Environmental and biological drivers of feeding and spatial dynamics in the green sea urchin, *Strongylocentrotus droebachiensis*

by

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ABSTRACT

In eastern Canada, the destruction of foundational kelp beds by dense aggregations (fronts) of the omnivorous green sea urchin, *Strongylocentrotus droebachiensis*, is a key determinant of the structure and dynamics of shallow reef communities. Current knowledge about factors affecting the ability of *S. droebachiensis* to exert top-down community control is based largely on observational studies of patterns in natural habitats, yielding fragmentary, and sometimes contradictory, results. The present research incorporated laboratory microcosm experiments and surveys of urchins in natural habitats to test the effects of abiotic (wave action, water temperature) and biotic (body size, population density) factors on: (1) individual and aggregative feeding on the winged kelp, *Alaria esculenta*; and (2) displacement, microhabitat use, distribution, and aggregation in food-depleted habitats. Wave action, water temperature, and body size strongly affected the ability of urchins to consume kelp: individual feeding increased with increasing body size and temperature, while aggregative feeding decreased with increasing wave action. Yet, feeding in large urchins dropped by two orders of magnitude between 12 and 18°C. Increasing wave action triggered shifts in urchin displacement, microhabitat use, distribution, and aggregation: urchins reduced displacement and abandoned flat surfaces in favour of crevices. They increasingly formed two-dimensional aggregations at densities ≥110 individuals m^{-2}. Collectively, results provide a foundational understanding of some of the drivers of feeding and spatial dynamics of *S. droebachiensis* and potential impacts on the formation of grazing fronts.

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CO-AUTHORSHIP STATEMENT

The work described in the present thesis was conducted by Desta Frey with guidance from Patrick Gagnon, Mark Abrahams, and Edward Miller. Desta Frey was responsible for field and laboratory data collection and analysis (with assistance by Patrick Gagnon) and contributed to modifications brought to the original design by Patrick Gagnon. All chapters were written by Desta Frey with intellectual and editorial input by Patrick Gagnon. Chapter II is published in *PLoS One*. Any additional publication in the primary literature resulting from work in the present thesis will be co-authored by Desta Frey and Patrick Gagnon.

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CHAPTER I

General introduction

Biological communities are shaped by interactions among organisms, and between organisms and the environment (Jones and Lawton 1995, Bertness et al. 2001, Begon et al. 2006). Physical factors such as salinity, light, water motion, and temperature affect the life history, physiology, behaviour, distribution, and abundance of marine organisms (e.g. Menge and Sutherland 1987, Siddon and Witman 2003, Wiencke et al. 2006). Hydrodynamic forces can reduce the ability of consumers to move body parts and displace, ultimately affecting foraging (Powers and Kittinger 2002, Gagnon et al. 2003, St-Pierre and Gagnon 2015). Because metabolic rates scale with temperature and body size (Gillooly et al. 2001, Brown et al. 2004), ectothermic consumers are, in general, particularly sensitive to changes in sea state and temperature (Huey and Kingsolver 1989, Angilletta et al. 2002). Experimental demonstrations of wave- and temperature-induced shifts in functionally important, ectothermic consumers are generally lacking. This knowledge gap limits the ability to formulate accurate predictions about the frequency and magnitude of changes in marine communities resulting from accelerating shifts in sea state and temperature (Scheffer et al. 2001, Wang et al. 2004, deYoung et al. 2008, Lauzon-Guay et al. 2009, Young et al. 2011).

Regime shifts are broadly defined as relatively abrupt, persistent changes from one community state to another (Scheffer et al. 2001, Folke et al. 2004, deYoung et al. 2008). One classical example of a marine regime shift is the switch from a “kelp bed” community state dominated by kelp, those large brown seaweeds of the order Laminariales (Tegner and Dayton 2000), to a “barrens” community state dominated by red coralline algae (Lawrence 1975, Breen and Mann 1976, Lubchenco and Gaines 1981, Dayton 1985). Shifts between kelp bed and barrens states are largely driven by grazing of kelp by sea urchins, which varies with urchin and kelp abundance (Lawrence 1975, Steneck et al. 2002, Filbee-Dexter and Scheibling 2014, Ling et al. 2015). In the northern hemisphere, barrens can be extensive and persist for decades provided urchin biomass is sufficiently high to prevent the recruitment of kelp sporophytes (Cowen et al. 1982, Himmelman 1984, Johnson and Mann 1988, Sivertsen 1997, Scheibling et al. 1999). Studies of kelp recruitment following experimental removal and natural die-offs of urchins established the importance of cyclical and episodic declines of urchin populations to kelp bed re-establishment (Himmelman et al. 1983, Miller 1985, Scheibling 1986, Leinaas and Christie 1996, Gagnon et al. 2004). Many ecologically and economically important invertebrate and fish species use kelp beds as a prime habitat to feed, reproduce, and reduce the risk of predation (Dayton 1985, Tegner and Dayton 2000, Steneck et al. 2002, Bégin et al. 2004). Urchins, therefore, can exert strong top-down community control through removal of foundational (*sensu* Bruno and Bertness 2001) kelp biomass (Breen and Mann 1976, Johnson and Mann 1988, Scheibling et al. 1999, Steneck et al. 2002, Gagnon et al. 2004).

