

Influence of spawning capelin *Mallotus villosus* on the distribution of green sea urchins *Strongylocentrotus droebachiensis* on the northeast Newfoundland coast

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ABSTRACT: Spawning capelin *Mallotus villosus* provide an abundance of nutrients in the form of fish eggs and dead fish that can be relied upon by numerous predatory and scavenging species. We investigated whether the annual resource pulse of spawning capelin influenced the distribution of green sea urchins *Strongylocentrotus droebachiensis* at capelin spawning sites on the northeast coast of Newfoundland, Canada. Sea urchin densities at capelin spawning sites were monitored using a remotely operated vehicle during the summers of 2013 and 2014 and were modeled against the presence or absence of substrate types (bedrock, cobble, and sediment waves) and food resources (capelin eggs, dead capelin, and drift algae). Mean (\pm SE) sea urchin densities associated with each predictor variable were highest on bedrock substrate (7.2 ± 0.6 urchins m^{-2}), dead capelin (3.7 ± 0.2 urchins m^{-2}), and drift algae (3.1 ± 0.2 urchins m^{-2}) and were <1.5 urchins m^{-2} on all other predictors. In accordance, transect segments containing bedrock, dead capelin, and drift algae were 3–20, 6–20, and 2–7 times more likely to have sea urchins, respectively. Contrary to what was predicted, transect intervals containing capelin eggs were 5–10 times more likely to have no sea urchins and had the lowest mean sea urchin densities out of all predictors (0.91 ± 0.1 urchins m^{-2}). In addition, sea urchins were more likely to be clumped in areas with patchily distributed food, with urchin clumps being 15–18 times more likely in areas with dead capelin and 4–9 times more likely in areas with drift algae. Overall, results suggest that capelin spawning provides an important food source for sea urchins in an otherwise nutrient-poor environment, and, additionally, that sea urchins may be important recyclers of capelin detritus.

KEY WORDS: Sea urchin · Capelin · Remotely operated vehicle · ROV · Transect · Density

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INTRODUCTION

Seasonal resource pulses that increase ecosystem productivity are important for numerous life processes of consumers in all ecosystems (Ostfeld & Keesing 2000, Yang et al. 2010). Pulse resources are especially important in nutrient-poor environments where food availability is scarce, and organisms residing in these habitats often exhibit greater responses to nutrient pulses and food subsidies (Anderson et al. 2008). For instance, the deep ocean

is extremely nutrient-poor, but whale carcasses that fall to the seafloor create entire ecosystems that can support communities for over a decade (Smith & Baco 2003). Similarly, annual spawning of anadromous salmon in the Pacific Northwest provides nutrients to freshwater scavengers as well as terrestrial animals and plants (Cederholm et al. 1999, Gende et al. 2004). Mobile consumers show the highest magnitude of response to pulse resources, due to their ability to move quickly to high resource areas, whereas slow-moving and sessile consumers only have access

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to nutrient subsidies deposited nearby (Yang et al. 2010).

In the northwest Atlantic, capelin *Mallotus villosus* is the main forage fish species (Carscadden & Vilhjálmsson 2002). Capelin mature and winter in areas near the continental shelf edge but migrate inshore in late spring and early summer to spawn (Nakashima 1992) at persistently used beach and deep (<50 m depth) water locations (Nakashima & Wheeler 2002, Penton & Davoren 2012). After capelin spawn, the substrate is covered in adherent capelin eggs (Nakashima & Wheeler 2002, Penton et al. 2012). Capelin eggs are energy-dense (Montevecchi & Piatt 1984) and provide an important food source for winter flounder *Pseudopleuronectes americanus* (Frank & Leggett 1984) and the amphipod *Calliopius laeviusculus*, whose fall biomass is correlated with capelin egg availability (DeBlois & Leggett 1993). High egg densities are often coupled with high densities of fish carcasses due to mass mortality of spawning capelin (Templeman 1948). The relative importance of capelin detritus in the diets of benthic invertebrate scavengers at spawning sites has not been examined; however, sea urchins have been observed scavenging on capelin carcasses discarded from fisheries (Himmelman & Steele 1971).

The green sea urchin *Strongylocentrotus droebachiensis* is common in inter- and sub-tidal marine habitats throughout its circumpolar distribution (Scheibling & Hatcher 2013). Green sea urchins are primarily found on hard substrates (i.e. bedrock or cobble) that provide a firm attachment surface (Himmelman 1986, Scheibling & Raymond 1990), as sea urchins on finer sediments are more vulnerable to dislodgement (Santos & Flammang 2006, 2007, Tuya et al. 2007, Kawamata et al. 2011) and movements are slower (Ebeling et al. 1985, Laur et al. 1986). Sea urchin densities vary with substrate type and depth, reaching densities in excess of 200 ind. m⁻² in dense foraging aggregations on rocky substrate (Meidel & Scheibling 2001) but are typically lower (<2 ind. m⁻²) on fine sediments in the deeper sub-tidal zone (>20 m depth; Filbee-Dexter & Scheibling 2012). Sub-tidal sand patches and rock outcrops are considered nutrient-poor habitats (Chapman 1981, Kelly et al. 2012), and sea urchins in these zones often rely on drift algal subsidies, evidenced by clumping on kelp that accumulates in sediment wave troughs (Britton-Simmons et al. 2009, Filbee-Dexter & Scheibling 2012), or on alternative prey when delivery of drift algae is infrequent (Kelly et al. 2012). Green sea urchins generally prefer a diet of macroalgae in most regions (Vadas 1977, Larson et al. 1980, Lemire &

Himmelman 1996, Lauzon-Guay & Scheibling 2007), but can consume a wide variety of animal protein (Himmelman & Steele 1971, Larson et al. 1980, Briscoe & Sebens 1988, Dumont et al. 2008). Kelly et al. (2012) provided evidence that sea urchins further away from kelp stands are more reliant on animal matter than on macroalgae. Even in cases when macroalgae are available, sea urchins aggregate in areas with abundant animal prey (e.g. fish carcasses near wharves; Himmelman & Steele 1971), illustrating that prey consumption is more related to availability of prey types rather than preference for specific prey types (Himmelman & Nédélec 1990).

