



Detrital kelp subsidy supports high reproductive condition of deep-living sea urchins in a sedimentary basin

K. Filbee-Dexter*, R. E. Scheibling

Department of Biology, Dalhousie University, Halifax, Nova Scotia B3H 4J1, Canada

ABSTRACT: Highly productive kelp beds off Nova Scotia, Canada export detrital material to adjacent sedimentary habitats in deeper waters. We evaluated the importance of this subsidy to sea urchins *Strongylocentrotus droebachiensis* in less productive habitats. Gonad index and gut content of urchins on sediments at 60 m depth were measured monthly from September 2010 to May 2013 in a large semi-protected bay, and compared to concurrent measurements of sea urchins at 8 m depth off a nearby headland. Detrital algal cover in the bay was measured using a towed camera system. Seasonal patterns in algal deposition and gut contents of deep-living urchins indicated that detritus was the predominant food source from March to October. We observed lower gonad indices in deep-living sea urchins compared to those at 8 m, but deep-living urchins spawned outside of the main spring season, suggesting periodic detrital subsidy enhances their reproductive condition. Food availability and temperature appear to control the timing of gametogenesis, and phytodetritus may cue gamete release in these deep habitats. To evaluate the response of deep-living urchins to detrital subsidy, and turnover time of this material, we deployed lines baited with kelp thalli at 45 and 60 m depth and measured rates of encounter and consumption of kelp detritus by sea urchins, using the towed camera. Sea urchins aggregated on kelp within hours of deployment, and consumed it after 3 to 5 mo. Our findings suggest kelp detritus represents an important energy source that can support a high reproductive capacity in deep-living urchins.

KEY WORDS: Kelp · *Strongylocentrotus droebachiensis* · Reproduction · Spawning · Kelp detritus · Sea urchin · Resource subsidy

INTRODUCTION

The flow of material and energy between habitats plays an important role in structuring marine communities (Polis et al. 1997, Nakano & Murakami 2001, Marczak et al. 2007). In kelp bed ecosystems, macroalgal primary production is largely restricted to the shallow subtidal zone (generally <25 m depth) because light is limiting in deeper waters. This shallow band of production can form a substantial proportion of the overall production in temperate coastal waters (Witman 1988). About 90% of organic material produced in kelp beds is not directly consumed, but enters detrital food webs where it rafts onto

beaches, is exported to pelagic ecosystems, or enters deeper benthic communities (reviewed by Krumhansl & Scheibling 2012a). This detrital material ranges from small particles that erode off the distal ends of kelp fronds to large fragments or whole thalli that are torn off during periods of high wave action or when tissue is weakened by grazing damage, encrustation or sporogenesis (Krumhansl & Scheibling 2011, de Bettignies et al. 2013).

On the Atlantic coast of Nova Scotia, the sea urchin *Strongylocentrotus droebachiensis* is a dominant herbivore in the rocky subtidal zone. At high population density, sea urchins overgraze kelp and create expansive coralline algal barrens (Scheibling 1986,

*Corresponding author: kfilbeedexter@gmail.com

Scheibling et al. 1999, Filbee-Dexter & Scheibling 2014). In the 1990s and 2000s, phase shifts to barrens occurred when sea urchins migrated from deeper regions and formed aggregations at the lower margin of kelp beds that advanced shoreward as destructive grazing fronts (Scheibling et al. 1999, Brady & Scheibling 2005). More recently, widespread kelp beds have been re-established following recurrent disease outbreaks caused by a pathogenic amoeba, *Paramoeba invadens*, which appears to be periodically introduced into coastal waters where it causes mass mortality of *S. droebachiensis* in shallow habitats (Scheibling & Hennigar 1997, Feehan et al. 2012, Scheibling et al. 2013). Sea urchins have a thermal refuge in deeper waters (>20 m depth), where temperatures remain below the 12°C threshold for propagation of paramoebiasis (Scheibling & Stephenson 1984). These urchins are a source of adult migrants and larval recruits that could repopulate the shallows (Brady & Scheibling 2005).

Off wave-exposed headlands in Nova Scotia, where rocky substrata usually extend to greater depths before burial by sediments, deep-living sea urchins inhabit persistent barrens (Brady & Scheibling 2005, Kelly et al. 2012). Sea urchins in deep barrens subsist mainly on microbial films and coralline algae (Johnson & Mann 1982). Deep-living urchins are also found in sedimentary habitats below the rocky subtidal zone at 25 to 90 m depth, particularly in depositional areas where kelp detritus accumulates. These can occur in protected embayments or within small depressions amid shoals or along exposed headlands (Brady & Scheibling 2005, Filbee-Dexter & Scheibling 2012, unpubl. data, Kelly et al. 2012). Brady & Scheibling (2006) found low rates of growth and reproduction in poorly nourished sea urchins in persistent barrens at 24 m depth along a wave-exposed headland, compared to urchins within or adjacent to kelp beds in shallower water. However, our general knowledge of the ecology of deep populations of *S. droebachiensis* off Nova Scotia and elsewhere is limited compared to populations in the shallow subtidal zone.

In less productive habitats below the depth limit of kelp beds, the spatial extent and duration of detrital subsidy can play an important role in supporting sea urchin populations (Rogers-Bennett et al. 1995, Basch & Tegner 2007, Britton-Simmons et al. 2009). Sea urchins associated with accumulations of kelp detritus have been documented in deep submarine canyons off central California (Harrold et al. 1998) and in other rocky subtidal habitats in Alaska (Duggins et al. 1989), Washington (Britton-Simmons et al. 2009) and Western Australia (Vanderklift & Wern-

berg 2008). Since gonadal production in sea urchins is tightly linked to food availability (Keats et al. 1987, Meidel & Scheibling 1999, Wahle & Peckham 1999, Christiansen & Siikavuopio 2007), detrital subsidy is expected to enhance the reproductive capacity of deep-living sea urchins, and hence their contribution to the supply of larvae to shallow populations. Patterns of detrital kelp production (Krumhansl & Scheibling 2011, Filbee-Dexter & Scheibling 2012) and degradation (Krumhansl & Scheibling 2012b) have been measured in Nova Scotia, however the seasonal variation and extent of detrital deposition to deep subtidal habitats have not been quantified. Kelly et al. (2012) found that sea urchins in habitats beyond the kelp bed edge (25 to 30 m depth and 240 m offshore) with access to kelp detritus had higher gonad indices than those living in barrens, but sea urchins at greater depths have not been studied.

In the North Atlantic, *S. droebachiensis* has an annual reproductive cycle with a major spawning period in March/April (reviewed by Scheibling & Hatcher 2013). Reproductive periodicity is primarily cued by changes in temperature (Walker & Lesser 1998, Garrido & Barber 2001, Kirchhoff et al. 2010), photoperiod (Böttger et al. 2006, Siikavuopio et al. 2007, Kirchhoff et al. 2010) and phytoplankton abundance (Starr et al. 1994, Gaudette et al. 2006, Himmelman et al. 2008). Some populations also spawn in late summer and autumn (August to November), but this second spawning event is thought to occur only in food-rich habitats (Keats et al. 1987, Meidel & Scheibling 1998, Lyons & Scheibling 2007). Gonads are the main energy storage organ in sea urchins, and in habitats with insufficient food the gonad can be re-absorbed and gametogenesis suspended without spawning (Guillou et al. 2000).

During video surveys off headlands and within large embayments between Halifax and Mahone Bay on the southwestern shore of Nova Scotia in 2010, we documented sea urchin populations in sedimentary basins at 40 to 100 m depth that were associated with deposits of kelp detritus (Filbee-Dexter & Scheibling 2012). We expected these sea urchins to have a higher reproductive capacity than populations remote from a source of attached or detrital kelp (Britton-Simmons et al. 2009, Kelly et al. 2012). Here, we describe the reproductive cycle of the deep-living population in St. Margarets Bay and compare it to a population in a shallow kelp bed. We measure the contribution of kelp detritus to the diet of deep-living urchins and document temporal patterns in detrital deposition over a 3 yr period. We also measure the response time of sea urchins to detrital kelp deposi-

tion and the turnover time of this material in a field experiment.

MATERIALS AND METHODS

Study sites

Our main study site was located off Owl's Head (44° 31.30' N, 64° 0.91' W) in St. Margarets Bay, a large semi-protected embayment 50 km southwest of Halifax, Nova Scotia. The shallow rocky subtidal zone (5 to 20 m depth) of the bay is typically dominated by kelp (*Saccharina latissima*, *Laminaria digitata* and *Agarum cribrosum*), and deeper regions (to ~100 m depth) consist of sedimentary bottom. Owl's Head is an exposed point along the western shore of St. Margarets Bay, where the granitic bottom shelves steeply into a deep basin (40 to 100 m depth) that is protected from the open ocean by a sill (50 m depth) extending across the bay's entrance. Our shallow-water (8 m depth) reference site was at Duncan's Cove (44° 29.54' N, 63° 31.20' W), a partially exposed headland at the western mouth of Halifax Harbour. The substratum at Duncan's Cove consists of granite ledges and boulders, covered by dense kelp (*S. latissima* and *L. digitata*). The deep and shallow sites were spatially separated (by 38 km) as shallow adult populations of *Strongylocentrotus droebachiensis* do not occur in St. Margarets Bay or along adjacent headlands where they have been eliminated by recurrent outbreaks of paramoebiasis.

Sea urchin collection and analysis

We monitored the reproductive cycle of *S. droebachiensis* at 60 m depth at Owl's Head and at 8 m depth at Duncan's Cove (hereon, deep and shallow urchins, respectively). Large adults (test diameter >35 mm) were collected at both sites at approximately monthly intervals between August 2010 and May 2013. Deep urchins were collected from June to October using small purpose-built traps (0.4 m diameter plastic trays, baited with sardines) or a trawl (2 cm nylon mesh bag within a 0.5 × 0.5 m metal frame, towed from a 5.5 m research vessel), and from November to May using commercial lobster traps baited with chum (fermented herring) and set by a local fisher. Bait was placed inside a perforated metal container to prevent sea urchins from consuming it; purpose-built traps were retrieved after 1 d and lobster traps after 1 or 2 d. Collection methods varied

seasonally as we were prohibited from deploying lobster traps outside the lobster fishing season, and we were unable to trawl or deploy our own traps during the season because of the large number of commercial traps and associated floating lines at Owl's Head. Measurements of sea urchin test diameter (8.5 to 111 mm) from each collection method revealed that lobster traps were able to catch smaller individuals than trawls or purpose-built traps. Consequently, sea urchins <35 mm were omitted from our analyses. Shallow urchins >35 mm were collected on encounter by divers at Duncan's Cove.