Urchins increase their ability to remove kelp biomass by forming feeding aggregations, termed “fronts”. Urchins in grazing fronts climb on kelp stipes and weigh down blades, which facilitates kelp consumption (Breen and Mann 1976, Scheibling et al. 1999, Gagnon et al. 2004, Lauzon-Guay and Scheibling 2007a, b). Such fronts typically form at the lower edge of kelp assemblages and advance through kelp at rates that depend largely on urchin and kelp biomass, but also on wave-induced movement of kelp fronds, which can deter urchins (Velimirov and Griffiths 1979, Scheibling et al. 1999, Konar and Estes 2003, Gagnon et al. 2006, Lauzon-Guay and Scheibling 2007a). The omnivorous green sea urchin, *Strongylocentrotus droebachiensis*, is one of the most conspicuous ectothermic consumers in shallow reef communities in the northern hemisphere (Scheibling and Hatcher 2007). It is found in arctic regions of the Atlantic and Pacific oceans, ranging as far south as Cape Cod and Oregon, USA (Jensen 1974, Ojeda and Dearborn 1989, Scheibling and Hatcher 2007). It can tolerate water temperatures as low as ~0 and as high as 22°C (Percy 1973), consuming a wide variety of food items including invertebrates, fish, and seaweeds with a clear preference for kelp (Himmelman and Steele 1971, Vadas 1977, Briscoe and Sebens 1988, Himmelman and Nédélec 1990).

In eastern Canada, green sea urchin fronts can advance over kelp beds at rates as high as 4 m month^{-1} (Scheibling et al. 1999, Gagnon et al. 2004, Lauzon-Guay and Scheibling 2007b), leaving behind extensive barrens colonized by red coralline algae (mainly *Clathromorphum*, *Lithothamnion*, and *Phymatolithon* spp.) and a few grazing-resistant fleshy seaweeds (mainly *Agarum clathratum*, *Desmarestia viridis*, and *Ptilota serrata*) (Gagnon et al. 2005, Gagnon et al. 2006, Adey and Hayek 2011, Blain and Gagnon 2014). Urchins can persist in these barrens for decades (Johnson and Mann 1982) by mainly consuming detrital kelp, corallines, and animal carcasses (Kelly et al. 2012). Laboratory and field studies suggest a threshold urchin biomass of 2 to 5 kg m^{-2} below which grazing fronts cannot reduce the limit of kelp beds (Scheibling et al. 1999, Gagnon et al. 2004). However, knowledge about how hydrodynamic and thermal environments affect the formation of grazing fronts, speed of kelp bed destruction by fronts, and foraging of *S. droebachiensis*, is sparse. A few observational field studies suggest that: (1) individual displacement, urchin density at the front, and rate of kelp bed destruction by fronts are negatively related to wave height and current speed [Dumont et al. 2006, Lauzon-Guay and Scheibling 2007a, b]; and (2) the wave environment has a much greater influence than temperature on the regulation of urchin-kelp interactions across the 0-18°C range [Lauzon-Guay and Scheibling 2007b, Feehan et al. 2012]. Laboratory studies found both positive (Larson et al. 1980, Siikavuopio et al. 2006) and negative (Himmelman 1984, Scheibling and Anthony 2001) relationships between temperature and individual (non-aggregative) feeding rate in *S. droebachiensis*. More studies are required to elucidate the relationships between water motion, temperature, and urchin-kelp interactions.

A number of studies established that the ability of *S. droebachiensis* to exert top-down community control depends primarily on displacement, distribution, and aggregation at the kelp-barrens interface (reviewed by Filbee-Dexter and Scheibling 2014, Ling et al. 2015). Far fewer studies have examined urchin displacement, distribution, or aggregation in barrens (but see Garnick 1978, Hagen and Mann 1994, Dumont et al. 2004, 2006, Lauzon-Guay et al. 2006), where food including kelp is scarce and less likely to influence urchin activity. Current evidence suggests that urchin populations in barrens are the primary source of new individuals to grazing fronts following disturbance (Scheibling et al. 1999, Brady and Scheibling 2005). This hypothesis stresses the need to conduct additional studies of urchin spatial dynamics in barrens. A few studies showed that urchin displacement in barrens is negatively related to wave height or current speed (Dumont et al. 2006, Lauzon-Guay et al. 2006, Lauzon-Guay and Scheibling 2007b, Morse and Hunt 2013). This finding suggests that the hydrodynamic environment mediates important components of the behavioural repertoire and foraging of *S. droebachiensis* in barrens that hinge on the ability to move. One such component is the ability to move and attach to different seabed topographies (microhabitats) in response to shifting hydrodynamic conditions. A few studies report that (1) green sea urchins can cluster in crevices and along the base of rocky outcrops during periods of strong wave action (Garnick 1978, Vadas et al. 1986, Scheibling et al. 1999); and (2) the degree to which urchins are aggregated in laboratory tanks and field cages generally increases with urchin density (Bernstein et al. 1983, Hagen and Mann 1994). Further research incorporating rigorous experimental testing is required to study the effects of wave action and urchin density on displacement, microhabitat use, distribution, and aggregation of *S. droebachiensis* in barrens.

