

FEATURE ARTICLE



Cannibalism among green sea urchins *Strongylocentrotus droebachiensis* in the laboratory and field

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ABSTRACT: The green sea urchin *Strongylocentrotus droebachiensis* plays an important ecological role as a consumer of kelp in temperate subtidal ecosystems, but is known to be omnivorous, and recent studies suggest it is potentially cannibalistic. This study examined cannibalism of small juvenile *S. droebachiensis* by larger conspecifics in the laboratory, and estimated rates of inter-cohort cannibalism in the field based on gut contents of adult sea urchins collected from subtidal sites in the Mingan Archipelago, St. Lawrence Estuary, Canada. Initial 48 h trials investigated factors (substratum, presence of food) that may influence cannibalism, and a subsequent 4 wk laboratory experiment found that adults and larger juveniles consumed 21 and 24% of small juveniles (3.5–6 mm test diameter), respectively, on cobble substratum when kelp was provided ad libitum. Frequencies of cannibalism from gut contents of urchins in the field were combined with an estimate of gut passage time determined in the laboratory and the densities of sea urchins at each site to estimate rates of cannibalism. The proportion of adults that had cannibalized ranged from (mean \pm SD) 0 ± 0 to 0.31 ± 0.12 across sites in 2013 and 2014, resulting in estimated rates of cannibalism from 0 ± 0 to 68.3 ± 0.60 small juveniles cannibalized $m^{-2} wk^{-1}$. This is the first study to report size-structured cannibalism among *S. droebachiensis*, and suggests that cannibalism can be a major source of mortality for small juvenile sea urchins in subtidal barren grounds.

KEY WORDS: Sea urchin · Cannibalism · *Strongylocentrotus droebachiensis* · Omnivorous · Gut analyses

INTRODUCTION

Subtidal temperate kelp beds are among the most productive communities on the planet (Mann 1973).



Dense aggregations of green sea urchins at subtidal sites in the Gulf of the St. Lawrence may promote cannibalism through increased conspecific interactions and competition for scarce kelp.

Photo: K. MacGregor

Kelp beds support complex food webs and provide habitat for many animal species (Steneck et al. 2002, Salomon et al. 2008). Globally, sea urchin herbivory has transformed large areas of kelp beds into coral-line algae-dominated 'barren grounds' (Breen & Mann 1976, Foreman 1977, Graham 2004, Foster & Schiel 2010).

Factors that regulate sea urchin population size are of ecological relevance because of the key role sea urchins play in reducing kelp abundance. Sea-urchin population is determined by the number of recruits and mortalities (Pfister & Bradbury 1996, Steneck et al. 2013). Recruitment reflects larval supply, settlement, and the survival and growth of newly settled juveniles (Cameron & Schroeter 1980). Predation by carnivores, such as crabs and shrimp, is an important source of mortality for the green sea urchin *Strongylo-*

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centrotus droebachiensis shortly after settlement (McNaught 1999, Scheibling & Robinson 2008). Small juvenile *S. droebachiensis* (3–6 mm test diameter [TD]) are also vulnerable to predation by rock crabs (*Cancer irroratus*), juvenile lobsters (*Homarus americanus*), and juvenile sculpins (*Myoxocephalus octodecemspinosus*), which can significantly reduce the abundance of recruits in the laboratory (Scheibling & Hamm 1991). Although predation by carnivores is the most frequently cited cause of post-settlement mortality for sea urchins, omnivorous grazers have recently been recognized as a potentially important source of mortality (Jennings & Hunt 2011). A field experiment in the Bay of Fundy, Canada (Jennings & Hunt 2011), and subsequent laboratory experiment (Jennings & Hunt in press) suggested that juvenile *S. droebachiensis* are a source of mortality for smaller conspecifics, though it is unclear whether the mortality occurred through 'bulldozing' (inadvertent crushing), or ingestion.

Cannibalism has been reported in several taxa of marine benthic invertebrates, including crabs (Luppi et al. 2001, Moksnes 2004, Long et al. 2012), lobsters (Jones 2009), gastropods (Kelley 1991, Kingsley-Smith et al. 2005, Chiu et al. 2010), polychaetes (Herringshaw et al. 2010), the sea urchins *Strongylocentrotus purpuratus* (Sonnenholzner et al. 2011) and *Lytechinus variegatus* (Richardson et al. 2011), and, occasionally, in sea stars (Witman et al. 2003). For many of these taxa, cannibalism can cause high mortality, particularly at the time of settlement or shortly afterwards—for example, up to 74% of crab settlers were cannibalized after 3 d in the field (Moksnes 2004). Settling cohorts of benthic marine invertebrates are particularly vulnerable to cannibalism due to the high density of the settlers, and the size asymmetry between established conspecifics and settlers. The high density of the cohort of new settlers may promote cannibalism either as a byproduct of normal feeding behavior (because frequent conspecific interactions can result in consumption) (Polis 1981), or through high levels of stress caused by crowding (Richardson et al. 2011), or as a manifestation of intense competition for limiting resources (e.g. Polis 1981, Witman et al. 2003). The large size-difference between the adults and recent settlers can also facilitate cannibalism. All species have a 'predation window', defined as the threshold size-difference between a predator and its prey, above which predation can occur (Claessen et al. 2002). Body size may be the main determinant of the prey items a given individual can consume, and may be more important than the species of the prey (Polis & Holt 1992, Woodward & Hildrew 2002). For sea urchin species, it has

not yet been investigated whether size-asymmetry facilitates higher levels of cannibalism.