The annual resource pulse of spawning capelin provides an abundance of capelin eggs and carcasses at spawning sites that may be important food for scavenging *S. droebachiensis*. We examined the influence this annual resource pulse has on the distribution of *S. droebachiensis* (hereafter referred to as 'sea urchins') at deep-water (15–40 m) capelin spawning sites that are otherwise nutrient-poor habitats. We hypothesized that the presence of food resources (i.e. capelin eggs, dead capelin, drift algae) and substrate type (i.e. bedrock, cobble, sediment waves) will influence sea urchin density (H_1) and dispersion (H_2) at deep-water spawning sites of capelin. We predicted that sea urchin densities would be higher when food resources and bedrock were present and, similarly, that sea urchins would be clumped more often when patchily distributed food (i.e. dead capelin, drift algae) and bedrock were present. Alternatively, we did not expect sea urchins to be clumped in areas with capelin eggs, as eggs are abundant and uniformly distributed at the scale of a spawning site when available. Overall, these results will illustrate whether the resource pulse of spawning capelin influences sea urchin distribution and provide insight into the ecological role of sea urchins at capelin spawning sites.

MATERIALS AND METHODS

Study area

Field work was conducted around a concentration of persistently used deep water (15–40 m) spawning sites of capelin off the northeast Newfoundland coast (Gull Island; 49° 15' N, 53° 25' W; Fig. 1) during July and August 2013 and 2014. Spawning beds are located in 100–150 m wide (Roy 2013) and >300 m long (K. A. Crook pers. obs.) depressions in the ocean floor that range from 2 to 10 m deeper than surround-

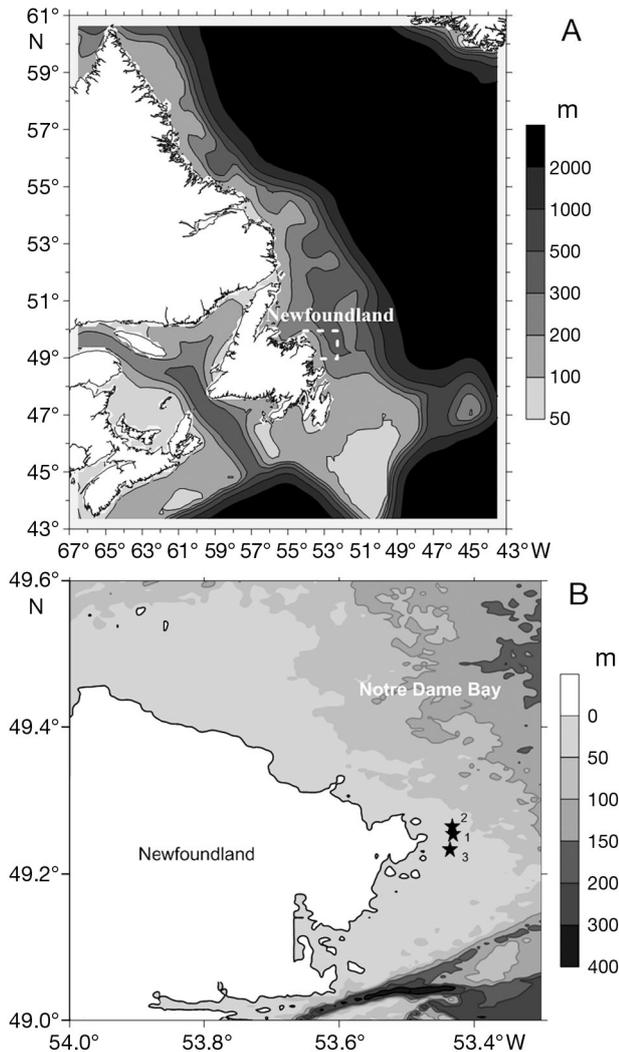


Fig. 1. Locations of (A) the study area (white box) on the northeast coast of Newfoundland (Canada) and (B) deep-water spawning sites (★) concentrated around Gull Island (Sites 1 and 2) and Site 3. Shading indicates depth contours

ing bedrock outcrops (Penton & Davoren 2012). Within depressions, the sediment consists primarily of coarse sand (sediment sizes ranging from 0.5–16 mm; Penton & Davoren 2012), which has been washed into waves with crests spaced ~1 m apart and troughs ~0.5–1 m deep. When capelin spawn, their eggs adhere to the substrate and remain at sites for 7 to 40 d, depending on water temperature (Penton et al. 2012). We focused on 3 spawning sites (Fig. 1); Site 3 was the shallowest (16–19 m), followed by Site 1 (24–27 m) and Site 2 (33–35 m). Sites 1 and 2 were located in close proximity around Gull Island (~400 m apart) and Site 3 was further away (~1.6 km from Gull Island). Water temperature varied among years, which likely caused capelin spawning activity

to differ among sites within and between years (Davoren 2013). Capelin spawned at Sites 1 and 2 in 2013 (mean \pm SE water temperature at Site 1: $4.66 \pm 0.07^\circ\text{C}$) but not in 2014 due to water temperatures ($0.92 \pm 0.05^\circ\text{C}$) below the estimated temperature threshold for capelin (2°C ; G. K. Davoren unpubl. data). Spawning only occurred at Site 3 in 2014 despite mean water temperature being within the 2 to 12°C range in both years (2013: $7.52 \pm 0.09^\circ\text{C}$; 2014: $4.95 \pm 0.08^\circ\text{C}$). Water temperature data were not available for Site 2 but were likely similar to those observed at Site 1.