The gonad index (GI) was calculated for each sample of sea urchins ($n = 9$ to 23 individuals per sample, depending on trawl and trap success) as gonad wet weight expressed as a percentage of the total body wet weight (including coelomic fluid). The sex of individuals was determined by examining a gonadal smear under a compound microscope. Sea urchins with little to no gonad, or without clear ovaries or testes, were designated unsexed (8.0% of dissected urchins). An index of the latency of response to spawning induction (LI) (either by collection, dissection, or addition of 1 to 2 ml (depending on sea urchin size) of 0.55 M KCl to excised gonads in a petri dish) was determined by recording the time (min) to gamete release on a 6-point scale: (1) not observed after 20 to 60 min following addition of KCl, (2) observed after 10 to 20 min following addition of KCl, (3) observed after 5 to 10 min following addition of KCl, (4) observed after 0 to 5 min following addition of KCl, (5) observed upon dissection, and (6) observed upon collection. For sea urchins collected between August 2011 and May 2013, fertilization rates of 5 ripe females (the first 5 to release eggs during dissection or after induction with KCl) were measured as the proportion of eggs ($n = 30$ eggs ind.⁻¹) showing an elevated perivitelline membrane 1 h after addition of 0.05 ml sperm. Sperm was collected from 1 to 3 ripe males (that were dissected around the same time as the females), checked for motility, mixed in a pipette and added to 100 ml vials of seawater containing eggs of individual females.

Gut contents of all collected specimens were macroscopically analyzed to determine the relative contribution of different food sources: macroalgae, coralline algae/sediment and invertebrate/animal matter. Approximately 2.5 ml of gut content collected from each sea urchin during dissection was spread across a 1 × 5 cm grid to estimate the percentage cover of each food source. Content that could not be macroscopically identified was examined with a dissecting microscope.

Detrital abundance

To monitor kelp and other macroalgal detritus available to deep urchins at Owl's Head, we surveyed the seabed throughout the reproductive-sampling period in 16 video transects between August 2010 and November 2013 (Table S1 in the Supplement at www.int-res.com/articles/suppl/b023p071_supp.pdf). Surveys were conducted using a digital video camera (Ocean Systems Deep Blue Pro II Color, Sea View Underwater Search Equipment) attached to a depressor dive wing (JW Fishers DDW-1 Deep Dive Wing, Sea View Underwater Search Equipment) that was towed at an average speed of 0.51 m s^{-1} from a 7 m research vessel (RV 'Nexus'). Two dive lights and 2 fixed lasers (spaced 20 cm apart) were attached to either side of the camera to light the bottom and provide scale in the video record. The camera was maintained at 1 m above bottom using a hydraulic slip-ring winch with a ship-board controller (Shark Marine Technologies). Video transects began at 45 m depth and extended perpendicular to shore to 75 m depth. For the surveys conducted between August 2010 and February 2011, we measured depth along the video transect using side-imaging sonar (1198c Side Imaging Sonar, Humminbird), lagged by 60 s to account for the positional offset between the camera and the vessel. For surveys after February 2011, we used an acoustic transponder to directly record the depth of the camera (Tracklink 1500 USBL tracking system, LinkQuest). The 60 s positional offset was determined by comparing records from the acoustic transponder and side-imaging sonar for the same video transects.

Each video transect was viewed in iMovie (version 9.0.4, Apple) in real time, and percentage cover of algal detritus along the transect was qualitatively assessed and entered into an Excel macro, synchronized with the video time. The Excel macro tabulated measurements in sample units of 1 s intervals, which was long enough to avoid frame overlap. The accuracy of the detritus measurement was evaluated by selecting 25 frames from the transect conducted on 21 June 2013, overlaying each image with a 100-point grid, measuring percentage cover of detritus, and comparing it to the qualitative measurement of the same frame (paired *t*-test, $p = 0.938$).

Environmental cues

Photoperiod over a 3 yr period (August 2010 to December 2013) was estimated for our study area

after Meeus (1999) using a web-interfaced calculator (www.gcstudio.com/suncalc.html). Temperature records from 8 and 60 m depth at the mouth of Halifax Harbour (~10 km SSE of Duncan's Cove) were acquired from the Coastal Time Series (CTS) database (<http://bluefin2.dfo-mpo.gc.ca/ctsqry/index-e.html>). To obtain a continuous record of phytoplankton concentration at Owl's Head and Duncan's Cove, we acquired 8 d composite chlorophyll *a* (chl *a*; mg m^{-3}) measurements in a 4 km^2 area at both sites from NASA's Ocean Color project SeaWiFS and MODIS satellite-based sensors (<http://oceancolor.gsfc.nasa.gov/cgi/l3>). Satellite-based measures at Duncan's Cove corresponded with chl *a* measures at the mouth of Halifax Harbour (~10 km SSE of Duncan's Cove), acquired from the CTS database at 1 m depth (Pearson's $r = 0.986$, $p < 0.001$, $n = 43$).

Field experiment: response to detrital kelp subsidy

To examine rates of encounter and consumption of kelp detritus by sea urchins in the sedimentary basin off Owl's Head, we deployed 2 weighted nylon lines, baited with single thalli of *S. latissima* attached at the holdfast (with plastic cable-ties) at 1 m intervals along a 40 m target section of each line, on 21 June 2013. Each line was marked at each interval with flagging tape for scale. *S. latissima* was collected from Splitnose Point (2.4 km southwest of Duncan's Cove) on 19 June 2013 and held in flowing sea water tanks for 36 h. Thalli of similar biomass and length were selected for the experiment (mean \pm SD, $227 \pm 89 \text{ g}$, $n = 90$). The lines were anchored at one end and stretched along the 45 and 60 m depth contours using our research vessel. A line without kelp also was placed ~3 m inshore of the experimental line at each depth as a procedural control to account for potential line effects on sea urchin behavior or trapping of kelp detritus. Surveys using a towed video camera were taken immediately following and 2 d after deployment of the experimental lines to examine the initial response of sea urchins. Subsequent surveys were conducted at 1 to 4 wk intervals (21 June to 4 October 2013) to examine the rate of kelp consumption and decomposition, and changes in sea urchin density over time (Table S1 in the Supplement). From 4 to 6 video transects were completed on every sampling day, each beginning in the kelp bed, intersecting the experimental lines (at different points along the 40 m target area) and ending at 80 to 100 m depth. Video data were exported from iMovie (version 9.0.4, Apple) into ImageJ (National Institute of Health) as

frames. For each video transect, we selected 1 or 2 frames with a clear image of a kelp thallus attached to the 45 or 60 m depth lines. We outlined the thallus in each frame in ImageJ and calculated the surface area of kelp (using the flagging tape for scale), and recorded the number of sea urchins in contact with kelp. Urchin density on the seafloor surrounding the experimental lines was measured in the 10 consecutive frames before and after the line appeared in the video for each transect.

Natural variation in abundance of macroalgal detritus and sea urchins also was documented during the experiment by measuring percentage cover of detritus and urchin abundance (ind. frame⁻¹) along an extended video transect, ranging from 135 to 227 m from the kelp edge. These video surveys followed the same GPS track as transects used to monitor the detrital algae cover at this site between August 2010 and November 2013.

RESULTS

Reproductive cycle of deep and shallow populations

Seasonal cycles in GI of *Strongylocentrotus droebachiensis* were more similar among years at 8 than 60 m depth, both in the timing and magnitude of GI peaks, and the occurrence of spawning periods (indicated by sharp declines in GI 1 to 2 mo after peaks). In general, peaks in GI occurred in late winter (February to March) and late summer or autumn (August to October) each year (Fig. 1). The maximum GI recorded was 33.1 and 38.9% in deep and shallow urchins respectively. The primary spawning period (greatest decline in GI) at 60 m generally occurred in autumn between September and November, and male and female spawning was less synchronized than in shallow populations (Fig. 1c). Spring spawning events differed substantially between sites, occurring in all 3 yr at 8 m, but only in 2011 at 60 m. Spawning events with smaller declines in GI occurred also during autumn at 8 m between August and October (Fig. 1b).

LI was positively correlated with GI over the sampling period for both deep and shallow sea urchins (Table 1), with rapid gamete release in spring and autumn and weak or no spawning in winter and summer (Fig. 1). This biannual

pattern was clearer in LI than GI and showed less variation in the timing and strength of peaks. LI measures were less consistent in the final sampling year, with increases lasting longer than usual at 60 m depth in October 2012 and occurring earlier at 8 m depth in January 2013 (Fig. 1c,d). The seasonal pattern of *in vitro* fertilization rate also was concordant with patterns of GI and LI, with the highest proportion of fertilized ova in spring and autumn (Fig. 2). The proportion of mature ova (without a nucleolus) was positively correlated with GI over the sampling period (Table 1). It was lowest in early winter and