Although there have been observations of adult *Strongylocentrotus droebachiensis* cannibalizing other individuals of the same size in the subtidal zone (Himmelman & Steele 1971), cannibalism has not been quantified for any sea urchin species in the field. This paper investigates the prevalence of cannibalism of small juvenile green sea urchins, *S. droebachiensis*, by larger conspecifics in the laboratory and the field. Cannibalism on small juvenile urchins (3.5–6 mm TD) was first investigated in the laboratory. Trials (48 h) were performed to determine if inter-cohort cannibalism occurs among *S. droebachiensis*, and to examine potential factors (the size of the urchin cannibal, the presence of alternate food, and substratum) affecting the level of cannibalism. A longer-term experiment determined the amount of inter-cohort cannibalism (by adults and large juveniles on small juveniles) after 4 wk under conditions similar to the field (cobble substratum with kelp was provided as an alternate food source). Gut analyses were then performed on adult urchins collected from 5 subtidal sites in the St. Lawrence estuary, in 2013 and 2014. Gut analyses are an effective method of determining the major predators of sea urchins in the field (Ojeda & Dearborn 1991, Clemente et al. 2010). In the present study, gut analyses along with gut passage time determined in the laboratory, and sea urchin densities from the field, were used to estimate the rate of cannibalism at the 5 sites. This is the first study to quantify cannibalism rates of a sea urchin species in the field.

MATERIALS AND METHODS

Cannibalism among green sea urchins in the laboratory

Specimen collection

Small juvenile (3.5–6 mm test diameter [TD]), large juvenile (15–20 mm TD), and adult (30–60 mm TD) green sea urchins *Strongylocentrotus droebachiensis* were collected at Pointe Mitis (48.6872°N, 68.0166°W), QC, Canada in the St. Lawrence estuary by SCUBA divers. Sea urchins were held in tanks at the Institut Maurice Lamontagne, Department of Fisheries and Oceans Canada (IML), in Mont Joli, QC, for an acclimation period of at least 48 h prior to experiments.

The small juveniles were likely to have been at least 1 yr old as no sea urchin settlement was

detected in collectors deployed at Pointe Mitis over the spring and summer prior to the experiment (K. LeGault unpubl. data). There is no information about the post-settlement growth rates of *S. droebachiensis* in the St. Lawrence estuary, but 3.5 to 6 mm is within the size range of 1-yr-old sea urchins on the Atlantic coast of Nova Scotia (Raymond & Scheibling 1987) and in the Bay of Fundy, NB (Jennings 2011).

Sand and cobbles (6–12 cm length) were collected on the shore by IML for use as substrata for the laboratory experiments. Kelps *Laminaria digitata*, *Saccharina latissima* and *Alaria esculenta* were collected on the North Shore of the St. Lawrence estuary at Ile du Havre in the Mingan Archipelago (50.2030° N, 63.5619° W) and frozen. Sea urchins were fed thawed kelp once a week while being held in the laboratory.

Laboratory set up

Two laboratory experiments were conducted at IML. Tanks were supplied with raw, unfiltered seawater from the St. Lawrence estuary at a flow rate of 3.6 l min⁻¹. The seawater temperature dropped from 4.8°C at the start of the experiments on October 25 to 2.4°C at the end of the experiments on November 23, 2012. Experiments were set up as a randomized block design in tanks measuring 90 cm long × 45.5 cm wide × 34 cm deep. Treatments were contained within sealed plastic containers (23 × 23 × 9 cm deep), which were placed in a single layer in the tanks. Panels were cut out of the sides and lids of the plastic containers and lined with 750 µm mesh attached with aquarium-safe silicone to improve water flow.

48 h cannibalism trials

Initial 48 h trials were conducted from October 23 to 25, 2012 to determine whether sea urchins are a source of mortality (through cannibalism or accidental 'bulldozing') of smaller conspecifics, and to investigate the factors that may influence cannibalism rates. Three tanks were used for the trials with one replicate container of each of 6 treatments placed in each tank. Ten small juveniles (3.5–6 mm TD) were placed in each container (189 urchins m⁻²), which is representative of densities at Ile Firmin (mean ± SD 132 ± 93 urchins m⁻²) in the Mingan Archipelago in the St. Lawrence (one of the study sites for the field measurements of cannibalism) but greater than measured juvenile densities at many other sites in the St. Lawrence estuary (C. Narvaez unpubl. data). The containers were randomly assigned a treatment. The first 3 of these treatments were compared to determine the effect of the presence of larger conspecifics: 2 large

juvenile (15–20 mm TD) or 2 adult (40–50 mm TD) conspecifics (density of 38 urchins m⁻²), and control containers with no added larger conspecifics; all of these treatments had no added substratum or food. The density of 38 large juvenile or adult sea urchins m⁻² was within the range of densities of adults (39–62 urchins m⁻²) but somewhat higher than that of larger juveniles (16–26 urchins m⁻²) in the rocky subtidal of the St. Lawrence estuary (C. Narvaez unpubl. data). Additional treatments were set up to test the effect of alternate food and substratum on the mortality rate of small juveniles in the presence of adult conspecifics (density of 38 urchins m⁻²) by comparing these treatments to the adult treatment with no substratum or food. The fourth treatment consisted of adult conspecifics (density of 38 urchins m⁻²) and *S. latissima* provided ad libitum for the duration of the 48 h experiment. Two additional treatments were lined with either 1 cm layer of sand, or cobbles (6–9 cobbles, creating a single layer) to determine whether the presence of substratum (sand and cobbles) affected the level of small juvenile mortality induced by adult urchins (density of 38 urchins m⁻²). With the exception of the kelp-added treatment, adults and large juveniles were last fed 6 d before the start of the experiment.