Video transects

Sea urchin densities at capelin spawning sites were quantified during transects using a remotely operated vehicle (ROV; VideoRay Pro 3 GTO) equipped with an underwater video camera. A 300 m tether connected the ROV to the control box onboard a 13 m commercial fishing vessel, displaying real-time video along with ROV depth (m) and heading (degrees), which were recorded on a camcorder for later analysis. The ROV was deployed off the starboard side of the vessel every 3 to 5 d throughout July and early August 2013 and 2014 ($8\text{--}10 \text{ d yr}^{-1}$). Transects were established at Sites 1 and 2 in both years but at Site 3 only in 2014 owing to differences in site use by spawning capelin. At least 2 transects were surveyed at each site on all sampling days: one moving north–south and another moving east–west. When sediment waves were present, east–west transects ran parallel to wave troughs and north–south transects ran perpendicular to sediment waves. When time allowed, a third north–south transect was conducted at the opposite end of the site to the previous north–south transect. The ROV heading was kept as constant as possible for the duration of each transect. To accurately identify sea urchins on the bottom, ROV depth was maintained at $<1 \text{ m}$ above the seafloor. Transect segments were excluded from analyses if the ROV was $>1 \text{ m}$ from the seafloor, could not maintain a consistent speed (i.e. high current), had moved off-site, or if visibility prevented reliable sea urchin counts. Although the tether length was fixed (300 m), transect length was variable as a result of surface currents, tidal currents, and wind causing the boat to drift. The date, site number, start/end times, start/end latitude and longitude, and heading were recorded on datasheets for each transect. The ROV was deployed at the same approximate location (latitude and longitude) at each site on

each sampling day; however, transects were not treated as repeated measures because they did not cover the exact same area due to varying boat drift across sampling days.

Transect analysis

Sea urchins were counted using the strip-transect method (Burnham & Anderson 1984), counting only sea urchins that passed through the bottom of the screen during video playback. Transects were analyzed in 2 s intervals which encompassed approximately 1 m² of seafloor (ROV speed ~1 m s⁻¹; field of view ~0.5 m wide). The number of sea urchins m⁻² was counted and the presence or absence of abiotic and biotic factors was simultaneously recorded. Factors of interest were bedrock, cobble, capelin eggs, dead capelin, drift algae, sediment waves, and sea urchin predators. When sediment waves were present, the number of sea urchins in troughs (i.e. bottom half of the wave) and on crests (i.e. top half of the wave) were recorded separately. Sea urchin dispersion patterns were also recorded as the presence or absence of sea urchin clumps (i.e. ≥3 sea urchins in physical contact with one another), defined to ensure 'clumped' sea urchins were using the same spatially limited resource (e.g. dead capelin). When possible, which predictor the sea urchins were clumped on was identified and recorded. During transects where the site edge (i.e. bedrock cliffs) was observed and the ROV was moving perpendicular to the edge, distance from the site edge was determined for each transect segment by setting the video time at the edge to 0 and increasing in 2 s (~2 m, ROV speed ~1 m s⁻¹) intervals as the ROV moved away from the edge.

Data analysis

Sea urchin counts had a skewed distribution, with 58.2% of all 1 m² transect segments containing zero sea urchins (Fig. 2). The high number of zeroes prevented analysis using generalized linear models as the data were overdispersed for both Poisson and negative binomial distributions. When sea urchins were observed in transect segments, they were most often observed at low densities, with 88.1% of 1 m² transect segments containing ≤3 sea urchins (Fig. 2). Thus, sea urchin density was categorized as presence or absence of sea urchins in transect segments. Generalized estimating equations were used to examine the autocorrelation structure in the data follow-

ing Zuur et al. (2009), and the independent error structure provided the best fit. Therefore, adjacent transect segments were treated as independent observations.

To test whether food resources or substrate type influenced sea urchin density (H_1), the odds of encountering sea urchins in transect segments were modeled using logistic regression with the presence or absence of substrate types (bedrock, cobble, and sediment waves) and food resources (capelin eggs, dead capelin, and drift algae) as predictor variables (Fig. 3). Potential sea urchin predators observed included ocean pout *Zoarces americanus*, sculpin (*Myoxocephalus* spp.), toad crabs *Hyas araneus*, rock crabs *Cancer irroratus*, and seastars *Asterias rubens*; however, even when combined, they were only observed in 1% of transect segments. Thus, the presence of predators was not included as a predictor in the analyses. Given that site use by spawning capelin differed among years, Site 3 was analyzed separately from Sites 1 and 2 (hereafter referred to as 'Gull Island' sites). The logistic regression for Gull Island sites also included site (Site 1/Site 2) and year (2013/2014) as predictor variables. For H_2 , logistic regressions were performed with the same predictors described above to determine whether the presence of food resources or substrate types influenced sea urchin dispersion. Only transect segments containing >2 urchins m⁻² were included in the analysis with sea urchin dispersion being considered 'clumped' or 'not clumped' in each segment. The best model for each analysis was chosen using Akaike's information criterion (AIC) with plausible models being considered if ΔAIC was <2. In the case of multiple plausible models, the most parsimonious model was consid-