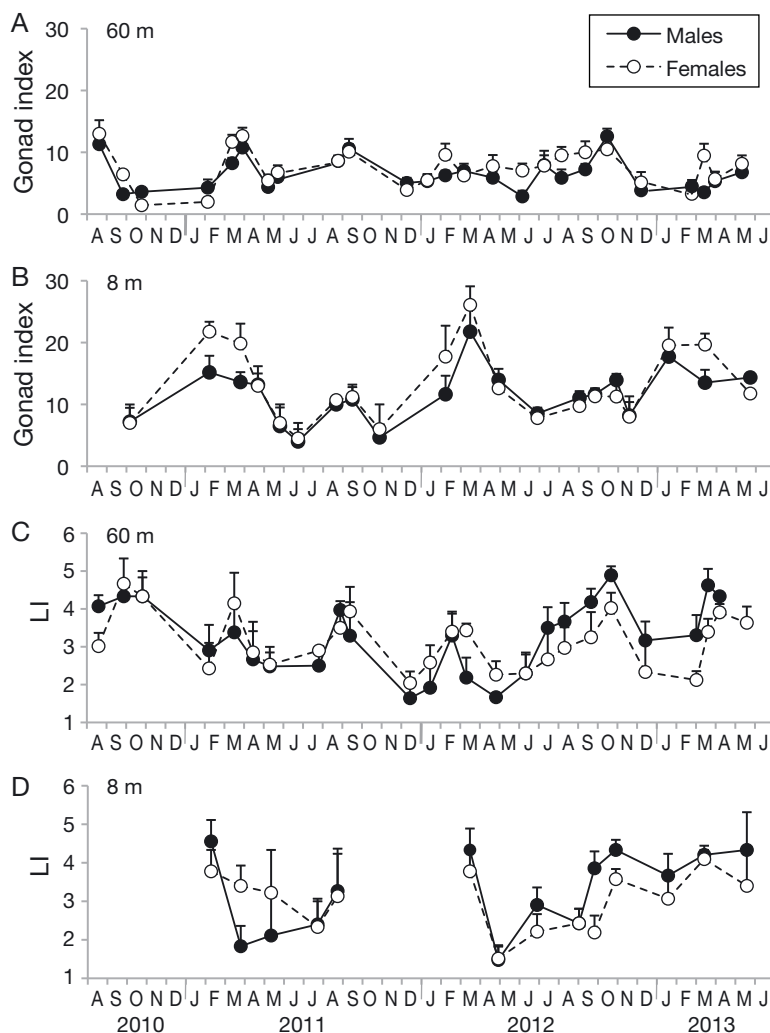


Fig. 1. *Strongylocentrotus droebachiensis*. Gonad index (% body weight that is gonad) of males and females at (A) Owl's head (60 m depth) from August 2010 to May 2013, and (B) Duncan's Cove (8 m depth) from February 2011 to May 2013; male $n = 1$ to 19, female $n = 2$ to 18. Latency of response index to spawning induction (LI) of males and females at (C) Owl's head (60 m depth) from August 2010 to May 2013, and (D) Duncan's Cove (8 m depth) from February 2011 to May 2013. LI ranges from 1 (did not spawn by 1 h after induction) to 6 (spawned during collection); male $n = 4$ to 20, female $n = 1$ to 19. Data are means \pm SE

Table 1. *Strongylocentrotus droebachiensis*. Correlation matrix (Pearson's r , * $p < 0.01$, ** $p < 0.001$; sample size in parentheses) for gonad index (GI), latency of response index to spawning induction (LI), proportion of mature ova (MO) and sea urchin test diameter (TD) at Owl's Head (OH, 60 m depth) and Duncan's Cove (DC, 8 m depth)

	OH				DC			
	GI	LI	MO	TD	GI	LI	MO	TD
GI	1.00				1.00			
LI	0.35** (566)	1.00			0.45** (226)	1.00		
MO	0.43** (136)	0.44** (136)	1.00		0.39* (41)	0.11 (41)	1.00	
TD	0.35** (518)	0.29** (518)	0.31** (136)	1.00	0.21* (211)	0.08 (211)	0.40* (41)	1.00

highest in spring and autumn, and remained relatively high in summer months between spawning periods (Fig. 2). The proportion of mature ova and GI both were positively correlated with urchin size (test diameter) for deep and shallow urchins; LI was correlated with size for only the deep location (Table 1). Mean adult size was similar in the deep (55.9 ± 5.14 mm) and shallow (58.3 ± 2.80 mm) populations, however maximum size was much greater for deep (112 mm) than shallow urchins (79.1 mm). Deep urchins also had long, brittle spines and tended to have lighter, thinner tests than shallow urchins. The ratio of males to females was similar in shallow (1.14, $n = 210$) and deep urchins (1.08, $n = 505$) and did not differ significantly from 1:1 at either depth ($\chi^2_{8m} = 0.933$, $p = 0.334$; $\chi^2_{60m} = 0.715$, $p = 0.398$).

Daily photoperiod during autumn and spring spawning periods was similar (10 to 13 h) but differed in the direction of change (Fig. 3a). Seawater temperature at 8 m depth at Duncan's Cove was warmest (12 to 20°C) between August and October, coinciding with the autumn spawning, and coldest (1 to 3°C) between February and March, coinciding with the spring spawning (Fig. 3a). Temperature at 60 m depth at Owl's Head ranged from 1 to 7°C, and was lowest between February and April, and highest between November 2011 and January 2012, and August 2012 and January 2013 (Fig. 3a). Chlorophyll concentration (a proxy for phytoplankton abundance) at Owl's Head showed substantial inter-annual variability. As expected, seasonal peaks in chlorophyll occurred in autumn 2010 to 2012, and spring 2011, with highest concentrations (>10 mg m^{-3}) in April, May, and November 2011 and October 2012, and lowest concentrations (<4 mg m^{-3}) during summer and in some winter months (Fig. 3b). Out-of-season peaks also occurred in January 2012 and 2013, and no phytoplankton increase was documented in spring 2012 and 2013 (Fig. 3b). Chlorophyll measures near Duncan's Cove were also variable, but tended to peak in autumn 2011 and 2012 and spring 2011 and 2012, with slight increases in September and October 2010, and March 2013 (Fig. 3b).

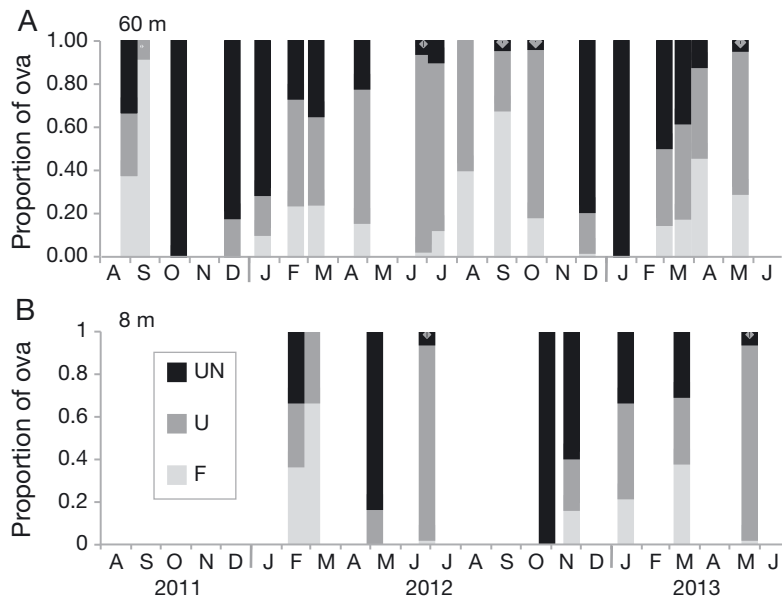


Fig. 2. *Strongylocentrotus droebachiensis*. Proportion of ova ($n = 60$) fertilized (F), unfertilized without nucleolus (U) or unfertilized with nucleolus (UN) 1 h after addition of sperm in sea urchins at (A) Owl's head (60 m depth) from August 2011 to May 2013, and (B) Duncan's Cove (8 m depth) from February 2012 to May 2013

Gut contents and availability of detrital algae for deep sea urchins

Algal material (mainly kelp and other brown algae) was present in the guts of 95% of sea urchins ($n = 533$) from 60 m depth at Owl's Head. Gut contents consisted almost entirely of algal detritus during spring/summer, while sediment, fila-

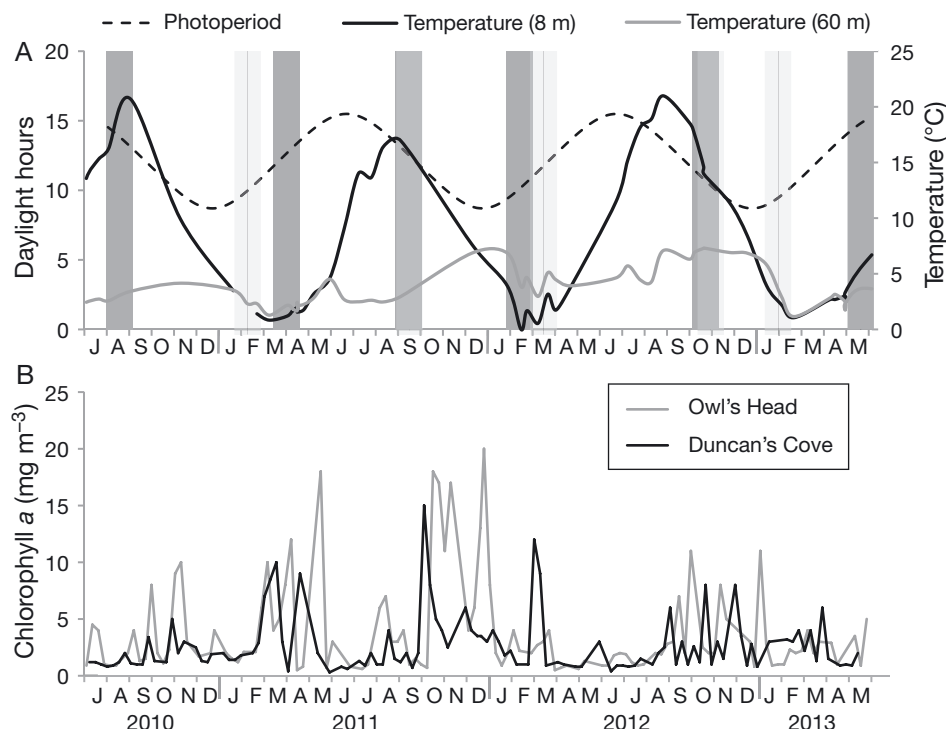


Fig. 3. *Strongylocentrotus droebachiensis*. (A) Mean daily temperature at 8 m and 60 m depth, and daylight hours, in the study area from July 2010 to June 2013. Shaded bars indicate spring and autumn spawning periods of sea urchins based on decreases in GI and increases in LI at Owl's Head (60 m depth, dark grey) and Duncan's Cove (8 m depth, light grey). (B) Chl *a* concentration at Duncan's Cove and Owl's Head from July 2010 to June 2013

mentous algae, and animal matter accounted for 15 to 27 % of the content in autumn/winter (Table S2 in the Supplement at www.int-res.com/articles/suppl/b023p071_suppl.pdf). Brown algae (mainly kelp) were present in the guts of all sea urchins ($n = 214$) along the kelp bed at 8 m depth at Duncan's Cove; 95 % of these urchins had no other observable material in the gut (Fig. 4a).