Hydrodynamic and thermal regimes can vary considerably in shallow coastal ecosystems in southeastern Newfoundland (SEN) (Blain and Gagnon 2013, Gagnon et al. 2013), making these systems particularly suitable for studies of the effects of wave action and temperature on feeding and foraging in *S. droebachiensis*. Kelp beds in SEN are primarily composed of *Alaria esculenta* interspersed with *Laminaria digitata* (Fig. 1.1, Keats et al. 1982, Chapman and Johnson 1990, Gagnon et al. 2013, Blain and Gagnon 2014). Beds are largely restricted to a refuge in shallow water where wave action presumably impedes urchin grazing (Himmelman and Steele 1971, Himmelman 1984, Keats et al. 1985, 1990, Keats 1991). Like in the northern Gulf of St. Lawrence and Nova Scotia (Scheibling et al. 1999, Gagnon et al. 2004), green sea urchins form grazing fronts that destructively graze the lower edge of kelp beds, leaving large tracts of barrens behind (Himmelman 1984, Keats et al. 1990). A few observational studies suggest that barrens in SEN can persist for >40 years, much longer than the 15-year lifespan of most barrens in Nova Scotia (Keats 1991, Filbee-Dexter and Scheibling 2014). This thesis investigates

Fig. 1.1. Transition between kelp (*Alaria esculenta*) bed and urchin (*Strongylocentrotus droebachiensis*) barrens on 25 June, 2011 at a depth of 3 m in Bay Bulls, southeastern Newfoundland (Photo: Patrick Gagnon).

the causes of feeding and foraging variability in *S. droebachiensis* by studying the effects of abiotic (wave action, water temperature) and biotic (body size, population density) factors on: (1) individual and aggregative feeding on *A. esculenta*; and (2) displacement, microhabitat use, distribution, and aggregation in food-depleted habitats. Work involves laboratory experiments in water baths and an oscillatory wave tank at the Ocean Sciences Centre of Memorial University of Newfoundland with *S. droebachiensis* collected from Bread and Cheese Cove (BCC) in Bay Bulls (SEN), as well as surveys of urchin populations and kelp-bed boundary dynamics at BCC and an adjacent site, Cape Boone Cove (CBC).

Chapter II integrates experimental, observational, and analytical approaches to test the hypothesis that water temperature can predict short-term (over a few months) kelp bed destruction by *S. droebachiensis* in calm hydrodynamic environments. Specifically, two laboratory experiments investigate effects of water temperature and urchin body size on individual feeding, as well as of wave velocity on aggregative feeding at two times of year. Variation in kelp-bed boundary dynamics, sea temperature, and wave height are also quantified over three months at CBC to study relationships between environmental variability and urchin density at the kelp-barrens interface. Results from the latter survey are used to generate data against which to test the validity of thermal tipping ranges and regression equations derived from laboratory results.

Chapter III reports on the results of two complementary experiments in an oscillatory wave tank, and observations over six months at two barrens sites at BCC, to examine effects of varying hydrodynamic conditions on displacement, microhabitat use, distribution, and aggregation in *S. droebachiensis*. The two experiments mimic barrens conditions, including the back-and-forth flow of waves, to identify velocities and urchin densities triggering shifts in displacement, microhabitat use, distribution, and aggregation. Field observations test the generality of the results from the laboratory experiments by examining variation in wave height and sea temperature, and associated changes in microhabitat use and distribution.

Chapters II and III are written in a format compatible with the publication of scientific articles, motivating the repetition of core information and use of first-person plural pronoun ("we") and possessive determiner ("our") throughout. Chapter IV presents a summary of main findings and their contribution to advancing knowledge about the factors influencing feeding and spatial dynamics in *S. droebachiensis*. It also discusses future research directions in this area.

CHAPTER II

Thermal and hydrodynamic environments mediate individual and aggregative feeding of a functionally important omnivore in reef communities

2.1 INTRODUCTION

Shallow reef communities in high-latitude seasonal seas are exposed to considerable variation in thermal and hydrodynamic environments (Menge and Sutherland 1987, Siddon and Witman 2003, Schiel et al. 2004). Mobile consumers in these environments typically exhibit behavioural shifts across gradients of water temperature and wave action to balance physiological requirements and biomechanical limitations (Rochette et al. 1994, Taylor and Collie 2003, Smee et al. 2010). Alterations to species interactions ensuing from behavioural shifts can ultimately shape population dynamics and biodiversity patterns (Lubchenco and Gaines 1981, Dayton et al. 1992, Menge et al. 1994). A number of studies show that displacement toward, and consumption of, prey in mobile solitary invertebrates are respectively positively and negatively related to water temperature and wave action (Sanford 2002, Rilov et al. 2005, Matheson and Gagnon 2012). Yet, we know much less about how temperature and wave action affect foraging in mobile gregarious invertebrates (Kawamata 1998, Jenkins and Hartnoll 2001, Robles et al. 2001). Understanding plasticity in foraging and interspecific interactions of functionally important consumers is a key step toward anticipating and mitigating alterations to reef communities resulting from ongoing global shifts in sea temperature and state (Halpern et al. 2008, Burrows et al. 2011, Kordas et al. 2011, Harley 2013).