4 wk cannibalism trials

A 4 wk experiment was run from October 26 to November 23, 2012 to determine the level of small juvenile mortality in the presence of adult and large juvenile conspecifics under more natural conditions (cobble substratum, presence of kelp) and over a longer time period. Containers identical to the ones used in the 48 h trials were lined with a single layer of cobbles ~5 cm high. This substratum is similar to the substratum at Pointe Mitis, QC: a bedrock bottom covered in cobbles and occasionally interspersed with patches of silt or sand (K. LeGault pers. obs.). The adults and juveniles were fed *S. latissima* ad libitum for 8 h up to the start of the experiment. After 6 d, 10 g of *L. digitata* was added to each container of all treatments. For the remaining 3 wk of the experiment, all containers received frozen and thawed *L. digitata* ad libitum. The kelp was washed and patted dry on paper towelling to remove secretions and water. When the containers were checked for mortality (approximately once per week), the kelp was replaced with another 10 g piece of *L. digitata*, as the kelp was never fully consumed, and would begin to degrade.

Seven tanks were used for this experiment, and each tank received 1 replicate container of each of

the 3 treatments. Twelve small juvenile sea urchins (3.5–6 mm TD) were added to each container, for a density of 227 urchins m^{-2} , and each container was randomly assigned one of 3 treatments: 2 adults (range 35–47 mm TD, mean \pm SD 40.91 \pm 3.40 mm), 2 large juveniles (range 15–20 mm TD, mean \pm SD 17.03 \pm 1.83 mm), or no added adult or juvenile sea urchins (serving as a control). Mortality was monitored once a week by determining the number of small juveniles missing from a container, or partially eaten. Missing sea urchins were not replaced. The tanks in which the containers were being held were also thoroughly inspected for any missing small juveniles each time the containers were checked, and the containers were inspected for any gaps in the mesh that could have allowed small juveniles to escape. No sea urchins escaped from their containers during any of the laboratory experiments.

Statistical analyses for laboratory studies

All statistical analyses were performed using the open-source software R 2.12.0 (The R Foundation for Statistical Computing, www.r-project.org). The 48 h trials and the 4 wk experiment were analyzed as a complete randomized block design, with treatment (Adult, Large Juvenile or Control) as the fixed factor, and tank as the random blocking factor, and percent mortality as the response variable. It was not possible to test for an interaction between treatment and block because there were no replicates within blocks. The assumptions of homogeneity of variances and normality were checked using Bartlett's Test and Quantile-Quantile plots, respectively. Bartlett's test indicated that the data from the 48 h trials violated the assumption of equal variances ($p = 2.2 \times 10^{-16}$). A linear mixed effects model in the nlme package in R was used to test for differences between group means for the data collected from the laboratory experiments, with heteroscedastic variances specified. When there was a significant treatment effect, Tukey contrasts using the MultComp command in R were performed.

Cannibalism on small juveniles by adults in subtidal St. Lawrence

Gut analyses of field-collected sea urchins

Cannibalism pressure was determined at 5 sites in the Mingan Archipelago, QC, in the St. Law-

rence estuary: Ile Firmin (50.2033°N, 63.69°W), and Ile aux Goelands (50.20029°N, 63.58613°W) in 2013 and 2014, and Petit Ile aux Marteau East (50.201389°N, 63.558889°W), Ile du Havre South (50.210556°N, 63.634722°W) and Ile du Havre North (50.23°N, 63.60222°W) in 2014 only. The sites were sampled at approximately 8 to 10 m depth. The substratum at these sites is characterized by a bedrock bottom covered in crustose coralline algae with infrequent cobbles and little to no kelp other than sparse clumps of *Desmarestia aculeata* (K. LeGault pers. obs.). In the Mingan Archipelago, kelp generally occurs only at depths <2 m. Gut analyses were performed on sea urchins collected in mid-July 2013 at Firmin and Goelands, and in June 2014 at all sites. All adult sea urchins (>20 mm TD) were collected from five or six 0.25 m^2 quadrats per site, which were haphazardly dropped in the area around the marker float at that site. The adults were euthanized by freezing within 4 h of collection. In 2013, 30 adult sea urchins (mean size \pm SD: Firmin 37.8 \pm 4.64 mm TD; Goelands 40.0 \pm 7.42 mm TD) randomly selected from the total frozen specimens from each site were dissected. In 2014, 13 to 22 urchins were dissected for each of the 5 sites (mean size \pm SD: Firmin 50.4 \pm 5.39 mm TD, $n = 16$; Goelands 45.7 \pm 5.59 mm TD, $n = 19$; Marteau East 45.5 \pm 2.94 mm TD, $n = 17$; Havre South 48.0 \pm 5.8 mm TD, $n = 22$; Havre North 49.3 \pm 6.67 mm TD, $n = 13$). Adult sea urchins dissected for evidence of cannibalism were thawed, and their entire digestive tract was removed and visually analyzed under a dissecting microscope. Only the presence of structures from the Aristotle's lantern (the feeding structure unique to sea urchins) was considered a positive indication of cannibalism. This limited the detection of cannibalism to inter-cohort cannibalism, because only the entire consumption of a sea urchin much smaller than the adult being dissected would have been detected.

To estimate the variance associated with the counts of cannibalistic sea urchins collected in the field, bootstrapping was performed in MATLAB (v. 2012b). For each site and year, a bootstrapping randomization was performed, which sampled randomly from each pool of urchins that had cannibalized (entered as '1') and urchins that did not cannibalize (entered as '0'), with replacement, to create a new vector of 1 and 0. This was done 1000 times for each site and date, and the mean number of sea urchins that had cannibalized and standard deviation were calculated.