Seasonal changes in gut contents of deep urchins at Owl's Head reflected the annual pattern of abundance of algal detritus in the study area between August 2010 and November 2013 (Fig. 4b). For paired samples ($n = 9$, <30 d apart), the proportion of algal material in urchin gut contents was positively related to detrital cover on the bottom, although the correlation coefficient was on the margin of statistical significance (Pearson's $r = 0.579$, $p = 0.051$). Mean cover of detritus increased in late summer/early autumn in 2012 and 2013, and decreased in late autumn/winter throughout the 3 yr sampling period. Detrital cover was greatest in August or October/November in each year, and lowest in January/February 2011 and 2013 (there was no winter sampling in 2012, but detrital cover was minimal in July) (Fig. 4b). A dredged sample of algal detritus from 60 m depth on 20 July 2012

was primarily composed of the kelp *Agarum cribrosum* with moderate amounts of other kelps (*Saccharina latissima*, *Laminaria digitata*), foliose red algae, and the annual brown alga *Desmarestia viridis*.

Experimental response of sea urchins to detrital kelp subsidy

The fate of kelp thalli attached to lines placed at 45 and 60 m depth at Owl's Head, and the density of *S. droebachiensis* that aggregated on these thalli over time, differed markedly between depths (Table 2, Fig. 5). Sea urchins located kelp at the 45 m line within 2 h of deployment, forming aggregations of 12 ind. thallus⁻¹, on average, within 2 d, which doubled in size by Day 21 (Figs. 5a & 6). The area of transplanted kelp thalli began to decline at that point, and fronds were fragmented and mostly consumed by Day 82. Sea urchins were not observed on kelp at the 60 m line by Day 34 and density was only 5 ind. thallus⁻¹ by Day 59, at which time there had been no significant decrease in thallus area and fronds were intact with no sign of degradation. Mean urchin density on kelp at the 60 m line increased to

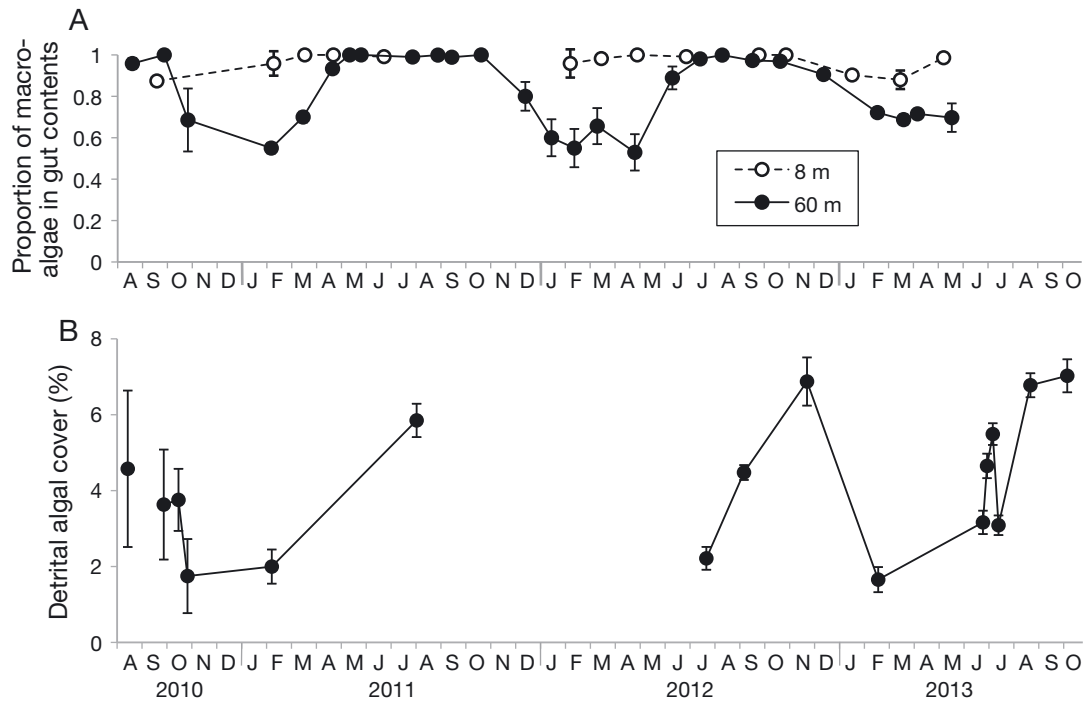


Fig. 4. *Strongylocentrotus droebachiensis*. (A) Proportion of algae (excluding coralline algae) in gut contents of sea urchins at Owl's Head (60 m depth) and Duncan's Cove (8 m depth) from August 2010 to November 2013. (B) Mean detrital algal % cover across a 45 to 75 m depth gradient at Owl's Head, near the collection site. Data are means \pm SE

Table 2. *Strongylocentrotus droebachiensis*. Two-way ANOVA of effects on area of kelp thalli or density of sea urchins on kelp (urchins thallus⁻¹) of fixed factors depth (45 and 60 m) and elapsed time (2, 14, 34, 59, 82, 105 d) at Owl's Head. Urchin density is square-root transformed to satisfy assumption of homoscedasticity (Levene's test, $\alpha = 0.01$). Significant post hoc comparisons (Tukey's test, $\alpha = 0.05$) are given

Source	df	MS	F	p	Tukey's post hoc tests
Kelp area					
Time	5	0.043	13.0	<0.001	Time
Depth	1	0.226	68.0	<0.001	2 = 14 = 34 > 59 = 82 > 105
Time \times Depth	5	0.006	1.81	0.129	
Error	48	0.003			
Urchin density					
Time	5	2.67	7.80	<0.001	Time \times Depth
Depth	1	79.5	232	<0.001	45 m: 105 < 82 = 59 = 34 = 14 = 2
Time \times Depth	5	7.58	22.1	<0.001	60 m: 105 > 82 = 59 > 14 = 34 = 2
Error	48	0.342			2, 14, 34, 59, 82 d: 45 > 60
					105 d: 60 > 45

12 ind. thallus⁻¹ by the end of the experiment on Day 105, by which time kelp cover had been reduced by half (Fig. 6). A 2-way ANOVA of kelp area showed a significant effect of both elapsed time and depth. Post hoc comparisons indicated that kelp area (pooled over depths) decreased significantly between 34 and 82 d after deposition. A 2-way ANOVA of urchin density on kelp (ind. thallus⁻¹) showed a significant interaction of time and depth.

Post hoc comparisons showed that urchin density was significantly lower on the 45 m line on Day 105 compared to all other sampling times, and urchin density significantly increased on the 60 m line 59 and 105 d after deposition (Table 2). Sea urchin density on kelp fronds was positively correlated with the number of urchins on the seafloor (ind. frame⁻¹) immediately before and after each line for data pooled throughout the experiment (Pearson's $r =$

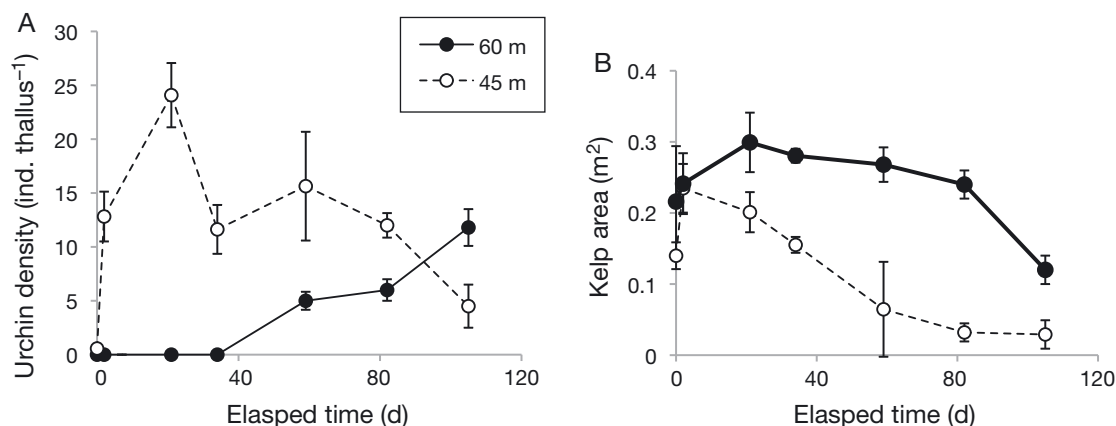


Fig. 5. *Strongylocentrotus droebachiensis*. Mean kelp area and density (urchin thallus⁻¹) on 45 and 60 m experimental lines at Owl's Head from 21 June to 4 October 2013. Data are mean \pm SE; $n = 6$ to 12. Note: kelp had not fully settled on the bottom when lines were surveyed directly after deployment, resulting in an increase in kelp area on Day 2

0.38, $p < 0.001$, $n = 175$). A 1-way ANOVA showed no effect of elapsed time on the number of urchins in contact with the procedural control line ($F_{6,7} = 0.738$, $p = 0.636$) and on the kelp area in contact with the procedural control line ($F_{6,7} = 0.458$, $p = 0.820$), indicating that the weighted lines did not influence sea urchin density or detrital kelp deposition.