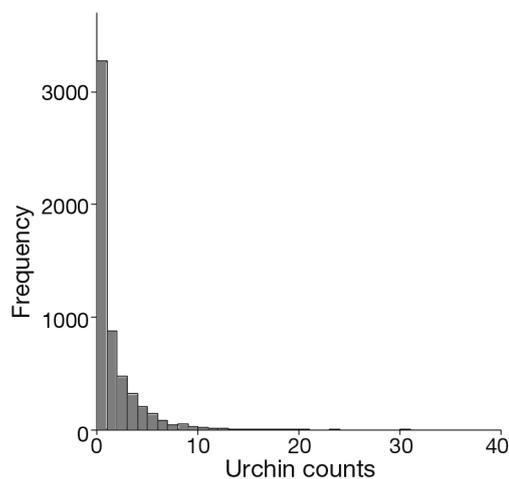


Fig. 2. Frequency of green sea urchin *Strongylocentrotus droebachiensis* counts in all 1 m² transect segments

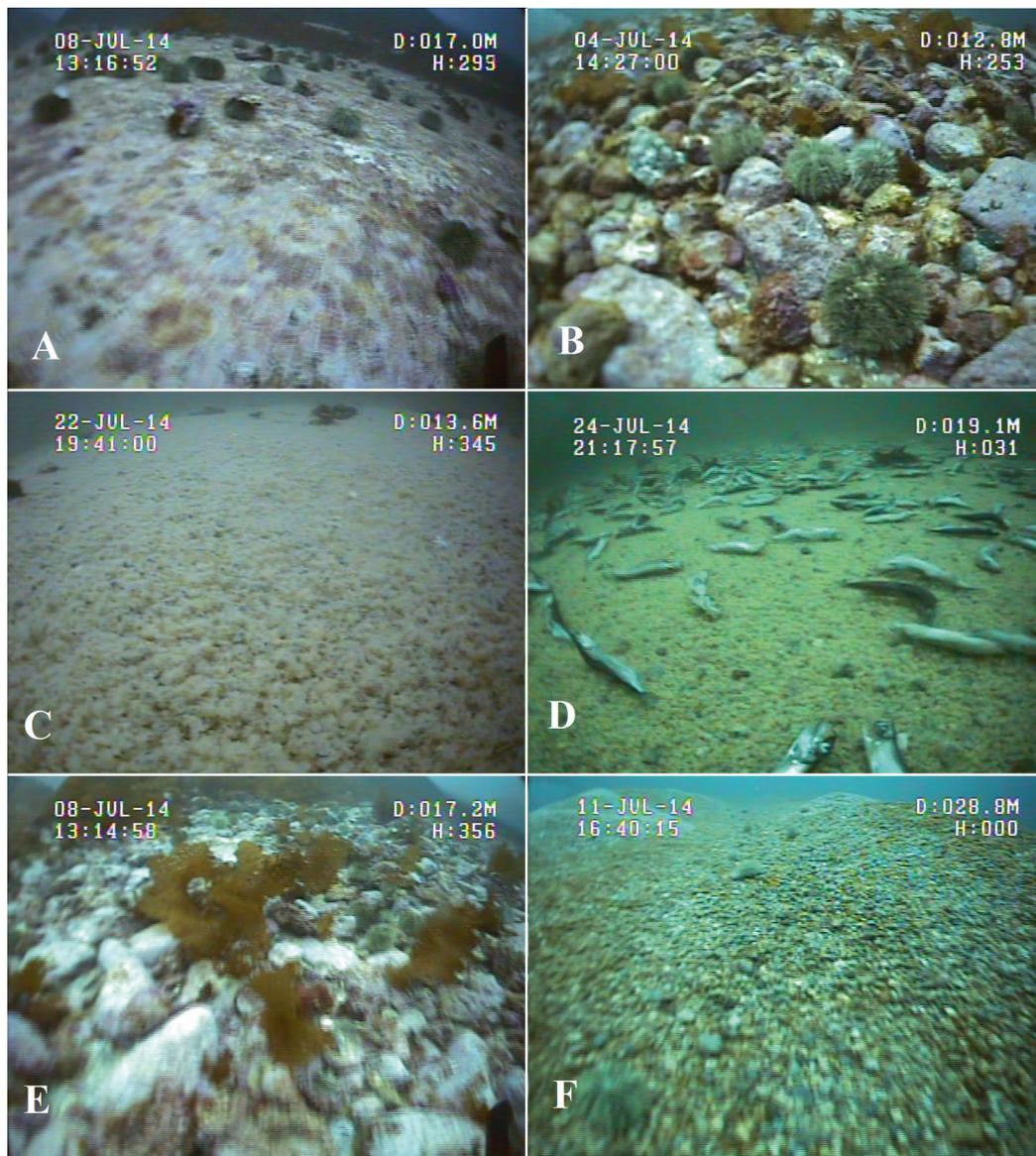


Fig. 3. Screenshots showing predictor variables: (A) bedrock, (B) cobble, (C) capelin eggs, (D) dead capelin, (E) drift algae, and (F) sediment waves observed during remotely operated vehicle transects

ered the best model. Variance inflation factors for predictor variables in all analyses were small (<3.5), indicating no collinearity among variables. All statistical analyses were performed using R statistical software v3.1.3 (R Core Team 2015) and the 'car' (Fox & Weisberg 2011), 'pgirmess' (Giraudoux 2014), 'MASS' (Venables & Ripley 2002), and 'geepack' (Højsgaard et al. 2006) packages.