Size of cannibalized sea urchins in the gut contents of adults

The Aristotle lantern demi-pyramids that were found in the gut contents of sea urchins from the field were measured using an ocular micrometer in a dissecting microscope. The size of the sea urchins that had been cannibalized was estimated using regressions of jaw length and test diameter determined for the green sea urchin in the Gulf of Maine by Russell et al. (1998): $TD = 3.38J^{1.20}$, where TD is test diameter and J is jaw length, in mm. As this relationship likely varies between sites, we used it only to obtain an estimate of the size range of the urchins found in the gut contents.

Rates of cannibalism in the field

A simple model equation was used to estimate cannibalism rates in the field by combining information on the proportion of sea urchins with conspecifics in their gut from the field, gut passage time of conspecifics, and density of adults in the field, for a specified time interval and area of interest. Wilcox (2012) used this model to estimate predation rates of green crabs on the American lobster *Homanus americanus*, modifying the equation from earlier work by Dempster (1960), who formulated the equation as the proportion of predators that consumed the prey item of interest, as indicated through gut smears, multiplied by the predator population density. The modified equation from Wilcox (2012) is given below:

$$N = \frac{pPt}{D} \quad (1)$$

where N is the predation rate, in this case the number of young sea urchins (<10 mm TD) consumed by adult conspecifics for the given time period and area, and is determined by the decaying probability of detection in the gut contents; D is the half-life of detection (Wilcox 2012); p is the proportion of individuals (in this case adult sea urchins) in the field sample that had consumed the prey item (cannibalized young sea urchins, as assessed by gut analyses), P is the density of predators (adult sea urchins), and t is the time period. The parameter D is determined from laboratory data (see the next section) and can be calculated by taking the integral of the logistic function relating the probability of detection to time, or by determining the half-life of detection, which relies on the assumption that the logistic function is symmetrical (Wilcox 2012). In order to calculate D for this study, the `dose.p` command in the MASS pack-

age of R was used, which calculates the time at which the probability of detection declines to 0.5 using the generalized linear model fit to the binomial data.

Gut passage time of juvenile sea urchins through adult conspecifics

The detection interval is the time over which cannibalism can be detected in the gut contents of a sea urchin that was known to have cannibalized at time zero. The probability of detecting cannibalism in the gut contents of a sea urchin will decline to zero when the cannibalized conspecific has passed through the gut or become too degraded to recognize. Cannibalism was only considered detectable if pieces of the Aristotle's lantern (demi-pyramids or teeth) of the consumed juvenile were found in the gut contents, because dissection of an adult can cause pieces of the test or spines to contaminate the gut contents.

Live juveniles fed to adult sea urchins in the laboratory was used to determine the detectable decay function for adult *S. droebachiensis* cannibalizing small juveniles. Adult sea urchins (mean size \pm SD 36 ± 2.9 mm TD, range 30–42 mm) were collected from Pointe Mitis, QC, and small juvenile sea urchins (7.2 ± 1.0 mm TD, 5.3–9 mm) were collected from the Mingan Archipelago, QC. All urchins were held in tanks at IML, where they were starved for 1 wk to ensure any food they had consumed in the field had passed through their digestive tracts, and to ensure they were in a state of hunger to readily cannibalize.

Adults were then placed in bare plastic containers with one small juvenile sea urchin of known size. The containers were checked hourly for the occurrence of cannibalism. When a cannibalism event occurred in which the small juvenile was completely consumed, the time was noted and the adult was then placed in a mesh-lined plastic container in a tank with flowing seawater. The sea urchins were then euthanized, by freezing, at a set time after cannibalism. Three adult sea urchins that had consumed a juvenile were euthanized 3, 6, 9, 12, 15, 18, 24, 36, 48, 54, 57, 60, 63, 66 and 72 h after cannibalism. After euthanasia by freezing, adults were thawed and dissected. For each sea urchin, the entire digestive tract was examined under a dissecting microscope. The presence of fragments of Aristotle's lantern was required for confirmation of cannibalism. At the time that the fragments of Aristotle's lantern of the cannibalized urchin were so degraded as to be unidentifiable or were completely absent, cannibalism was considered no longer detectable. The presence (Aristotle's lantern

fragments detected) or absence (no detectable fragments) of cannibalism was used to generate a curve of the probability of detection over time and a logistic regression was fit to the detection data. The upper time limit of the detection of cannibalism occurred when the detectability of cannibalism declined to zero, corresponding to the detection interval.

Determining the adult density in the field

To determine the parameter P , density of predators, for the model equation, estimates of the population density of adult sea urchins were required for all sites from which sea urchins were collected for gut analyses. SCUBA divers dropped a marker float at each site, and a 30 m transect line was laid out parallel to shore, starting at the marker float. All sea urchins within 0.25 m² quadrats placed to the right side of the transect line were collected at 5, 10, 15, 20, and 25 m along the transect ($n = 5$ quadrats at each site). All the sea urchins were taken back to the laboratory, and their test diameter was measured using calipers. The density of adults was calculated as the number of sea urchins >20 mm TD m⁻².

RESULTS

Cannibalism among green sea urchins in the laboratory

48 h trials

There was no mortality in the control. No small juveniles were found outside the containers in the tanks at any point during the trials. Therefore, any small juveniles missing from the other treatments at the end of the experiment were considered consumed by conspecifics. Over the course of the 48 h trials, several incidences of cannibalism were observed.

Treatment explained a significant proportion of the variation in survival, and the blocking factor, tank, was not significant (Table 1). The proportional survival of small juveniles in the adult + kelp treatment (mean \pm SD 0.467 \pm 0.231) was significantly lower than in the control, adults + no substratum, adults + sand, adults + cobble, and large juveniles + no substratum treatments (mean \pm SD proportional survival: 1.0 \pm 0, 0.80 \pm 0, 0.867 \pm 0.153, 0.933 \pm 0.115, and 0.833 \pm 0.115, respectively) (Tukey's HSD; $p < 0.05$), but none of these treatments differed significantly from each other (Fig. 1).