The extended video transects that intersected the experimental lines revealed patches of macroalgal

detritus on sedimentary bottom, and accumulations of sea urchins on and around these deposits (Fig. 7). The effect of detrital cover on urchin abundance (ind. frame⁻¹) along these transects was examined with a generalized linear model (GLM) performed using R software (MASS package). GLM residuals were modelled with a negative binomial distribution and a log-link function. Likelihood ratio (LR) tests showed no significant effect of sampling date ($LR_4 = 3.84$, $p =$

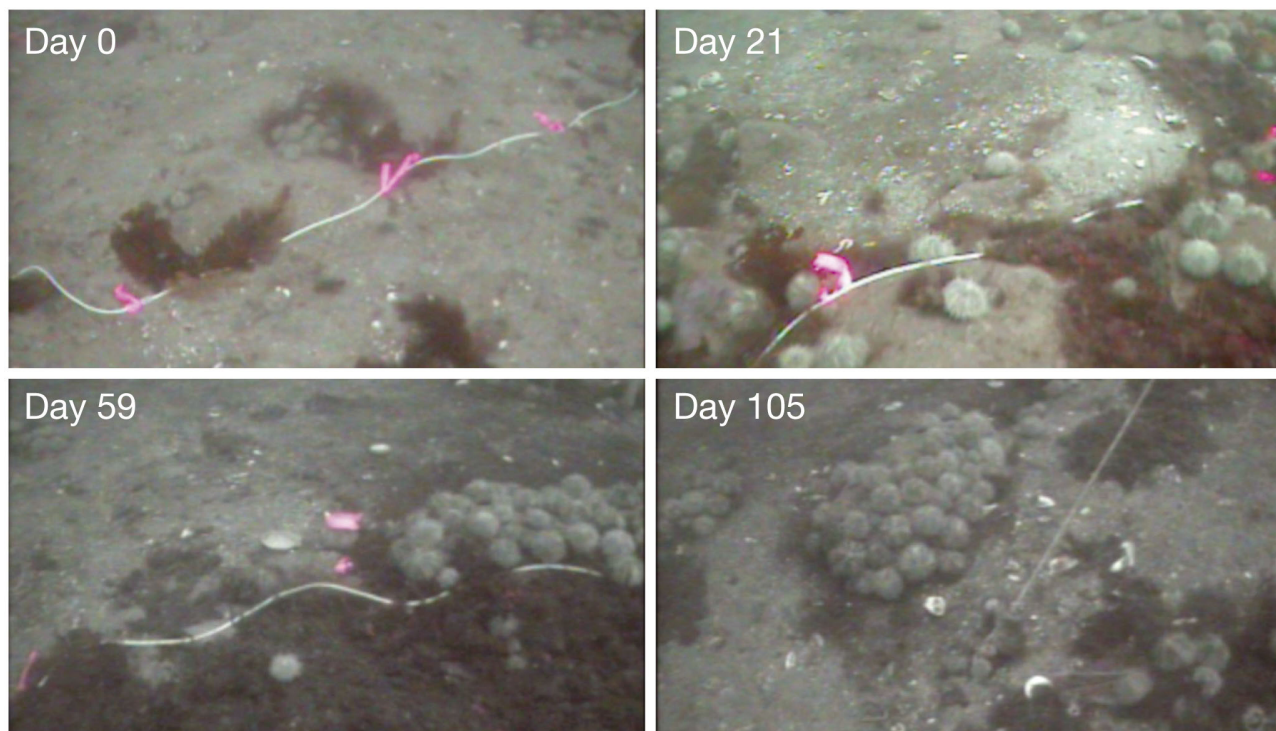


Fig. 6. Video frame grabs of weighted lines baited with kelp fronds at 45 m depth on Days 0, 21, 59 and 105 of the field experiment at Owl's Head in 2013, showing rapid detection of kelp by *Strongylocentrotus droebachiensis* within 2 h, dense urchin aggregations and kelp degradation after 21 and 59 d, and bare line by 105 d after deployment. Flagging tape indicates 1 m intervals along a line

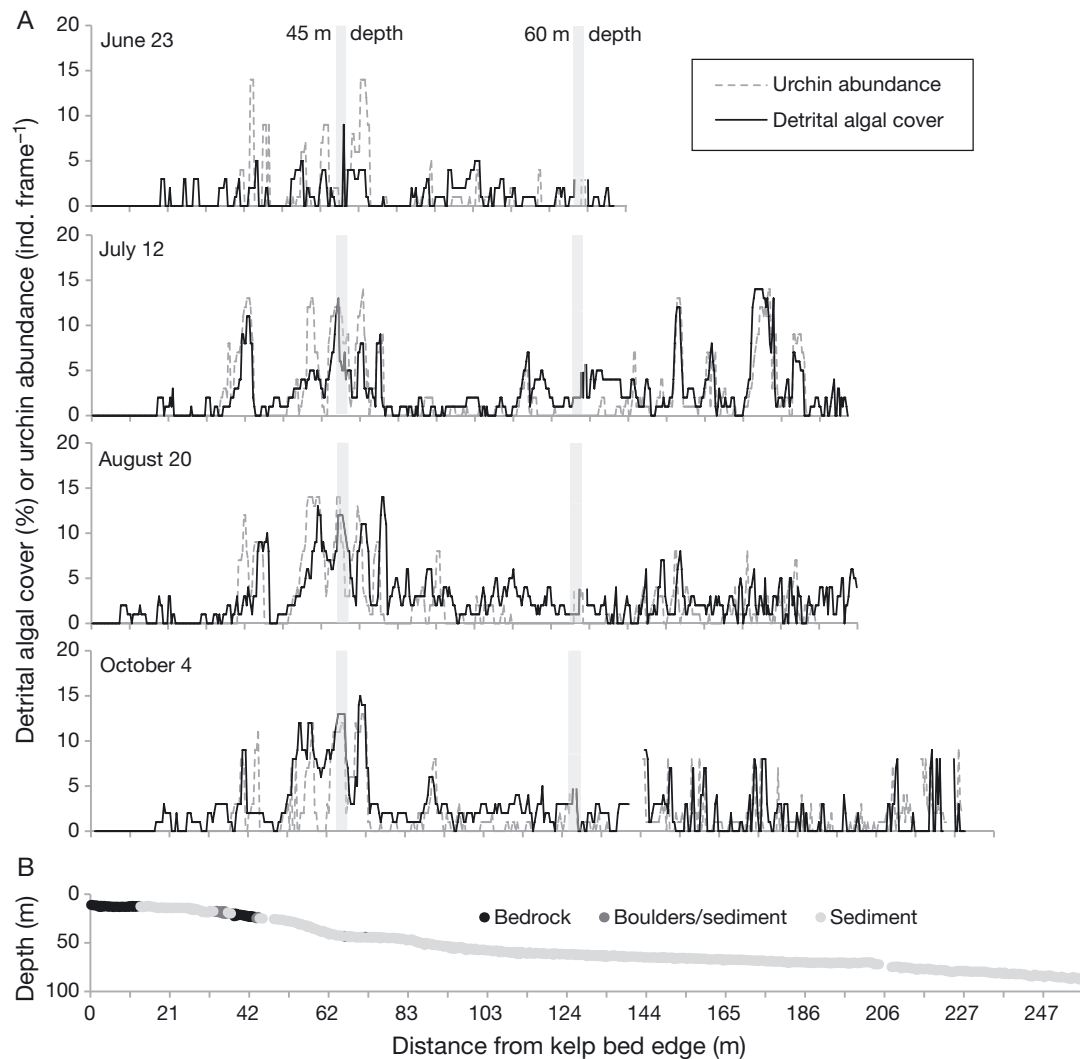


Fig. 7. (A) Detrital algal cover and sea urchin abundance along video transects on 23 Jun, 12 Jul, 20 Aug and 4 Oct at Owl's Head. Experimental lines baited with kelp fronds (deployed on 21 Jun) are indicated by shaded grey bars at 45 and 60 m depth. (B) Substratum type along the depth profile on video transects. Transects began in the kelp bed at 8 m depth and extended offshore to 95 m depth

0.427) and no interaction between detrital cover and date ($LR_4 = 1.37$, $p = 0.848$) on urchin abundance; therefore data were pooled over the duration of the experiment. To reduce spatial autocorrelation due to continuous sampling along video transects, an effective sample size of $N/12$ estimated using the autocorrelation function (ACF) and yielding 240 frames or 5 frames min^{-1} of video, was used. This analysis showed a significant positive effect of detrital cover on urchin abundance along these transects ($z = 5.74$, $p < 0.001$, deviance explained = 15.8%). The seafloor surrounding the 45 m line had a greater number of sea urchins and cover of detritus than the 60 m line (Fig. 7). Total detrital cover increased along these transects during the experiment, although the general pattern of distribution was maintained (Fig. 7).

DISCUSSION

Detrital kelp subsidy and reproductive condition of deep-living urchins

Previous studies have recorded a decrease in gonad size and fecundity with increasing depth and distance from macroalgal beds for *Strongylocentrotus droebachiensis* (Keats et al. 1984, Bertram & Strathmann 1998, Wahle & Peckham 1999, Brady & Scheibling 2006, Kelly et al. 2012) and congeneric species (Rogers-Bennett et al. 1995, Wahle & Peckham 1999, Konar & Estes 2003). In contrast, we found that sea urchins at 60 m depth in a sedimentary basin can have comparable or in some cases greater reproductive effort (mean GI at spring or autumn peak: 10

to 12%) than those living in rocky barrens at 6 to 24 m depth adjacent to kelp beds at other sites in St. Margarets Bay (8 to 10%; Meidel & Scheibling 1998) or at the mouth of Halifax Harbour (6 to 9%; Brady & Scheibling 2006) in past decades. Kelly et al. (2012) observed a similar increase in mean GI of sea urchins (from 11 to 22%), and supply of detrital kelp, within a depositional basin at 25 m depth along transects running offshore from a kelp bed near Duncan's Cove in 2009. Britton-Simmons et al. (2009) found that *S. franciscanus* feeding on macroalgal detritus at 24 m depth also had a similar GI compared to sea urchins in barrens at 6 m depth in the San Juan Islands, Washington, USA. The maximum GI of shallow and deep urchins in our study (39 and 33% respectively) was comparable to the highest measures recorded for *S. droebachiensis* under optimized feeding conditions (35 to 38%; Meidel & Scheibling 1999, Siikavuopio et al. 2007). The supply of detrital macroalgae, mainly kelp, likely explains the relatively high GI in deep urchins. Not only is kelp a high quality and preferred food of *S. droebachiensis* (Scheibling & Hatcher 2013), but the nutritional quality of kelp detritus is also enriched by microbial degradation (Duggins & Eckman 1997, Norderhaug et al. 2003, Krumhansl & Scheibling 2012b).