Because of its high destructive potential, the omnivorous green sea urchin, *Strongylocentrotus droebachiensis*, has become one of the most scrutinized organisms in studies of subtidal community dynamics in the northern hemisphere (Scheibling and Hatcher 2007). In eastern Canada, the destruction of foundational (*sensu* Bruno and

Bertness 2001) kelp beds by dense green sea urchin aggregations (fronts) is a key determinant of the structure and dynamics of shallow reef communities (Breen and Mann 1976, Himmelman 1984, Johnson and Mann 1988, Scheibling et al. 1999, Steneck et al. 2002, Gagnon et al. 2004). In Nova Scotia and the northern Gulf of St. Lawrence, fronts can destroy kelp beds and associated biota at rates as high as 4 m month^{-1}, leaving behind pavements of grazing-resistant, red coralline seaweeds termed “barrens” (Scheibling et al. 1999, Gagnon et al. 2004, Lauzon-Guay and Scheibling 2007b). Recent studies of relationships among urchin front formation, kelp bed destruction by fronts, and environmental variability in Nova Scotia suggest that wave action has a much greater effect than sea temperature on the regulation of urchin-kelp interactions across the 0-18°C range. For example, urchin density at fronts has been negatively correlated with wave height, with no detectable effect of water temperature on the rate of advance of, and urchin density at, fronts below a suggested threshold of ~17°C (Lauzon-Guay and Scheibling 2007a, b). Feehan et al. (2012) propose that the lack of a density threshold for destructive grazing in pre-existing gaps in kelp canopies, which is inconsistent with other studies in eastern Canada (Breen and Mann 1976, Scheibling et al. 1999, Gagnon et al. 2004, Lauzon-Guay and Scheibling 2007a), was due to insufficient wave action allowing urchins to aggregate and feed upon kelp more readily. Temperature in the latter study also did not appear to explain any of the observed variation in urchin-kelp dynamics (Feehan et al. 2012).

The notion that temperature has virtually no effect on these relationships challenges the tenets of the metabolic theory of ecology (MTE), which links the performance of individual organisms to the ecology of populations, communities, and ecosystems (Brown et al. 2004). According to the MTE, individual performance, and hence species interactions, is largely determined by (1) temperature, which affects biochemical reactions; and (2) body size, which affects the minimal rate of energy expenditure necessary for survival (Gillooly et al. 2001, Brown et al. 2004). In general, rates of biochemical reactions are optimized as temperature and body size increase, so long as temperature is within the range of normal activity, which for most organisms lies between 0 and 40°C (Brown et al. 2004). This, in theory, makes ectothermic organisms such as urchins particularly sensitive to variations in the thermal environment. Some studies show or suggest a positive relationship between water temperature and rates of displacement and feeding in individual (non-aggregated) urchins across the 0-18°C temperature range (Vadas 1977, Larson et al. 1980, Siikavuopio et al. 2006). Yet, that a few other studies show contradictory results, whereby individual feeding rates peak at low, rather than higher, temperatures (Himmelman 1984, Scheibling and Anthony 2001) further attests to the complexity of the factors and processes that control individual and aggregative feeding in the green sea urchin. We argue that the apparent lack of a relationship between sea temperature and rates of individual and aggregative feeding in *S. droebachiensis*, may be because: (1) most of the studies yielding this conclusion are observational, which does not allow for proper testing and partitioning of causal links between temperature, wave action, and feeding; (2) wave conditions over which urchin-kelp interactions were measured were generally too high for temperature to emerge as a significant factor; and (3) effects of temperature on individual and aggregative urchin performance (in this case displacement and feeding), and how they may change temporally, have been largely overlooked.

In the present study, we integrate experimental, observational, and analytical approaches to test the hypothesis that water temperature can predict short-term (over a few months) kelp bed destruction by *S. droebachiensis* in calm hydrodynamic environments. This hypothesis stems from the argument that under low hydrodynamic forces, urchin displacement, and hence the capacity to aggregate at the lower margin of kelp beds and consume kelp, should increase proportionally with temperature. It assumes that short-term changes in density at the front result primarily from increased immigration or emigration of urchins from or to the adjacent barrens and kelp bed, as opposed to broader-scale processes such as mortality or the recruitment of new individuals from reproductive events. Specifically, we carry out two laboratory experiments to investigate effects of water temperature and urchin body size on individual feeding, as well as of wave action on aggregative feeding at two times of year. We quantify variation in kelp-bed boundary dynamics, sea temperature, and wave height over three months at one subtidal site in Newfoundland to study relationships between environmental variability and urchin density at the kelp-barrens interface. We use results from the latter survey to generate data against which we test the validity of thermal tipping ranges and regression equations derived from laboratory results.