4 wk cannibalism trials

After 4 wk, survival of small juvenile sea urchins in the control treatment was 100%, indicating that no intra-cohort cannibalism occurred, and that environmental conditions and food were favourable for survival of the small juveniles. The proportion of small juveniles surviving was 0.785 \pm 0.13 SD in the presence of adults and 0.762 \pm 0.18 in the presence of larger juveniles (Fig. 2). The linear mixed effects model indicated that treatments varied significantly in survival of small juvenile sea urchins (Table 2). Survival in the control treatment was significantly higher than survival in the adult and large juvenile treatments (Tukey contrasts; $p = 0.0039$ and $p = 0.00102$, respectively), which did not significantly differ from one another ($p = 0.932$). The blocking factor, tank, was not significant (Table 2). All 3 treatments had cobble substratum and kelp as an alternative food source.

Cannibalism by adults at subtidal sites in the St. Lawrence estuary

Adult gut analyses and size of cannibalized urchins

Gut analyses indicated that the proportion of adult sea urchins that had cannibalized (p in Eq. 1) at each site ranged from (mean \pm SD) 0 \pm 0 (SD estimated by bootstrapping) at Havre North to 0.31 \pm 0.12 at Firmin in 2014 (Table 3). The average proportion of adult sea urchins that had cannibalized across sites was 0.14 \pm 0.12.

Regressions of demi-pyramid jaw length and test diameter using the equation from Russell et al. (1998) predict test diameters of cannibalized sea urchins of

Table 1. Linear mixed effects model for 48 h laboratory trials, where the dependent variable was the survival of small juvenile green sea urchins *Strongylocentrotus droebachiensis* (3.5–6 mm test diameter [TD]), the random factor was tank and the fixed factor was treatment (levels: no larger conspecifics or added substratum, no added substratum with adults, no added substratum with large juveniles, no added substratum with adults and kelp, cobble substratum and adults, sand substratum and adults). Alpha = 0.05 (significant value in **bold**). $n = 3$ containers per treatment

	df	MS	F	p
Treatment	5,10	0.103	5.87	0.0087
Tank	2,10	0.015	0.85	0.46
Residual error	10,10	0.018		

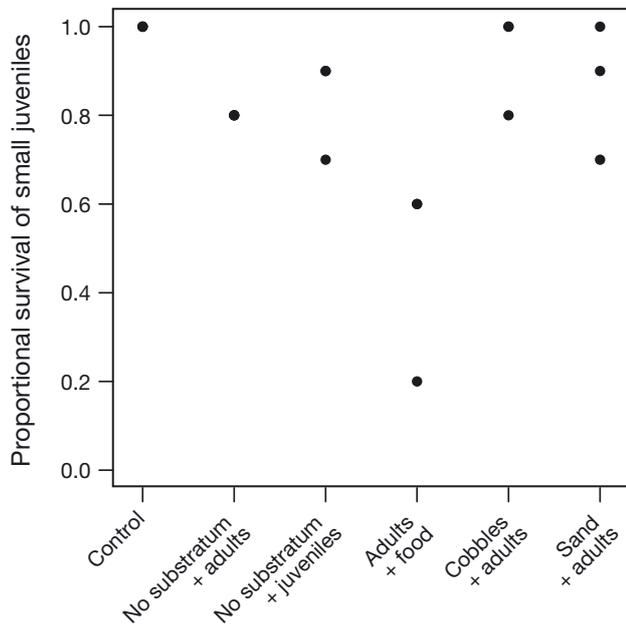


Fig. 1. Proportional survival of small juvenile green sea urchins *Strongylocentrotus droebachiensis* (3.5–6 mm test diameter [TD]) in the control treatment (no conspecifics or substratum); in the presence of adult sea urchins (35–50 mm TD) with no substratum; juveniles (15–20 mm TD) with no substratum; adults and kelp (adults + food) with no substratum; adults with cobble substratum; and adults with sand substratum, after 48 h. All of the treatments with the exception of adults and kelp had no alternative food. Each point is 1 replicate container (n = 3). Multiple points may overlap

1.1 to 28.4 mm TD (mean ± SD: 7.34 ± 6.06 mm TD). If this relationship, developed for Gulf of Maine sea urchins, is applicable in the St. Lawrence then this suggests that the size of cannibalized juveniles spans a wide range.

Gut passage time of cannibalized conspecifics

Starved, adult sea urchins (30–42 mm TD) in bare containers readily cannibalized small juveniles (5.3–9 mm TD) in the laboratory. The ability to detect Aristotle’s lantern fragments in the gut contents of adult sea urchins decreased with time since cannibalism. The fragments became increasingly degraded, until cannibalism was no longer detectable in any of the 3 adult sea urchins sampled 63 h after cannibalism. From this laboratory experiment, the half-life of the detection interval (*D*) of small juveniles in the gut contents of adult sea urchins was calculated to be 50.6 h (Fig. 3).