To determine whether distance from the site edge influenced sea urchin density, transect segments were divided into 3 categories: close (0–62 m), mid (63–155 m), and far (≥ 156 m) from the site edge. Distance categories were defined to include an equal

number of 2 m segments in each category. These data were then analyzed separately due to the limited number of transects fitting the criteria for measuring distance to the site edge. A Kruskal-Wallis test and post hoc pairwise comparisons were used to determine significance and between-group differences, as sea urchin counts could not be normalized. Similarly, sea urchin counts in troughs versus on crests were analyzed using Wilcoxon signed-rank and rank sum tests to determine if sea urchins were aggregating in sediment wave troughs. A sequential Bonferroni correction was applied to multiple Wilcoxon tests to avoid inflating the probability of type I error.

RESULTS

A total of 88 transects were surveyed (40 in 2013, 48 in 2014), of which 64 were used in the analyses (27 in 2013; 37 in 2014; Table 1). In 2013, the majority of transects were at Site 1 (Table 1) owing to difficulty maintaining the ROV ≤ 1 m from the seafloor due to greater water depth at Site 2 (>30 m deep). In 2014, the majority of transects were conducted at Site 3 and fewer at Sites 1 and 2 (Table 1). Sea urchin density (ind. m^{-2}) differed significantly between sites in 2013 ($W = 312145.5$, $p < 0.0001$) and among sites in 2014 ($\chi^2_2 = 57.78$, $p < 0.0001$). In both years, sea urchin density was significantly higher at Site 2 relative to other sites but did not differ between Sites 1 and 3 in 2014 (Fig. 4). Sea urchin densities were also significantly higher at Site 2 in 2013 than in 2014 ($W = 1527781$, $p < 0.0001$) but did not differ between years at Site 1 (Fig. 4).

Table 1. Number of days on which ROV transects were conducted, total number of transects, and the mean \pm SE number (and range) of 1 m^2 segments per transect at each spawning site of capelin *Mallotus villosus* in 2013 and 2014

Year	Site	Transect days	Total no. transects	No. transect segments
2013	1	9	20	76.7 ± 8.54 (23–132)
	2	5	7	77.9 ± 17.1 (20–141)
2014	1	5	11	96.2 ± 15.3 (30–204)
	2	3	7	70.1 ± 14.2 (23–138)
	3	8	19	102 ± 11.4 (9–190)

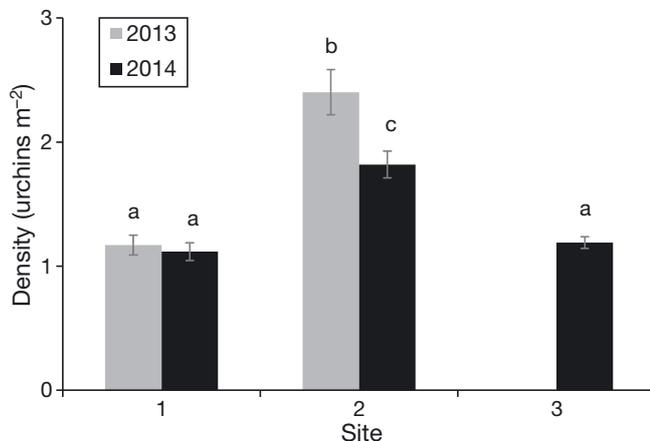


Fig. 4. Mean \pm SE green sea urchin *Strongylocentrotus droebachiensis* density in 1 m^2 transect segments at each sampled deep-water spawning site of capelin *Mallotus villosus* (see Fig. 1 for site locations). Bars not sharing the same letter differed significantly at $\alpha = 0.05$

Table 2. Percentage of 1 m^2 transect segments containing each predictor variable in 2013 at Sites 1 and 2, and in 2014 at Sites 1, 2, and 3. Rows do not add up to 100% because predictor variables were often observed together

Year	Site	Bedrock	Cobble	Capelin eggs	Dead capelin	Drift algae	Sediment waves
2013	1	1.20	31.4	73.8	8.15	3.10	31.1
	2	5.13	11.2	83.5	5.49	4.58	15.6
2014	1	0.66	30.4	0.00	1.23	2.08	76.3
	2	9.17	24.4	0.00	0.00	11.0	83.7
	3	2.06	52.6	38.2	12.8	18.4	38.0

Bedrock was the least common substrate type on capelin spawning sites and was most commonly observed at Site 2 (Table 2). Cobbles and sediment waves were encountered in a higher proportion of transect segments, with cobbles being most common at Site 3 and sediment waves being most common at Gull Island sites in 2014 (Table 2). Although bedrock was the least common substrate type, mean (\pm SE) sea urchin densities were highest in transect segments containing bedrock (7.19 ± 0.57 urchins m^{-2}) but were near average when cobbles and sediment waves were present (Fig. 5). Capelin eggs were the most commonly observed food resource relative to dead capelin and drift algae (Table 2), both of which were more patchily distributed over the spawning sites. The presence of dead capelin and capelin eggs differed among years at Gull Island sites because capelin only spawned at those sites in 2013. Mean sea urchin densities were higher than average when dead capelin and drift algae were present (3.68 ± 0.21 and 3.10 ± 0.16 urchins m^{-2} , respectively), but were below average when capelin eggs were present (0.91 ± 0.05 urchins m^{-2} ; Fig. 5).