2.2 MATERIALS AND METHODS

2.2.1 Study and collection sites

The present study was conducted with *Strongylocentrotus droebachiensis* and *Alaria esculenta* at, or collected from, two adjacent sites on the north shore of Bay Bulls, Newfoundland (Canada): Bread and Cheese Cove (BCC, 47°18'30.8" N, 52°47'19.1" W) and Cape Boone Cove (CBC, 47°18' 30.4" N, 52°47' 11.1" W). The BCC and CBC sites are separated by a rocky outcrop, Bread and Cheese Point, which extends ~150 m into the bay along a north-south axis. The seabed at both sites is composed of gently sloping bedrock, to a depth of ~15 m (chart datum), with scattered boulders between 3 and 5 m at BCC. At BCC, kelp beds, mainly *A. esculenta* and *Laminaria digitata*, dominate the 0-2 m depth range, followed by an extensive urchin (*S. droebachiensis*) barrens to a depth of ~15 m. Transient beds of the annual, acidic, brown seaweed *Desmarestia viridis* establish every year in this barrens (Blain and Gagnon 2014) and are interspersed with a few stands of the grazing-resistant kelp *Agarum clathratum* (Gagnon et al. 2005). At CBC, an extensive (several 100s of m^2) kelp bed dominated by *A. esculenta* establishes to a depth of ~9 m during spring, followed in deeper water by an urchin barrens. Scattered patches of *L. digitata* develop in the *A. esculenta* bed between 0 and 4 m.

2.2.2 Collection and acclimation of urchins prior to experimentation

Urchins used in the two laboratory experiments described below were hand collected by divers at depths of 3 to 6 m at BCC between 18 April and 27 September, 2012. They were transported in large containers filled with seawater to the Ocean

Sciences Centre (OSC) of Memorial University of Newfoundland. Upon arrival at the OSC (<5 hours after collection), urchins were transferred to 330-L holding tanks supplied with ambient flow-through seawater pumped in from a depth of ~5 m in the adjacent embayment, Logy Bay. Each holding tank contained one group of 200 urchins fed every two days with 25 g (wet weight) of freshly collected blades (including midribs) of *Alaria esculenta* cut into pieces of ~2.5 x 2.5 cm (in the present study all organisms were weighed with the same balance with a precision of ±0.1 g; PB3002-S/FACT; Mettler Toledo). Urchin feces and unconsumed kelp, if any, were removed from the holding tanks prior to adding new kelp. Urchins were used in the experiments within 1-2 weeks after collection.

2.2.3 Experiment 1: water temperature, body size, and individual urchin feeding

To investigate effects of water temperature and body size on individual feeding, we used a factorial experiment, Experiment 1, in which small, 25-35 mm in test diameter (t.d.), and large, 45-60 mm t.d., urchins were allowed to graze *Alaria esculenta* in seawater at six temperatures: 3, 6, 9, 12, 15, and 18°C. Our objective was to examine individual feeding during the first few weeks of summer, when urchin aggregation and grazing increase at the lower margin of kelp beds in eastern Canada (Scheibling et al. 1999, Gagnon et al. 2004, Lauzon-Guay and Scheibling 2007b). We chose these temperature treatments because sea temperature in coastal Newfoundland, including at BCC, generally increases by 10-15°C between June (~1-2°C) and early August (~12-16°C) (Caines and Gagnon 2012, Blain and Gagnon 2013).

We ran the experiment from 22 June to 28 July, 2012. Trials lasted 22 h (preliminary trials showed demonstrable kelp consumption over this period), and were conducted in three adjacent water baths (GD120L; Grant) that contained a solution with a 1:1 ratio of water to anti-freeze. Each water bath held three 5-L plastic containers, which were filled with new seawater before each trial and maintained at the appropriate treatment temperature by the anti-freeze solution circulating between the three containers. The volume of each bath enabled running simultaneously one replicate of six of the 12 experimental treatments. Each full run was therefore completed over two consecutive days by applying three randomly chosen temperature treatments on the first day and the remaining three temperatures on the second day. Temperature treatments were assigned randomly to each bath on each day. On each day, one group of three small urchins and one group of three large urchins were each introduced to one of two 5-L plastic containers in each bath pre-filled with seawater from the holding tanks. Mean daily water temperature at BCC and in the holding tanks supplied from Logy Bay varied simultaneously from 4.2°C to 12.4°C, meaning that urchins were exposed to the same thermal conditions as in their natural habitat prior to being used in the experiment. As a result, urchins in ~12% of the trials were exposed to changes in temperature of up to 10-13°C. Changes of this magnitude may qualify as a shock. However, they do occur in coastal Newfoundland (including BCC) in early summer, with relatively frequent drops and rises of up to 10°C over the course of only a few hours to days (Caines and Gagnon 2012, Blain and Gagnon 2013). We did not acclimate the urchins to the experimental temperature treatments because (1) incorporating the natural thermal history of urchins into trials was a more accurate representation of natural processes affecting individual urchin feeding over the short term; and (2) the variable thermal environment to which they were exposed prior to trials made it impossible to determine a proper acclimation time for each temperature treatment. Nevertheless, the water in each container was gradually cooled or warmed to the desired experimental temperature over the four hours preceding the onset of all trials to facilitate the thermal transition of urchins.