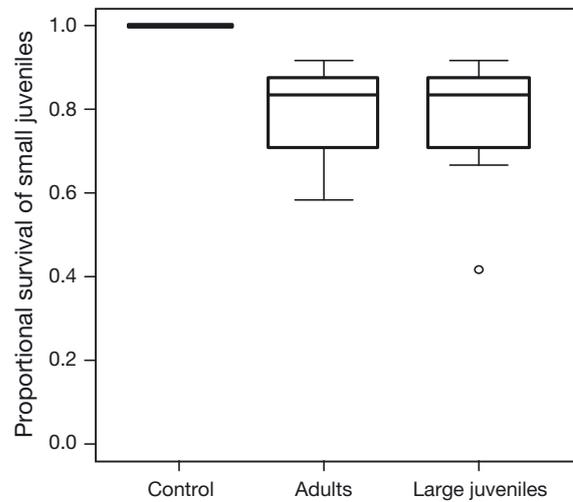


Fig. 2. Boxplot of proportional survival of small juvenile green sea urchins (3.5–6 mm TD) after 4 wk without other conspecifics (control), and in the presence of adults (35–50 mm TD) or large juveniles (15–20 mm TD). All treatments were fed kelp and provided a cobble substratum. Mid-line: median; box limit: 1st and 3rd quartiles; whiskers: range of data; open circle: outlier

Cannibalism rates

The density of adult sea urchins (>20 mm TD) at the study sites in the Mingan Archipelago ranged from 16.0 to 66.4 urchins m⁻² (Table 3). A calculation of cannibalism rate was made separately for each site in each year. For all sites, the half-life of detectability (*D*) was estimated to be 50.6 h using the equation from the general linear model fit to the laboratory data. The time period of interest (*t*) was specified as 24 h, to determine cannibalism rate per day. The data on the proportion of dissected urchins that had cannibalized, *p*, and the density of adult urchins, *P*, (Table 3) were entered into the model equation (Eq. 1), which predicted rates of cannibalism from 0.79 ± 1.22 urchins

Table 2. Linear mixed effects model of small juvenile sea urchin survival at the end of the 4 wk laboratory experiment. Treatment (fixed factor; levels: addition of adults, large juveniles, or no other conspecifics [control]) and tank (random factor) were the factors. All treatments had a cobble substratum and kelp was provided as food. Alpha = 0.05 (significant value in **bold**). n = 7 containers per treatment

	df	MS	F	p
Treatment	2,12	1203.7	6.64	0.011
Tank	6,12	106.9	0.59	0.733
Residual Error	12	181.33		

Table 3. Estimated rates of cannibalism based on the presence of fragments of Aristotle's lanterns of conspecifics in gut analyses of adult (> 20 mm TD) green sea urchins collected from 5 subtidal sites in the Mingan Archipelago, QC, in the St. Lawrence estuary in summer 2013 and 2014. Cannibalism rates were estimated using Eq. (1) using a detection interval $D = 50.6$ h determined from a laboratory experiment; adult density = P and proportion of adults that had cannibalized = p in Eq. (1). Juveniles: <20 mm TD. Where applicable, values are mean \pm SD

Site	Date of collection	Adult density (urchins m^{-2})	Adults collected (n)	Proportion of adults that had cannibalized	Rate of cannibalism (urchins $m^{-2} wk^{-1}$)	Juvenile density (urchins m^{-2})
Firmin	July 2013	44.8 \pm 22.7	30	0.13 \pm 0.062	19.3 \pm 0.70	274 \pm 135
	June 2014	66.4 \pm 30.5	16	0.31 \pm 0.12	68.3 \pm 0.60	107 \pm 69.1
Goelands	July 2013	41.6 \pm 25.9	30	0.066 \pm 0.044	9.12 \pm 0.91	188 \pm 32
	June 2014	32.0 \pm 23.9	19	0.052 \pm 0.050	5.52 \pm 1.22	76.8 \pm 45.2
Petit Marteau	June 2014	16 \pm 9.38	21	0.29 \pm 0.096	15.4 \pm 0.67	213 \pm 71.2
Havre South	June 2014	26.7 \pm 5.0	16	0.12 \pm 0.083	10.6 \pm 0.72	3.33 \pm 5.77
Havre North	June 2014	14.4 \pm 7.66	13	0 \pm 0	0	0 \pm 0

$m^{-2} d^{-1}$ (at Goelands in 2014) to 9.76 ± 0.60 urchins $m^{-2} d^{-1}$ (at Firmin in 2014) at the sites at which cannibalism was detected (no cannibalism detected at Havre North). Over the longer timescale of 1 wk ($t = 168$ h), this corresponds to mean \pm SD cannibalism rates ranging from 5.52 ± 1.22 urchins $m^{-2} wk^{-1}$ at Havre North to 68.3 ± 0.60 urchins $m^{-2} wk^{-1}$ at Firmin. See Table 3 for a summary of cannibalism rates from each site and date.

DISCUSSION

The results of these experiments show that the green sea urchin *Strongylocentrotus droebachiensis* cannibalizes smaller conspecifics both in the laboratory and in the field. The laboratory experiments

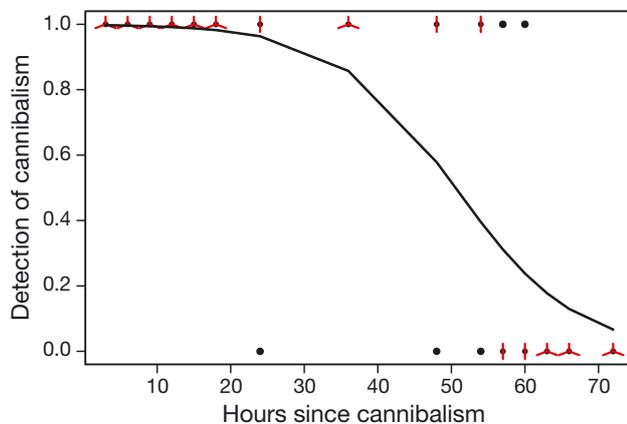


Fig. 3. The declining probability of detecting cannibalism of small juvenile (5–9 mm TD) sea urchins in the gut contents of adult *S. droebachiensis*, as indicated by the presence of Aristotle's lantern fragments, with increasing time since ingestion (at time 0) in the laboratory. The red branches indicate overlapping data points. The curve was fit by a logistic regression

demonstrated that cannibalism by adults (30–50 mm TD) and large juveniles (15–20 mm TD) of small 3–6 mm TD conspecifics ranged from 20–25% over 4 wk in the presence of an alternate food source (kelp), suggesting that larger conspecifics can be an important source of mortality for the small juveniles. Survival of the small juveniles did not differ significantly in the presence of larger juveniles (76.2%) compared to adults (78.6%).