S. droebachiensis generally does not form dense populations below 30 m depth as it does in the shallow barrens along the coast of Nova Scotia (Scheibling et al. 1999, Brady & Scheibling 2005). This likely is because the rocky substratum off the wave-exposed headlands does not accumulate substantial quantities of detrital macroalgae as it slopes continuously into deeper sedimentary areas. Ideally, we would have included a site at 60 m depth with minimal deposition of kelp detritus in our sampling design to directly test the effect of this subsidy on sea urchin reproductive capacity and periodicity. However, in extensive video surveys along the coast, we have found that in areas with little or no detritus sea urchins are so sparsely distributed (Filbee-Dexter & Scheibling 2012, unpubl. data) that regular collections for reproductive analyses would have been impossible within the logistical constraints of this study. This observation in itself supports our conclusions about the importance of detrital subsidy for deep urchin populations.

Sea urchin abundance was positively related to detrital cover in video surveys, and our field experiment indicates that *S. droebachiensis* can locate and consume this food resource for months. The presence of macroalgal detritus on the seafloor and in the guts of deep-living urchins varied seasonally throughout

our 3 yr study at Owl's Head, with peaks in late summer and autumn. High wave action, storm events, and heavy encrustation by the bryozoan *Membranipora membranacea* combine to increase dislodgment, fragmentation and erosion of kelp resulting in increased detrital deposition during this period (Scheibling & Gagnon 2009, Krumhansl & Scheibling 2011, Filbee-Dexter & Scheibling 2012). The non-uniform pattern of macroalgal detritus along our video transects indicates subtle bottom features that may retain detritus in certain areas. For example, a large amount of detritus accumulated amid sparse boulders and a decrease in slope at 40 to 45 m depth, which in turn was associated with high sea urchin densities.

The rapid response to kelp detritus on our experimental line at 45 m depth demonstrates that *S. droebachiensis* can locate a nearby subsidy within hours, and may be constantly searching for food in deeper waters. The slower response to the 60 m line (59 d had elapsed before the first urchins were observed there) suggests that sea urchins are unable to detect or respond to detritus 10s to 100s of meters distant, and may only encounter it through random movement. Once deposited, kelp detritus degrades slowly at depth and persists as a food source for macrofaunal communities for up to 4 mo in the absence of sea urchins (Krumhansl & Scheibling 2012b). We also observed minimal loss of transplanted kelp at the 60 m experimental line over nearly 2 mo before sea urchins located it. Even for kelp on the 45 m line that was immediately located by sea urchins, the turnover rate was slow (on the scale of months). In a caging experiment at 41 m depth off Owl's Head in 2011, we found that sea urchins consumed detached kelp at a rate of $1.4 \text{ g ind.}^{-1} \text{ d}^{-1}$ (Filbee-Dexter & Scheibling 2012), which is within the range recorded for *S. droebachiensis* grazing in shallow water (Lauzon-Guay & Scheibling 2007a). From these results, we estimated that it would take ~2 mo for sea urchins off Owl's Head to consume an average deposit of detrital kelp (Filbee-Dexter & Scheibling 2012), which approximates the time in which the majority of kelp was consumed on both experimental lines in our present study.

Laboratory feeding studies have shown that while a critical nutritional level is required for the initiation and progression of gametogenesis in *S. droebachiensis*, changes in food availability at later stages of the reproductive cycle affect gonad growth but do not influence the timing of gamete release (Minor & Scheibling 1997, Meidel & Scheibling 1998, 1999). Under optimal environmental conditions, gametogenesis can take about 6 mo (Walker & Lesser 1998).

Maximum food availability occurred at Owl's Head during peaks in macroalgal detritus between September and November, ~6 mo prior to spring peaks in GI. This subsidy may have been supplemented with phytodetritus from the autumn phytoplankton bloom, which is expected to reach 60 m depth within 1 to 2 d of cell death, assuming a sinking rate of 100 m d^{-1} for coastal aggregates (Alldredge & Gotschalk 1990). Likewise, phytodetritus from the spring bloom deposits between March and April, in time for initiation of gametogenesis. At Owl's Head in 2012, the spring phytodetritus subsidy was 2 mo later than in previous years, and was followed by an autumn peak in GI that occurred 1 to 2 mo later than in previous years. The late phytoplankton bloom, combined with limited detrital kelp deposition between March and April 2012, may have delayed gametogenesis.

Gonad growth in sea urchins is the result of either a build-up of nutrient reserves in nutritive phagocytes prior to gametogenesis, or an increase in the size or number of germinal cells in the gonad during gametogenesis (Walker et al. 2013). The higher spring peak in GI at 8 m (particularly in females) compared to 60 m depth may reflect a better overall nutritional environment at the shallow site, where sea urchins generally had continuous access to attached and detrital kelp within and around the kelp bed. Likewise, increases in GI in deep regions may reflect energy storage (rather than gametogenesis) following periods of abundant food. This may have occurred in early autumn 2012 following the late summer supply of detritus.

Trophic linkages between algal beds that export detritus and the recipient species typically occur on the scale of kilometers and can have an important influence on community structure (Kirkman & Kendrick 1997, Vanderklift & Wernberg 2008, Britton-Simmons et al. 2012). For example, kelp detritus that rafts onto beaches can allow fauna to reach high abundance in a habitat where local production is low (reviewed by Colombini et al. 2003). Detached kelps such as *Macrocystis pyrifera* and *Ecklonia radiata* can be transported 10s to 100s of kilometers by along-shore currents and thereby provide spores or food to neighboring areas (Harrold & Lisin 1989, Vanderklift & Wernberg 2008). Detrital kelp is an important food source for sea urchins that passively trap and consume drifting fronds along the Pacific coast of the USA, the central Chilean coast, and the coast of Western Australia (Krumhansl & Scheibling 2012a). In the Northwest Atlantic, *Strongylocentrotus pallidus* has been observed consuming fronds of *Saccharina latissima* at 2500 m depth off the Scotian

Shelf (A. Metaxas pers. comm.), indicating that this subsidy occurs over much larger spatial scales than is documented in our study.

Another important linkage between shallow and deep sea urchin populations could be their contribution to larval production in the rocky subtidal ecosystem. Kelp detritus not only provides energy that deep sea urchins use to produce gonads, but also aggregates them at high densities on detrital deposits. This can increase fertilization rate (Lauzon-Guay & Scheibling 2007b) by increasing both the number of spawning individuals and synchrony of gamete release (Starr et al. 1990, Wahle & Peckham 1999, Lauzon-Guay & Scheibling 2007b). A positive relationship between test size and GI for both deep and shallow urchins, combined with a larger maximum size for deep urchins, suggests that per capita gonadal production is greater in the deep.

Environmental cues and reproductive periodicity

Previous studies in Alaska, Eastern Canada, the Gulf of Maine, Norway and the Barents Sea have documented a distinct annual reproductive cycle for shallow populations (<25 m depth) of *S. droebachiensis*, with a peak in GI in March/April followed by a sharp decline, indicating relatively synchronous spawning in late winter or early spring (Himmelman 1978, Falk-Petersen & Lønning 1983, Keats et al. 1984, Munk 1992, Meidel & Scheibling 1998). Populations in the St. Lawrence Estuary, Canada have been observed to spawn in June/July (Starr et al. 1993, Oganessian 1998). Histological analysis of the gonads of sea urchins from Nova Scotia indicates that gametogenesis commences in summer and is fueled in part by nutritive phagocytes produced in spring (Meidel & Scheibling 1998). For shallow populations of *S. droebachiensis*, changes in photoperiod (Böttger et al. 2006, Siikavuopio et al. 2007, Kirchhoff et al. 2010) or temperature (Walker & Lesser 1998, Garrido & Barber 2001, Kirchhoff et al. 2010) appear to control the timing of gametogenesis.

The presence of seasonal increases in GI of *S. droebachiensis* in spring and autumn, and the high proportion of mature ova and short response time to spawning induction at these peaks, indicates that deep-living urchins, like those in the shallow kelp bed, may be capable of spawning outside of the main spring season documented for shallow populations. This generally has been observed only under optimal feeding (Shpigel et al. 2004) or manipulated environmental conditions (Walker & Lesser 1998) in labora-

tory experiments, or under conditions of high food availability in the field (Keats et al. 1987, Meidel & Scheibling 1998, Brady & Scheibling 2006). The high proportion of sea urchins that readily spawned upon dissection ($LI > 5$) in both autumn and spring suggest that individuals can spawn twice a year. At 8 m depth, a higher spring peak in GI is consistent with previous studies of *S. droebachiensis* in shallow, food-rich habitats (Meidel & Scheibling 1998, Brady & Scheibling 2006), and indicates that the autumn peak likely reflects a secondary spawning period.

GI increases in our study coincided roughly with rapid changes in photoperiod, albeit in opposing directions in spring and fall (see also Brady & Scheibling 2006). Gattuso et al. (2006) measured irradiance reaching the seafloor in coastal oceans using satellite (SeaWiFS) data collected between 1998 and 2003. They calculated that approximately 0.004 to $0.023 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ reached 60 m depth within 25 km of Owl's Head (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/b023p071_supp.pdf). Tube feet of *S. droebachiensis* in shallow water react to low light irradiances of $5 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ (Lesser et al. 2011), which approximates light levels at 35 to 40 m depth at Owl's Head. Therefore, it is likely that photoperiod does not play a role in reproductive timing at 60 m depth, although it may indirectly influence spawning by affecting phytoplankton production (Platt & Jassby 1976).