Each trial began with the introduction, in each bath, of 10±0.5 g (wet weight) of freshly collected *A. esculenta* blades cut in ~2.5 x 2.5 cm pieces to each of the two containers with urchins and a third container with no urchins. Containers with kelp but no urchins were used to correct kelp tissue loss to grazing for autogenic loss or gain. The order of the three containers in each bath was determined randomly. The unconsumed kelp was wet weighed at the end of trials. We used the equation: Kelp loss = $((T_o \times C_f / C_o) - T_f)$ to obtain the corrected kelp loss in each container with urchins, where T_o and T_f are the initial and final weights of kelp tissues exposed to urchins, respectively, and C_o and C_f are the initial and final weights of the corresponding autogenic control, respectively (Blain and Gagnon 2014).

We used feeding rates in each container to calculate the mean feeding rate for each temperature and urchin body size treatment. Feeding rate was obtained by dividing the corrected kelp tissue loss by the number of urchins (three) and duration of trial (22 h). Each trial was run with new urchins and kelp. A gentle stream of air bubbles was continuously injected in each container with aquaria pumps (Maxima, Hagen) to maintain oxygenation, since the 5-L containers were not configured with flow-through seawater.

The 12 experimental treatments were replicated eight times, and each trial was run with urchins not used previously.

2.2.4 Experiment 2: wave action, season, and aggregative urchin feeding

In the present study, “wave action” refers to the combined effects of hydrodynamic forces, which affect the ability of mobile consumers to move toward (direct effect) and contact (indirect effect) sweeping algal fronds. Urchins undergo both effects in natural habitats, which ultimately modulate foraging (Gagnon et al. 2006). Accordingly, we studied the overall impact of wave action on feeding, rather than the direct and indirect effects separately.

To investigate effects of wave action on aggregative feeding, we conducted a microcosm experiment, Experiment 2, in an oscillatory wave tank (Fig. 2.1), which simulated the wave-induced sweeping motion of kelp blades in natural habitats (Gagnon et al. 2003). The experiment was conducted in spring 2012, and again in late summer 2012, to test the prediction that aggregative feeding is generally lower in spring than summer. Groups of 118 large (40-60 mm t.d.) urchins, corresponding to 292 individuals m^{-2} at the onset of trials, were allowed to graze *Alaria esculenta* sporophytes at four wave velocities: 0.0 m s^{-1} (Null), 0.1 m s^{-1} (Low), 0.2 m s^{-1} (Intermediate), and 0.3 m s^{-1} (High) (peak longitudinal velocity measured in the centre of, and at ~5 cm above, the surface of the experimental area with a Doppler current meter [Vector Current Meter; Nortek]; see Appendix A for specifications of the wave tank system and general pattern of water flow at each velocity). Wave velocity was changed