The best logistic regression model predicting sea urchin presence included all predictor variables at Gull Island sites and all variables except cobble at Site 3. At Gull Island sites, the presence of bedrock in transect segments increased the odds of encountering sea urchins by 20.0 times relative to when bedrock was absent (Table 3). The presence of patchily distributed food resources (dead capelin and drift algae) also increased the odds of encountering sea urchins by 6.18 and 2.42 times, respectively (Table 3). At Site 3, the presence of dead capelin and drift algae had the strongest influence, increasing the odds of encountering sea urchins by 19.5 and 7.42 times, respectively, relative to when absent (Table 3). Transect segments containing bedrock also increased the odds of encountering sea

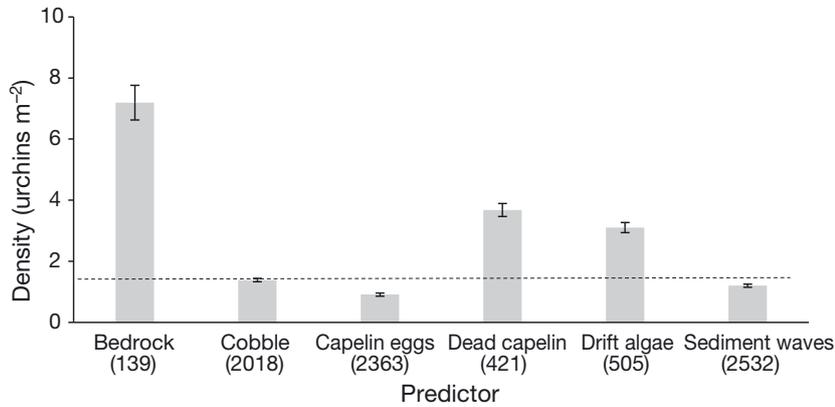


Fig. 5. Mean \pm SE green sea urchin *Strongylocentrotus droebachiensis* density in 1 m² transect segments in which each predictor variable was present. Numbers in parentheses indicate the total number of transect segments containing each predictor variable. Dashed line indicates the mean sea urchin density across all transect segments (1.34 ± 0.04 urchins m⁻²)

Table 3. Odds ratios (OR) and 95% confidence intervals (CI) for predictor variables that increased (+) or decreased (-) the odds of encountering green sea urchins *Strongylocentrotus droebachiensis* when present in 1 m² transect segments at Gull Island sites (Sites 1 and 2: 2013, 2014) and Site 3 (2014). Site comparisons are for Site 2 relative to Site 1 and Year for 2013 relative to 2014. Note that all confidence intervals exclude 1 and, thus, are deemed significant at $\alpha = 0.05$

Predictor	Gull Island			Site 3		
	OR	95% CI	Influence	OR	95% CI	Influence
Bedrock	20.0	(8.16, 66.26)	+	3.10	(1.31, 8.55)	+
Cobble	1.36	(1.14, 1.61)	-			
Eggs	5.12	(3.93, 6.66)	-	9.52	(7.12, 12.75)	-
Dead capelin	6.18	(4.23, 9.24)	+	19.5	(12.61, 30.93)	+
Sediment waves	2.05	(1.67, 2.53)	-	1.90	(1.49, 2.41)	-
Drift algae	2.42	(1.67, 3.57)	+	7.42	(5.26, 10.63)	+
Site (Site 2)	2.55	(2.18, 2.99)	+			
Year (2013)	1.55	(1.24, 1.93)	+			

urchins by 3.10 times. Contrary to what was predicted, the presence of capelin eggs significantly decreased the odds of encountering sea urchins at all sites (5.12 and 9.52 times at Gull Island sites and Site 3, respectively; Table 3). Sea urchins were also more likely to be absent in transect segments with sediment waves at all sites (Table 3). There was a small positive influence of cobble on sea urchin presence at Gull Island sites (1.36 times) but cobble was excluded from the best model at Site 3. Both year and site influenced the odds of encountering sea urchins at Gull Island sites, with urchins 2.55 times more likely to be present at Site 2 than at Site 1 and 1.55 times more likely to be present in 2013 versus 2014 (Table 3).

Although sea urchins were less likely to be found in transect segments with sediment waves, when sea

urchins were present, densities were significantly higher in sediment wave troughs relative to on crests both when food (i.e. dead capelin or drift algae) was absent in the trough ($V = 261641$, $p < 0.0001$) and when food was present ($V = 10254.5$, $p < 0.0001$; Fig. 6). Sea urchin densities in sediment wave troughs were higher when food was present relative to when food was absent ($W = 154542.5$, $p < 0.0001$). The presence of food resources in sediment wave troughs also influenced sea urchin densities on wave crests, with densities on the crest being lower when food was present in the troughs ($W = 277616$, $p = 0.0003$; Fig. 6).

In total, 14 ROV transects were examined to determine whether proximity to the site edge influenced sea urchin density at deep-water spawning sites of capelin. Sea urchin density differed significantly among the 3 proximity categories ($\chi^2_2 = 96.67$, $p < 0.0001$). Pairwise comparisons revealed that sea urchin density was highest close to the site edge (2.36 ± 0.17 urchins m⁻²) and decreased further away from the edge (mid: 1.68 ± 0.15 urchins m⁻²; far: 0.72 ± 0.07