Gut analyses in the laboratory showed that the presence of cannibalized juveniles in the gut contents of adults was a persistent signal that was detectable until 63 h after cannibalism. Previous studies of gut passage time in sea urchins have used a diet consisting of soft tissue, and much higher temperatures, and reported much faster gut passage times of 7.5 h for the urchin species *Eucidaris tribuloides* (Lares & McClintock 1991), and under 24 h for *Lyttechinus variegatus* (Klinger et al. 1994). Increased temperature increases gut passage time (Lares & McClintock 1991), as well as sea urchin metabolism (Brockington & Clarke 2001). Differences in seawater temperature may explain the discrepancy between the gut passage time reported in this study compared to previous studies, although the effect of hardness of the material being digested on sea urchin gut passage time is unknown and could also play a role.

This was the first study to quantify the cannibalism rate of small juvenile sea urchins in the field. Of the adult sea urchins collected from the north shore of the St. Lawrence estuary, the proportion that had cannibalized ranged from (mean \pm SD) 0.052 ± 0.05 to 0.31 ± 0.12 at the 5 sites over 2 summers, as well as 1 site (Havre North) where no sea urchins had cannibalized. The model equation predicted cannibalism rates of 5.52 ± 1.22 to 68.3 ± 0.60 urchins cannibalized $m^{-2} wk^{-1}$ (Table 3). The rates of cannibalism

estimated in the present study could represent a significant predation pressure on small sea urchins, particularly considering that there are few other predators of sea urchins in the St. Lawrence estuary. Measuring the demi-pyramids found in the gut contents suggested that adults consumed juveniles ranging from at least 1.1 to 28 mm TD in the field, a size range that occurred at a high density at Firmin, Goelands, and Petit Marteau: 274 ± 135 , 118 ± 69 , and 213 ± 71.2 urchins m^{-2} , respectively. The rates of cannibalism estimated using the model equation (Eq. 1) may be conservative, as our methods excluded cannibalism of sea urchins that were too large to have been fully ingested, and the field gut analyses had no way of determining whether >1 sea urchin had been cannibalized. The high rate of cannibalism estimated at the field sites in our study suggests that a cohort of small sea urchins from a given year's settlement could be completely consumed before being replenished by annual settlement. Settlement is spatially patchy in the St. Lawrence estuary, and can vary a great deal between years (K. LeGault unpubl. data). Low and patchy settlement combined with high cannibalism rates (due to high adult densities) could lead to missing cohorts. However, *S. droebachiensis* can live for 45 yr (Blicher et al. 2007), and their long lifespan likely reduces variability in adult population densities despite large variability in recruitment.

Previous reports of cannibalism among green sea urchins have been descriptive accounts of intra-cohort cannibalism in the field and laboratory among adults, where it was observed that the cannibal creates a small hole in the side of the test, typically the apical side of the victim, by removing the spines and test, then consumes the contents of the sea urchin, leaving the majority of the test, including the Aristotle's lantern, unconsumed (Himmelman & Steele 1971; K. LeGault pers. obs.). Cannibalism by larger juvenile sea urchins was hypothesized to be a possible mechanism of mortality in a field experiment where 1 to 3 mm TD *S. droebachiensis* settlers were placed in cages along with the suite of organisms (chitons, scale worms and larger sea urchins) found on the cobble bottom surrounding the cages in the Passamaquoddy Bay, New Brunswick (Jennings & Hunt 2011). In cages with the suite of organisms, sea urchin mortality was 25% higher than in cages without the suite (Jennings & Hunt 2011, Jennings & Hunt 2014). A follow-up laboratory experiment by Jennings & Hunt (in press) found that survival of 1 to 3 mm *S. droebachiensis* in cages with potential predators was lowest (70% after 8 wk) in the juvenile conspecific (mean \pm SD size: 8.8 ± 2.2 mm TD) treatment.

The survival of small juveniles in our study was similar to the survival of settlers in the presence of small juvenile conspecifics, despite the shorter duration (4 vs. 8 wk) compared to Jennings & Hunt (in press). At the conclusion of their laboratory experiment, Jennings & Hunt (in press) were unsure whether the mortality of 1 to 3 mm TD sea urchins was due to cannibalism by the juveniles, or bulldozing, the inadvertent crushing of conspecifics. The present experiment confirms that cannibalism can account for the settler mortality reported by Jennings & Hunt (2014) in the field, and Jennings & Hunt (in press) in the laboratory, and we found no evidence of bulldozing as there were no dead but unconsumed sea urchins found in any of the replicates. The present study is the first to examine the prevalence of inter-cohort cannibalism among *S. droebachiensis* systematically in the laboratory, as well as corroborate these results with empirical data from the field.