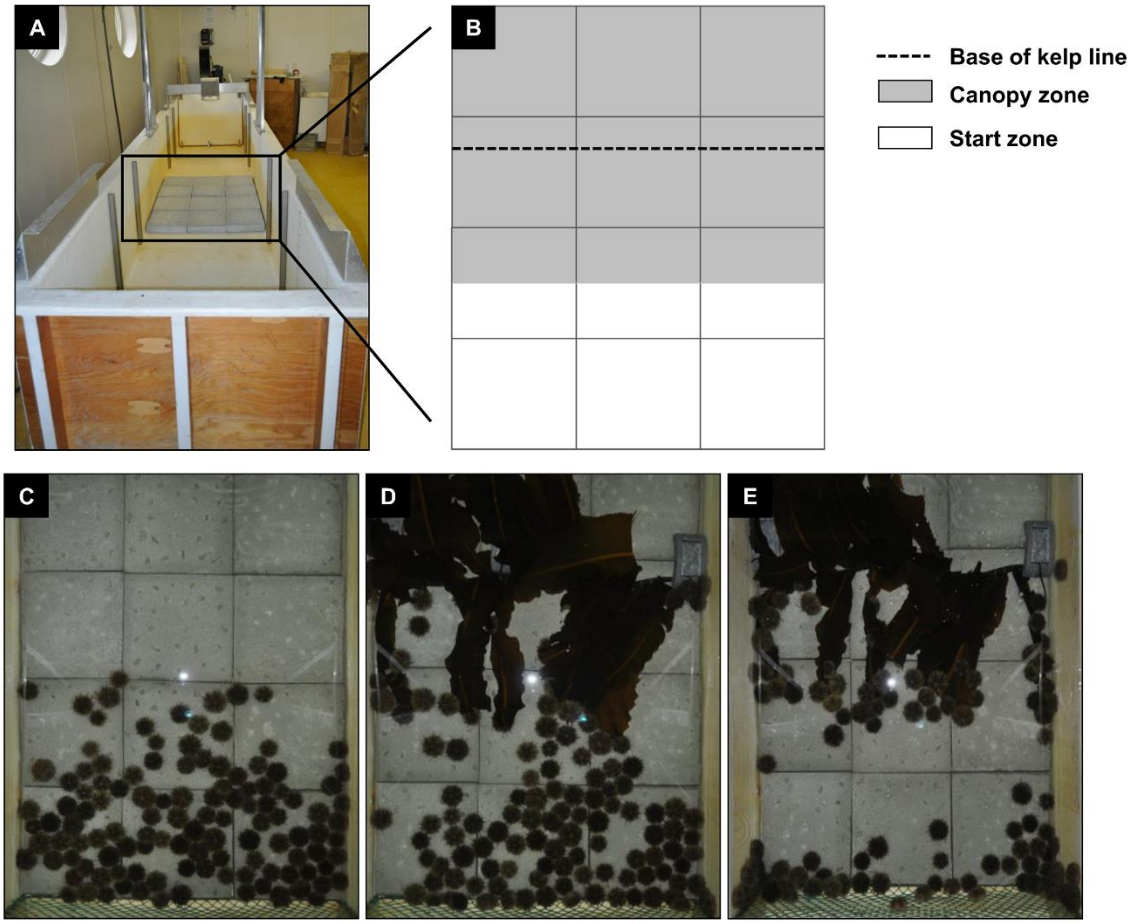


Fig. 2.1. Oscillatory wave tank used in Experiment 2. (A) Position of the experimental area [3×4 grid of concrete tiles of 0.3×0.3×0.05 m each], and (B) relative positions of the kelp (*Alaria esculenta*) line, zone of maximum canopy cover [Canopy zone], and zone to which green sea urchins (*Strongylocentrotus droebachiensis*) were introduced prior to the onset of trials [Start zone]. The sequence at the bottom shows urchins at (C) t=0 [prior to introducing the kelp line], (D) t=1 h, and (E) t=6 h [end] of a trial at a wave velocity of 0.1 m s^{-1} (see Section 2.2.4 for details).

by adjusting water depth in the tank (see Appendix A for water depth at each velocity). Urchin density was similar to that at fronts at the lower edge of *A. esculenta* beds in the northern Gulf of St. Lawrence (Himmelman 1986, Gagnon et al. 2004). Wave velocity included the threshold value of ~0.3 m s^{-1} above which displacement in *S. droebachiensis* virtually ceases (Gagnon et al. 2006). Sporophytes formed a line similar to the lower edge of a kelp bed (see below). We used a fixed frequency of 14 wave cycles min^{-1} in treatments with waves because (1) we were interested in the effects of water velocity on aggregative feeding, rather than the effects of wave frequency per se; and (2) it reflects the general wave frequency under moderate winds at our collection and survey sites.

Trials were conducted on a 3 x 4 grid arrangement of concrete tiles (12 tiles, each 0.3 x 0.3 x 0.05 m), yielding an experimental area of 1.08 m^2 (Fig. 2.1). The grid was located in the centre of the wave tank, where sinusoidal waves caused kelp blades to sweep back and forth at the onset of trials, when none of the urchins were in contact with the blades (Fig. 2.1). The grid was delimited longitudinally by the tank walls, and transversally by nylon netting with 2.5-cm mesh to restrict urchins to the experimental area. Preliminary measurements of water velocity with and without netting showed no perceptible changes along the *u*, *v*, and *w* vectors (in the *x*-, *y*-, and *z*-direction, respectively). The upper surface of the tiles was sculpted with holes, cracks, and waves to simulate natural bedrock heterogeneity. The kelp line consisted of *A. esculenta* sporophytes (40 cm in length), with stipes wedged into a split (at 1.5 cm intervals) made along a rubber hose (84 cm in length, 1.5 cm in diameter) and held in place by winding electrical tape around the hose. During trials, the hose was anchored down by 3-kg lead weights, and oriented so as to maintain kelp stipes at an angle of ~45° to the bottom of the tank, towards the urchins. In this position, the blade tips touched the bottom, mimicking what happens with kelp at the lower edge of the kelp fringe. We made two kelp lines, which we used in alternation from one trial to another. Between trials, the lines were maintained in holding tanks supplied with ambient flow-through seawater and new sporophytes were added to each line to replace those grazed during trials. The wet weight of the kelp line (including hose and tape) was determined before and after trials after shaking the line gently until no water came off. Kelp weight on the line was standardized at the onset of each trial by trimming a few sporophytes to a total line weight of 650 (±32.5) g.