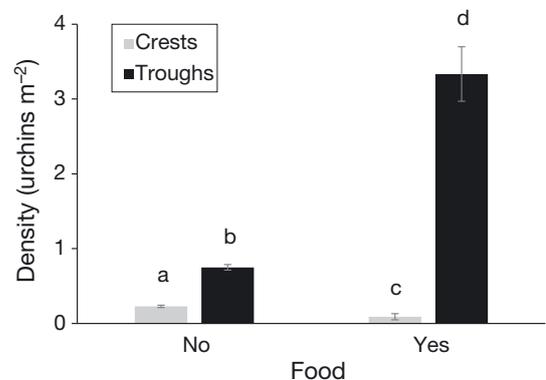


Fig. 6. Mean \pm SE green sea urchin *Strongylocentrotus droebachiensis* density in sediment wave troughs and on crests in 1 m² transect segments when food (dead capelin *Mallotus villosus* or drift algae) was present ('yes') or absent ('no') from wave troughs. Bars not sharing the same letter differed significantly at $\alpha = 0.05$

urchins m^{-2}). In one transect off the spawning site (not included in analyses), sea urchin density was much higher off-site on bedrock outcrops (24.1 ± 2.7 urchins m^{-2} ; $n = 64$ transect segments) than on the spawning sediment (1.1 – 2.4 urchins m^{-2}). The highest observed off-site density was 95 urchins m^{-2} , but this is likely an underestimate due to difficulty counting urchins when densities exceeded 30 urchins m^{-2} .

Which resource sea urchins were clumped on could be determined in 80% of transect segments containing urchin clumps. Of these, 86.4% of clumps occurred on dead capelin (44.8%), drift algae (25.6%), or both dead capelin and drift algae (16%). Similarly, presence of dead capelin and drift algae in transect segments were the best predictors of urchin clumps in logistic regression models. The odds of encountering sea urchin clumps were 18.3 and 8.77 times higher when dead capelin and drift algae were present at Gull Island sites and 14.9 and 4.39 times higher, respectively, at Site 3 (Table 4). The best logistic regression model for Gull Island sites also included bedrock and year as significant predictors of urchin clumps with cobble and capelin eggs being non-significant (Table 4). Sea urchin clumps were 4.93 times more likely in transect segments containing bedrock and 6.01 times more likely in 2013 relative to 2014 (Table 4). At Site 3, bedrock and cobble were excluded from the best logistic regression model but capelin eggs and sediment waves were included. The presence of capelin eggs and sediment waves at Site 3 increased the odds of encountering sea urchin clumps by 5.67 and 2.56 times, respectively (Table 4).

Table 4. Odds ratios (OR) and 95% confidence intervals (CI) for predictor variables that increased (+) or decreased (–) the odds of encountering green sea urchin *Strongylocentrotus droebachiensis* clumps (i.e. ≥ 3 sea urchins in physical contact) in 1 m^2 transect segments at Gull Island sites (Sites 1 and 2: 2013, 2014) and Site 3 (2014). Year comparisons are for 2013 relative to 2014. Confidence intervals excluding 1 are deemed significant at $\alpha = 0.05$ and are indicated in **bold**

Predictor	Gull Island			Site 3		
	OR	95% CI	Influence	OR	95% CI	Influence
Bedrock	2.14	(1.11, 4.10)	+			
Cobble	1.58	(0.91, 2.72)	+			
Eggs	1.49	(0.88, 2.54)	+	5.67	(2.84, 11.84)	+
Dead capelin	18.30	(9.60, 37.27)	+	14.87	(7.89, 29.45)	+
Drift algae	8.77	(4.44, 17.79)	+	4.39	(2.38, 8.45)	+
Year (2013)	6.01	(3.18, 11.35)	+			
Sediment waves				2.56	(1.25, 5.39)	+

DISCUSSION

Mean sea urchin densities observed at deep-water spawning sites of capelin (1.1 – 2.4 urchins m^{-2} ; Fig. 4) are similar to those observed on fine sediment at similar depths in other regions (e.g. St. Margarets Bay, Nova Scotia: 2 urchins m^{-2} ; Filbee-Dexter & Scheibling 2012). Sand is thought to be less preferred by sea urchins than hard substrates, such as cobble or bedrock (Himmelman 1986, Scheibling & Raymond 1990), as sea urchins cannot attach to sand well (Kawamata et al. 2011) and may have decreased locomotory ability (Ebeling et al. 1985, Laur et al. 1986). Indeed, sea urchins were most likely to be encountered in areas with bedrock, and sea urchin densities were highest in segments containing bedrock. On finer sediment, urchin densities were lower, as were the odds of encountering urchins, suggesting sea urchins that encounter areas of bedrock when moving over fine substrates may remain there until some stimulus causes them to leave. Similarly, Blicher et al. (2007) found that sea urchin abundance in the high Arctic was directly related to the amount of rocky substrate available. Interestingly, bedrock was more commonly observed at Site 2 than at Site 1, which may have contributed to sea urchins being encountered in higher densities at Site 2. Along the borders of the spawning site, sea urchins were observed in high densities on bedrock cliffs where the rock met the fine sediment of the capelin spawning sites. These high densities on the site edge visually resembled a foraging front (Meidel & Scheibling 2001), although movement could not be determined and no kelp was associated with the aggregation. Ebeling et al. (1985) observed foraging fronts of *Strongylocen-*

trotus franciscanus on the California (USA) coast being halted where bedrock met sandy substrate, with sea urchins only moving onto the sand when drift algal subsidies became available. This suggests that food availability on spawning sites may influence individual-level decisions of sea urchins to leave bedrock substrate and move onto sandy substrate.