Differences in temperature between 8 and 60 m depth also may account for differences in GI peaks between shallow and deep urchins. Gonadal production increases with temperature up to $\sim 10^\circ\text{C}$, beyond which temperatures are too warm for oocyte maturation (Walker & Lesser 1998, Garrido & Barber 2001, Siikavuopio et al. 2006). Seawater temperature at 8 m dropped from 10 to 7°C from October to December, enabling oocyte maturation before the spring spawn, but exceeded 10°C from July to October, which could inhibit maturation and limit the autumn spawn (Brady & Scheibling 2006). Sea urchins at 60 m at Owl's Head experience consistently cold bottom temperatures (3 to 7°C). The lower summer temperatures at this depth are more conducive to oocyte maturation and autumn spawning compared to shallow waters. Moderately warm temperatures between September and January should enable gonad growth at 60 m, however, low detrital abundance and meager gut contents indicate that sea urchins are food-limited during this period.

Phenolic compounds associated with phytoplankton have been shown to induce spawning in *S. droebachiensis* from shallow populations under labora-

tory conditions (Starr et al. 1994), although this relationship is less clear in compiled field observations (Starr et al. 1993, Scheibling & Hatcher 2013). Phytodetritus following a bloom may provide an important cue at 60 m depth where changes in temperature, photoperiod and lunar cycles are damped. Reproductive periodicity in the deep-sea urchin *Echinus affinis* is strongly linked to seasonal pulses of phytodetritus (Tyler & Gage 1984, Campos-Creasey et al. 1994). Possible mechanisms to explain this association are: (1) sea urchins utilize phytodetritus for rapid gametogenesis and spawn shortly thereafter, (2) sea urchins time gamete release with favorable conditions for planktonic larval development, or (3) sea urchins initiate and synchronize gametogenesis with phytodetritus and spawn after a constant period of vitellogenesis (Eckelbarger & Watling 1995). Decreases in GI at 60 m in our study occurred 1 to 2 wk following phytoplankton blooms in autumn of all sampling years, and in spring 2011. This suggests that phytodetritus triggers gamete release in deep urchins, and may explain why spawning events were not documented at Owl's Head during spring 2012 and 2013, when blooms were not recorded on satellite imagery. The proportion of mature ova and LI remained high during summer 2012, indicating that gametogenesis occurred prior to the spring, but deep urchins did not spawn and retained their mature gonads until autumn. Similarly, a strong spawning event did not occur at 8 m depth in autumn 2012 even though GI and LI were high, and winter increases in GI and LI occurred earlier in 2013 than in other years, possibly because ripe gametes were retained from the autumn. It appears that although sea urchins have the capacity to release gametes in spring and autumn, spawning may only take place if it is cued by favorable environmental conditions.

Ecological implications of detrital subsidies for deep-living sea urchin populations

Our study underscores the importance of energy subsidies, originating in highly productive kelp beds within a relatively narrow rocky coastal zone, on the secondary productivity of adjacent communities in sedimentary habitats in deeper waters. Krumhansl et al. (2014) modelled the historical and future production of detritus in Nova Scotian kelp beds, and predicted that changes in ocean climate (increasing temperature and storm severity) will decrease detrital production. This would have negative effects on growth and reproduction of populations in adjacent

habitats, such as deep-living urchins that receive a detrital subsidy.

Our findings demonstrate that reproductive capacity of deep-living *S. droebachiensis* is substantial in areas with an abundant supply of detritus, and can rival that of sea urchins in the shallow kelp beds that are a major source of this subsidy. The degree to which larvae produced by these deep populations are either locally retained or contribute to recruitment in kelp beds warrants further exploration. Interestingly, the vast body of research on sea urchin–kelp interactions in Nova Scotia and elsewhere (Filbee-Dexter & Scheibling 2014) has focused almost entirely on a narrow band of rocky bottom between the intertidal zone and ~25 m depth. To a large extent, this reflects logistical constraints to direct observation within a ‘blind zone’ that exists between the deep (offshore) limit of non-technical scuba diving and the shallow (onshore) limit of camera platforms or submersibles deployed from large oceanographic vessels. Using a towed camera system deployed from a small coastal vessel has enabled us to visualize this blind zone for the first time off Nova Scotia. Our observations indicate that deep-living sea urchins, and the detrital subsidy upon which they rely, likely play a key role in the connectivity between adjacent habitats that influence ecosystem dynamics on a much broader scale than previously recognized.

Acknowledgements. We thank J. Lindley, C. Feehan, K. Krumhansl, F. Francis, and C. Robertson for field and laboratory assistance, and B. Miller for winter sea urchin collections. A. Metaxas and 3 anonymous reviewers provided helpful comments on earlier drafts of the manuscript. This research was funded by a Discovery Grant and a Strategic Networks Grant (Canadian Healthy Oceans Network) to R.E.S. from the Natural Sciences and Engineering Research Council (NSERC) of Canada. K.F.-D. was supported by a NSERC Canada Graduate Scholarship and a Dalhousie Kilam Scholarship.

LITERATURE CITED

- Allredge AL, Gotschalk CC (1990) The relative contribution of marine snow of different origins to biological processes in coastal waters. *Cont Shelf Res* 10:41–58
- Basch LV, Tegner MJ (2007) Reproductive responses of purple sea urchin (*Strongylocentrotus purpuratus*) populations to environmental conditions across a coastal depth gradient. *Bull Mar Sci* 81:255–282
- Bertram DF, Strathmann RR (1998) Effects of maternal and larval nutrition on growth and form of planktotrophic larvae. *Ecology* 79:315–327
- Böttger SA, Devin MG, Walker CW (2006) Suspension of annual gametogenesis in North American green sea urchins (*Strongylocentrotus droebachiensis*) experiencing invariant photoperiod—applications for land-based aquaculture. *Aquaculture* 261:1422–1431
- Brady SM, Scheibling RE (2005) Repopulation of the shallow subtidal zone by green sea urchins (*Strongylocentrotus droebachiensis*) following mass mortality in Nova Scotia, Canada. *J Mar Biol Assoc UK* 85:1511–1517
- Brady SM, Scheibling RE (2006) Changes in growth and reproduction of green sea urchins, *Strongylocentrotus droebachiensis* (Müller), during repopulation of the shallow subtidal zone after mass mortality. *J Exp Mar Biol Ecol* 335:277–291
- Britton-Simmons KH, Foley G, Okamoto D (2009) Spatial subsidy in the subtidal zone: utilization of drift algae by a deep subtidal sea urchin. *Aquat Biol* 5:233–243
- Britton-Simmons KH, Rhoades AL, Pacunski RE, Galloway AW and others (2012) Habitat and bathymetry influence the landscape-scale distribution and abundance of drift macrophytes and associated invertebrates. *Limnol Oceanogr* 57:176–184
- Campos-Creasey LS, Tyler PA, Gage JD, John AWG (1994) Evidence for coupling the vertical flux of phytodetritus to the diet and seasonal life history of the deep-sea echinoid *Echinus affinis*. *Deep-Sea Res I* 41:369–388
- Christiansen JS, Siikavuopio SI (2007) The relationship between feed intake and gonad growth of single and stocked green sea urchin (*Strongylocentrotus droebachiensis*) in a raceway culture. *Aquaculture* 262:163–167
- Colombini I, Chelazzi L, Gibson RN, Atkinson RJA (2003) Influence of marine allochthonous input on sandy beach communities. *Oceanogr Mar Biol Annu Rev* 41:115–159
- de Bettignies T, Wernberg T, Lavery PS, Vanderklift MA, Mohring MB (2013) Contrasting mechanisms of dislodgement and erosion contribute to production of kelp detritus. *Limnol Oceanogr* 58:1680–1688
- Duggins DO, Eckman JE (1997) Is kelp detritus a good food for suspension feeders? Effects of kelp species, age and secondary metabolites. *Mar Biol* 128:489–495
- Duggins DO, Simenstad CA, Estes JA (1989) Magnification of secondary production by kelp detritus in coastal marine ecosystems. *Science* 245:170–173
- Eckelbarger KJ, Watling L (1995) Role of phylogenetic constraints in determining reproductive patterns in deep-sea invertebrates. *Invertebr Biol* 114:256–269
- Falk-Petersen IB, Lønning S (1983) Reproductive cycles of two closely related sea urchin species, *Strongylocentrotus droebachiensis* (OF Müller) and *Strongylocentrotus pallidus* (GO Sars). *Sarsia* 68:157–164
- Feehan C, Scheibling RE, Lauzon-Guay JS (2012) An outbreak of sea urchin disease associated with a recent hurricane: support for the ‘killer storm hypothesis’ on a local scale. *J Exp Mar Biol Ecol* 413:159–168
- Filbee-Dexter K, Scheibling RE (2012) Hurricane-mediated defoliation of kelp beds and pulsed delivery of kelp detritus to offshore sedimentary habitats. *Mar Ecol Prog Ser* 455:51–64
- Filbee-Dexter K, Scheibling RE (2014) Sea urchin barrens as alternative stable states of collapsed kelp ecosystems. *Mar Ecol Prog Ser* 495:1–25
- Garrido CL, Barber BJ (2001) Effects of temperature and food ration on gonad growth and oogenesis of the green sea urchin, *Strongylocentrotus droebachiensis*. *Mar Biol* 138:447–456
- Gattuso JP, Gentili B, Duarte CM, Kleypas JA, Middelburg JJ, Antoine D (2006) Light availability in the coastal ocean: impact on the distribution of benthic photo-

