitat for capelin.

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Contributions

L.M.B. was responsible for data generation, survey design, project design, data analysis, fieldwork, and manuscript preparation. Further, L.M.B acquired additional funding from the University of Manitoba.

G.K.D. contributed to project design, acquired the majority of the funding from Fisheries and Oceans Canada through the Coastal Environmental Baseline Program, provided edits and feedback on the project as it developed and established the original idea for the project.

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