In transects where the site edge was observed, sea urchin density was highest close to the edge but decreased as distance from the edge increased. The relationship between sea urchin density and distance from the bedrock edge

suggests that sea urchins clumped at the rock–sand interface may slowly be dispersing onto the spawning sediment. Dispersed browsing is a foraging strategy whereby mobile sea urchins in low densities rely on food sources other than kelp stands (Scheibling & Hatcher 2013). In the present study, sea urchins were encountered and were clumped more often in areas with dead capelin and drift algae, suggesting that urchins dispersed over the spawning site are being attracted to patchily distributed food resources. Despite the capability of sea urchins to detect prey sources using chemosensation from distances of several meters (Vadas 1977, Larson et al. 1980, Bernstein et al. 1981, 1983, Klinger & Lawrence 1985, Vadas et al. 1986, Briscoe & Sebens 1988), dispersing urchins typically exhibit random movements and do not move directly to available food sources (Lauzon-Guay et al. 2006, Dumont et al. 2007). Locating the source of a chemical signal can be difficult in natural settings with turbulent flow, such that urchins may rely more on kinesis to locate prey (Lauzon-Guay et al. 2008, Harding & Scheibling 2015); however, chemical cues emanating from a prey item are stronger when another sea urchin is consuming it (Garnick 1978). Thus, the foraging activity of sea urchins may release chemical cues detectable from greater distances that may attract other urchins to forage in the same location. If dead capelin accumulate close to the site edge and are encountered and fed upon by sea urchins, this may create enough of a chemical cue for urchins to move off the bedrock cliffs to forage on the spawning site.

Dispersed browsing over fine sediments may be energetically expensive due to reduced locomotory ability (Laur et al. 1986). Therefore, once sea urchins reach a certain distance from the site edge or cannot detect prey cues, they may switch to a passive feeding strategy. Passive detritivory is characterized by seeking shelter in topographic refuges and relying on food items that settle after drifting in ocean currents (Scheibling & Hatcher 2013). Several studies have shown that sea urchins in low-productivity habitats rely on drift algal subsidies that settle in sediment waves or rock outcrops (Filbee-Dexter & Scheibling 2012, Kelly et al. 2012). While sediment waves did not strongly influence sea urchin density along transects in the present study, significantly higher sea urchin densities were observed in the troughs of sediment waves relative to on the crests, possibly providing refuge from ocean currents. In addition, densities in the troughs were higher still when dead capelin or drift algae were present in the wave trough. Therefore, sea urchins aggregated in troughs may represent those using a passive feeding strategy, re-

lying on drift algal subsidies or dead fish that accumulate in the sediment wave troughs. A similar strategy may be employed by sea urchins clumped on small patches of bedrock situated within patches of spawning sediment. Generally, food supply in this type of habitat is low, but dead capelin and capelin eggs provide a pulse of protein-rich food that sea urchins on spawning sites can rely on while available.

Interestingly, sea urchin density was lowest and urchins were less likely to be encountered when capelin eggs were present. Sea urchins feed more efficiently on food that is attached to the substrate (Himmelman 1984, Dumont et al. 2008) and although capelin eggs adhere to the substrate (Penton & Davoren 2012), the small size of the sediment may not fix eggs strongly enough for sea urchins to consume them efficiently. While dead capelin and drift algae are also not fixed to the substrate, sea urchins clumped on these resources may provide enough stability for sea urchins to consume them efficiently. Due to the small size of capelin eggs (0.5–0.8 mm; Penton & Davoren 2013) as well as high egg densities (~1500 eggs cm⁻²; Penton et al. 2012) distributed uniformly over a spawning site, clumping on eggs would unlikely improve sea urchin foraging efficiency. Indeed, sea urchin clumping was not influenced by capelin eggs at Gull Island sites, but was positively influenced by eggs at Site 3. This apparent discrepancy may be due to difficulty determining what sea urchins were clumped on, which was the case in 20% of transect segments with sea urchin clumps. Thus, it is likely that sea urchins were actually clumped on dead capelin or drift algae, which was obscured by the urchin clump, when clumps were observed in the presence of capelin eggs. In addition, the chemical compounds in some fish eggs are insoluble in water and detectability of eggs decreases once the eggs have become water-hardened (Dittman et al. 1998). Strength of chemical cues emanating from capelin eggs has not been studied; however, results from the present study suggest the chemosensory cues emanating from dead capelin or drift algae may be stronger than eggs. Overall, the apparent lack of preference for capelin eggs may be due to decreased detectability and palatability of eggs, although this requires further study.

The observed sea urchin densities at deep-water spawning sites of capelin in the present study are similar to previous estimates of sea urchin density on sub-tidal sandy bottom. On a fine scale within spawning sites, sea urchin density is concentrated in areas with bedrock substrate and patchily distributed food resources, primarily dead capelin and drift

algae. The observed pattern of sea urchin distribution suggests that these sea urchins have flexible feeding strategies, which appeared to be primarily influenced by the availability of dead capelin and drift algae. Future studies should examine the influence of spawning capelin on a larger scale, particularly to investigate whether sea urchins migrate onto spawning sites from adjacent bedrock cliffs once capelin resources become available. Our findings also show that sea urchins may consume more dead capelin than drift algae and capelin eggs. Sea urchins have rapid gut passage times (Lawrence et al. 2013), and consumption of capelin detritus may aid in the nutrient recycling process through release of fecal pellets. With warming ocean temperatures, capelin are predicted to rely more heavily on deep-water spawning relative to beach spawning (Nakashima & Wheeler 2002, Davoren 2013), which may increase the importance of nutrient recycling by sea urchins. Reliance on annual forage fish subsidies by sea urchins has not been explored in many habitats and may be a common occurrence throughout their range. Future studies examining sea urchin diets throughout their range, specifically where sea urchins overlap with forage fish spawning activities, may reveal that sea urchins play a more important role as nutrient recyclers in marine ecosystems than previously thought.

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