Although this is the first study quantifying cannibalism among *S. droebachiensis*, cannibalism has been reported in the laboratory in other species of sea urchins. Laboratory experiments of aquaculture-reared sea urchins *Lytechinus variegatus* (Richardson et al. 2011) and *S. purpuratus* (Sonnenholzner et al. 2011) demonstrated that intra-cohort cannibalism (the cannibal and its victim are of the same approximate size) occurs when sea urchins are starved, causing 18% mortality of *L. variegatus* and 50% mortality of *S. purpuratus* over a 4 wk period. In contrast to these cannibalizing species, some sea urchins have positive conspecific relationships such as the red sea urchin *S. franciscanus* (Nishizaki & Ackerman 2005, Nishizaki & Ackerman 2007, Zhang et al. 2011) and *Heliocidaris erythrogramma* (Smoothey & Chapman 2007).

Omnivory may predispose sea urchins to a highly generalist diet, which potentially includes cannibalism. *S. droebachiensis* is an omnivorous grazer that consumes the mussel *Mytilus edulis* (Briscoe & Sebens 1988, Meidel & Scheibling 1999) as well as other invertebrate infauna associated with kelp forests (Knip & Scheibling 2007), in addition to macroalgae (Steneck et al. 2013). Macroalgae (*Laminaria saccharina*) is a better energy source for green sea urchins, resulting in higher growth rates compared to sea urchins fed a mussel diet (Briscoe & Sebens 1988), although a combined diet of mussel and macroalgae can result in greater reproductive output than a diet of macroalgae alone (Meidel & Scheibling 1999). In contrast, Britton-Simmons et al. (2009) found that the red sea urchin *S. franciscanus*, which has positive associations between juveniles and adults, rarely supplements their diet of drift kelp

with invertebrates. *Heliocidaris erythrogramma*, another sea urchin species with positive adult–recruit interactions, has an exclusively macroalgal diet, and is classified as an herbivore, unlike 2 sympatric species, *Phyllacanthus irregularis* and *Centrostephanus tenuispinus*, which consume animal tissue (Vanderklift et al. 2006). An association between omnivory and cannibalism suggests that cannibalism may be an opportunistic feeding strategy for sea urchin species. The degree to which a sea urchin species is omnivorous may affect the likelihood that cannibalism occurs among conspecifics, which may then mediate the relationship between adults and recruits. Omnivorous species of sea urchins, such as *S. droebachiensis*, may be unselective feeders and consume any food item they encounter that is of an appropriate size, including conspecifics.

Food availability is the most important environmental variable linked to cannibalism (Dong & Polis 1992). Low food availability, low densities of alternate prey, hunger and/or fear of starvation may trigger cannibalism, or promote the evolution of cannibalism in a species (Polis 1981, Folkvord 1997, Nishimura & Hoshino 1999, Duarte et al. 2010). All treatments in the 4 wk laboratory experiment were supplied kelp (*Laminaria* spp.) ad libitum throughout the duration of the experiments. The occurrence of cannibalism despite the addition of kelp to all treatments suggests that cannibalism among green sea urchins may not be driven directly by energetics. In fact, in the 48 h trials, consumption of small juveniles was greatest in the treatment where kelp was provided as an alternative food. It is possible that the higher mortality of the small juveniles in the presence of kelp may be due to a higher encounter rate between the adults and the small conspecifics. Our field estimates of cannibalism were primarily for barren grounds where food availability is typically lower compared to kelp beds and grazing fronts, as indicated by differences in growth rates, gonad indices and food quantity indices determined by gut analyses (Lang & Mann 1976, Keats et al. 1984, Meidel & Scheibling 1998), and may therefore be an area where cannibalism occurs more frequently than in grazing fronts or in kelp beds. However, cannibalism still occurred at 1 site that is proximate to a large kelp bed (K. LeGault pers. obs.), Havre South, where the cannibalism rate was (mean \pm SD) 10.6 ± 0.72 urchins $m^{-2} wk^{-1}$. Although cannibalism may not be driven by starvation in the green sea urchin, the consumption of conspecifics may provide an important nutritional supplement to a kelp-based diet in the form of proteins. In *S. droebachiensis*, the gonad index of female urchins increases with

the consumption of the invertebrate fauna associated with kelp holdfasts (mussels, clams, ophiuroids, asteroids) (Knip & Scheibling 2007), as well as the addition of mussels to a diet of kelp (*Laminaria* spp.) (Meidel & Scheibling 1999). Cannibalism may be another animal supplement that benefits urchin reproductive output and/or somatic growth.

The 48 h laboratory trial did not indicate that substratum influenced cannibalism rate, as there were no significant differences between treatments with a substratum (cobble or sand) and the treatment with small juveniles and adults on bare containers. However, it is possible that effects of substratum would be detected over a longer time interval or with a larger number of replicates.

This is the first study to examine cannibalism of different size classes of any species of sea urchin in the laboratory, and the first study to quantify cannibalism in any species of sea urchin in the field. Adult and large juvenile green sea urchins cannibalized small juveniles (3–6 mm TD) in the laboratory on the order of 20 to 25% over a 4 wk period, and cannibalized a range of sizes of small juveniles (2–9 mm TD) in the field. Cannibalism may be a significant source of mortality for small juvenile sea urchins in subtidal barren grounds where adults and juveniles coexist (mean \pm SD: 5.52 ± 1.22 to 68.3 ± 0.60 urchins consumed $m^{-2} wk^{-1}$), and does not occur where juveniles are absent (no cannibalism at Havre North). In subtidal habitats where adult densities are high, cannibalism may be an important source of mortality for small juveniles, potentially driving a cohort to very low levels before the next period of settlement. Further work should focus on the demographic importance of cannibalism by estimating cannibalism rates from gut analyses over a wider range of sites and over multiple sampling periods. Additional laboratory studies should address the factors that could influence cannibalism among green sea urchins, including density, starvation state, and the size window between the cannibal and its conspecific victim over which cannibalism occurs.

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