- synthetic organisms and their contribution to primary production. *Biogeosciences* 3:489–513
- Gaudette J, Wahle RA, Himmelman JH (2006) Spawning events in small and large populations of the green sea urchin *Strongylocentrotus droebachiensis* as recorded using fertilization assays. *Limnol Oceanogr* 51:1485–1496
- Guillou M, Lumingas LJ, Michel C (2000) The effect of feeding or starvation on resource allocation to body components during the reproductive cycle of the sea urchin *Sphaerechinus granularis* (Lamarck). *J Exp Mar Biol Ecol* 245:183–196
- Harrold C, Lisin S (1989) Radio-tracking rafts of giant kelp: local production and regional transport. *J Exp Mar Biol Ecol* 130:237–251
- Harrold C, Light K, Lisin S (1998) Organic enrichment of submarine-canyon and continental-shelf benthic communities by macroalgal drift imported from nearshore kelp forests. *Limnol Oceanogr* 43:669–678
- Himmelman JH (1978) Reproductive cycle of the green sea urchin, *Strongylocentrotus droebachiensis*. *Can J Zool* 56:1828–1836
- Himmelman JH, Dumont CP, Gaymer CF, Vallières C, Drolet D (2008) Spawning synchrony and aggregative behaviour of cold-water echinoderms during multi-species mass spawnings. *Mar Ecol Prog Ser* 361:161–168
- Johnson CR, Mann KH (1982) Adaptations of *Strongylocentrotus droebachiensis* for survival on barren grounds in Nova Scotia. In: Lawrence JM (ed) *Echinoderms: proceedings of the international conference*. AA Balkema, Rotterdam, p 277–283
- Keats DW, Steele DH, South GR (1984) Depth-dependent reproductive output of the green sea urchin, *Strongylocentrotus droebachiensis* (OF Müller), in relation to the nature and availability of food. *J Exp Mar Biol Ecol* 80:77–91
- Keats DW, Hooper RG, Steele DH, South GR (1987) Field observations of summer and autumn spawning by *Strongylocentrotus droebachiensis*, green sea urchins, in eastern Newfoundland. *Can Field Nat* 101:463–465
- Kelly JR, Krumhansl KA, Scheibling RE (2012) Drift algal subsidies to sea urchins in low-productivity habitats. *Mar Ecol Prog Ser* 452:145–157
- Kirchhoff NT, Eddy S, Brown NP (2010) Out-of-season gamete production in *Strongylocentrotus droebachiensis*: photoperiod and temperature manipulation. *Aquaculture* 303:77–85
- Kirkman H, Kendrick GA (1997) Ecological significance and commercial harvesting of drifting and beach-cast macroalgae and seagrasses in Australia: a review. *J Appl Phycol* 9:311–326
- Konar B, Estes JA (2003) The stability of boundary regions between kelp beds and deforested areas. *Ecology* 84:174–185
- Krumhansl KA, Scheibling RE (2011) Detrital production in Nova Scotian kelp beds: patterns and processes. *Mar Ecol Prog Ser* 421:67–82
- Krumhansl KA, Scheibling RE (2012a) Production and fate of kelp detritus. *Mar Ecol Prog Ser* 467:281–302
- Krumhansl KA, Scheibling RE (2012b) Detrital subsidy from subtidal kelp beds is altered by the invasive green alga *Codium fragile* ssp. *fragile*. *Mar Ecol Prog Ser* 456:73–85
- Krumhansl KA, Lauzon-Guay JS, Scheibling RE (2014) Modeling effects of climate change and phase shifts on detrital production of a kelp bed. *Ecology* 95:763–774
- Lauzon-Guay JS, Scheibling RE (2007a) Seasonal variation in movement, aggregation and destructive grazing of the green sea urchin (*Strongylocentrotus droebachiensis*) in relation to wave action and sea temperature. *Mar Biol* 151:2109–2118
- Lauzon-Guay JS, Scheibling RE (2007b) Importance of spatial population characteristics on the fertilization rates of sea urchins. *Biol Bull (Woods Hole)* 212:195–205
- Lesser MP, Carleton KL, Böttger SA, Barry TM, Walker CW (2011) Sea urchin tube feet are photosensory organs that express a rhabdomeric-like opsin and PAX6. *Proc R Soc B* 278:3371–3379
- Lyons DA, Scheibling RE (2007) Differences in somatic and gonadic growth of sea urchins (*Strongylocentrotus droebachiensis*) fed kelp (*Laminaria longicruris*) or the invasive alga *Codium fragile* ssp. *tomentosoides* are related to energy acquisition. *Mar Biol* 152:285–295
- Marczak LB, Thompson RM, Richardson JS (2007) Meta-analysis: trophic level, habitat, and productivity shape the food web effects of resource subsidies. *Ecology* 88:140–148
- Meeus JH (1999) *Astronomical algorithms*. Willmann-Bell, Richmond, VA
- Meidel SK, Scheibling RE (1998) Annual reproductive cycle of the green sea urchin, *Strongylocentrotus droebachiensis*, in differing habitats in Nova Scotia, Canada. *Mar Biol* 131:461–478
- Meidel SK, Scheibling RE (1999) Effects of food type and ration on reproductive maturation and growth of the sea urchin *Strongylocentrotus droebachiensis*. *Mar Biol* 134:155–166
- Minor MA, Scheibling RE (1997) Effects of food ration and feeding regime on growth and reproduction of the sea urchin *Strongylocentrotus droebachiensis*. *Mar Biol* 129:159–167
- Munk JE (1992) Reproduction and growth of green urchins *Strongylocentrotus droebachiensis* (Müller) near Kodiak, Alaska. *J Shellfish Res* 11:245–254
- Nakano S, Murakami M (2001) Reciprocal subsidies: dynamic interdependence between terrestrial and aquatic food webs. *Proc Natl Acad Sci USA* 98:166–170
- Norderhaug KM, Fredriksen S, Nygaard K (2003) Trophic importance of *Laminaria hyperborea* to kelp forest consumers and the importance of bacterial degradation to food quality. *Mar Ecol Prog Ser* 255:135–144
- Oganesyan SA (1998) Reproductive cycle of the echinoid *Strongylocentrotus droebachiensis* in the Barents Sea. In: Mooi R, Telford M (eds) *Echinoderms*. AA Balkema, Rotterdam, p 765–768
- Platt T, Jassby AB (1976) The relationship between photosynthesis and light for natural assemblages of coastal marine phytoplankton. *J Phycol* 12:421–430
- Polis GA, Anderson WB, Holt RD (1997) Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. *Annu Rev Ecol Syst* 28:289–316
- Rogers-Bennett L, Bennett WA, Fastenau HC, Dewees CM (1995) Spatial variation in red sea urchin reproduction and morphology: implications for harvest refugia. *Ecol Appl* 5:1171–1180
- Scheibling RE (1986) Increased macroalgal abundance following mass mortalities of sea urchins (*Strongylocentrotus droebachiensis*) along the Atlantic coast of Nova Scotia. *Oecologia* 68:186–198
- Scheibling RE, Gagnon P (2009) Temperature-mediated outbreak dynamics of the invasive bryozoan *Membranipora*

- membranacea* in Nova Scotian kelp beds. *Mar Ecol Prog Ser* 390:1–13
- Scheibling RE, Hatcher BG (2013) *Strongylocentrotus droebachiensis*. In: Lawrence JM (ed) *Edible sea urchins: biology and ecology*, 3rd edn. Elsevier Science, Amsterdam, p 381–412
- Scheibling RE, Hennigar AW (1997) Recurrent outbreaks of disease in sea urchins *Strongylocentrotus droebachiensis* in Nova Scotia: evidence for a link with large-scale meteorologic and oceanographic events. *Mar Ecol Prog Ser* 152:155–165
- Scheibling RE, Stephenson RL (1984) Mass mortality of *Strongylocentrotus droebachiensis* (Echinodermata: Echinoidea) off Nova Scotia, Canada. *Mar Biol* 78: 153–164
- Scheibling RE, Hennigar AW, Balch T (1999) Destructive grazing, epiphytism, and disease: the dynamics of sea urchin–kelp interactions in Nova Scotia. *Can J Fish Aquat Sci* 56:2300–2314
- Scheibling RE, Feehan CJ, Lauzon-Guay JS (2013) Climate change, disease and the dynamics of a kelp-bed ecosystem in Nova Scotia. In: Fernández-Palacios JM, Nascimiento LD, Hernández JC, Clement S, González A, Díaz-González JP (eds) *Climate change perspectives from the Atlantic: past, present and future*. Servicio de Publicaciones de la Universidad de La Laguna, Tenerife, p 41–81
- Shpigiel M, McBride SC, Marciano S, Lupatsch I (2004) The effect of photoperiod and temperature on the reproduction of European sea urchin *Paracentrotus lividus*. *Aquaculture* 232:343–355
- Siikavuopio SI, Christiansen JS, Sæther BS, Dale T (2006) Effects of temperature and season on gonad growth and feed intake in the green sea urchin (*Strongylocentrotus droebachiensis*). *Aquaculture* 255:389–394
- Siikavuopio SI, Christiansen JS, Sæther BS, Dale T (2007) Seasonal variation in feed intake under constant temperature and natural photoperiod in the green sea urchin (*Strongylocentrotus droebachiensis*). *Aquaculture* 272: 328–334
- Starr M, Himmelman JH, Therriault JC (1990) Direct coupling of marine invertebrate spawning with phytoplankton blooms. *Science* 247:1071–1074
- Starr M, Himmelman JH, Therriault JC (1993) Environmental control of green sea urchin, *Strongylocentrotus droebachiensis*, spawning in the St Lawrence Estuary. *Can J Fish Aquat Sci* 50:894–901
- Starr M, Therriault JC, Conan GY, Comeau M, Robichaud G (1994) Larval release in a sub-euphotic zone invertebrate triggered by sinking phytoplankton particles. *J Plankton Res* 16:1137–1147
- Tyler PA, Gage JD (1984) The reproductive biology of echinothuriid and cidarid sea urchins from the deep sea (Rockall Trough, North-East Atlantic Ocean). *Mar Biol* 80:63–74
- Vanderklift MA, Wernberg T (2008) Detached kelps from distant sources are a food subsidy for sea urchins. *Oecologia* 157:327–335
- Wahle RA, Peckham SH (1999) Density-related reproductive trade-offs in the green sea urchin, *Strongylocentrotus droebachiensis*. *Mar Biol* 134:127–137
- Walker CW, Lesser MP (1998) Manipulation of food and photoperiod promotes out-of-season gametogenesis in the green sea urchin, *Strongylocentrotus droebachiensis*: implications for aquaculture. *Mar Biol* 132:663–676
- Walker CW, Lesser MP, Unuma T (2013) Sea urchin gametogenesis – structural, functional and molecular/genomic biology. In: Lawrence JM (ed) *Edible sea urchins: biology and ecology*, 3rd edn. Elsevier Science, Amsterdam, p 25–43
- Witman JD (1988) Stability of Atlantic kelp forests. *Trends Ecol Evol* 3:285–286

Editorial responsibility: Alistair Poore,
Sydney, Australia

Submitted: April 30, 2014; Accepted: September 22, 2014
Proofs received from author(s): December 1, 2014