Each trial lasted six hours to allow sufficient time for urchins to form fronts and consume detectable amounts of kelp at all wave velocities as determined with preliminary trials. All (118) urchins were introduced, oral surface down, to the “Start zone”, defined by the surface area (0.405 m^2) of the outermost 1.5 rows of cross-current tiles in the grid (Fig. 2.1). Urchins were allowed to explore the experimental area in the absence of waves for one minute following the placement of the last individual. In trials with waves, the motor was turned on to create an initial wave velocity of 0.1 m s^{-1}. The velocity was gradually increased over the next two and five minutes in the 0.2 and 0.3 m s^{-1} treatments, respectively, by adding water to the tank. This gradual increase was necessary to allow urchins in these two treatments to adapt to higher hydrodynamic forces and avoid dislodgement (in preliminary trials a few urchins detached from the tank bottom when velocity was increased more quickly). Urchins at all velocity treatments were allowed to move for a total of 6 min, with no change in velocity in the 0.0 and 0.1 m s^{-1} treatments. Waves were then stopped, and urchins that had left the start zone (generally <10 individuals in the 0.2 and 0.3 m s^{-1} treatments) were moved back into it to standardize the initial urchin distribution among trials. The onset of the trial (t=0) was marked by the introduction of the kelp line to the other end of the grid, so as to have a space of ~40 cm between the kelp blades and nearest urchins. The motor was turned on again in treatments with waves. At the end of the trial (t=6 h) we stopped waves (as required), counted and removed urchins that were consuming kelp, and removed the kelp line. We then photographed the experimental area with a digital camera (D5000; Nikon) located 1.3 m above the water surface, and weighed the kelp line. The tank was emptied, and feces and occasional kelp debris were removed. New seawater was added to the tank in the hour preceding each trial.

Kelp loss to feeding was corrected for autogenic loss or gain as determined from trials in which kelp lines were exposed for 2 h to the same velocity treatments as above (n=5 [spring] and 3 [summer] for each wave treatment), except no urchins were introduced to the tank. Preliminary trials showed no difference in kelp loss or gain between 2-h and 6-h trials. The same equation as in Experiment 1 was used to determine the corrected kelp loss in each trial. We used feeding rates in each trial to calculate the mean feeding rate for each velocity treatment in each season. Feeding rate was obtained by dividing the corrected kelp tissue loss by the number of urchins (118) and duration of trial (6 h). We used direct counts, images of the experimental area at the end of trials, and PhotoImpact v6.0 (Ulead Systems, Inc.), to determine the numbers of urchins: (1) feeding on kelp; (2) underneath [and not feeding] the kelp canopy; (3) on the tiles, outside of the area swept by kelp; and (4) on the longitudinal walls of the tank and transverse nettings, collectively termed “the walls”. Urchins in the latter three categories respectively provided an indication of the tendency and ability of urchins to penetrate the kelp line at the lower margin of kelp beds, remain more or less stationary on a flat surface like in urchin barrens, and displace and take higher risks of dislodgement by climbing on vertical surfaces like rocks in barrens and kelp within beds.

Each wave velocity treatment was replicated eight times during spring (23 April to 30 May), and seven times during late summer (26 August to 3 October), 2012. We blocked trials over time within each season by running one replicate of each treatment on four consecutive days (one trial per day). The order of the treatments among days was randomized in each block of four days. We alternated the position of the kelp line between the two transverse edges of the experimental area (and hence that of the start zone for urchins) between trials. The tiles were reshuffled randomly within the grid before the start of each trial. Each trial was run with new urchins. Water temperature in the wave tank during the spring and summer trials was 5.1 (±0.2) °C and 13.9 (±0.4) °C, respectively.

2.2.5 Field observations: water temperature, wave action, and kelp-bed boundary dynamics

To test the hypothesis that water temperature can predict short-term kelp bed destruction by *Strongylocentrotus droebachiensis* in calm hydrodynamic environments, we studied changes over three months in: (1) the absolute position of the lower limit of the kelp bed at CBC; (2) urchin density at the front and fixed distances from the shifting position of the lower limit of the bed; (3) kelp biomass in the bed; and (4) temperature and wave height.

In June 2012, we established a linear series of benchmarks by setting into the bedrock 11 steel eyebolts at 1-m intervals in the barrens, ~3 m from the lower edge of the kelp bed. On 3 July, 2012, we attached one vinyl tape to the first benchmark of the series, and a second vinyl tape to the next benchmark. Both tapes were extended to the bed until they gave the same measure (±1 cm) when superimposed over the point marking the lower edge of the bed. This measure was subsequently converted by triangulation into a perpendicular distance between the lower edge of the bed and midway between the benchmarks. This procedure was repeated for each successive pair of benchmarks along the benchmark line, therefore yielding 10 absolute positions of the lower limit of kelp. Urchin density was measured in one quadrat (50 × 50 cm) placed at four distances along a transect line, which extended from the midpoint between each successive pair of benchmarks, up to ~3 m into the bed, for a total of 40 quadrats (four quadrats × 10 transects). The four distances were (1) 0.2 m from the benchmarks [hereafter termed "Barrens" zone]; (2) 2 m from the lower edge of the bed ["Pre-front" zone]; (3) at the leading edge of the urchin front ["Front" zone]; and (4) 2 m into the kelp bed ["Bed" zone]. Kelp biomass (wet weight of all sporophytes cut at the holdfast with a knife) was measured in five quadrats (50 × 50 cm) placed at 2-m intervals, ~2 m into the kelp bed. Accordingly, quadrats to measure urchin density in the Barrens zone were spatially fixed

(0.2 m from the benchmarks). Quadrats to measure urchin density in the three other zones, as well as those to measure kelp biomass, shifted from one sampling event to the next because they were at fixed distances from the shifting edge of the kelp bed. These sampling procedures were repeated every 12 to 17 days until 25 September, 2012, for a total of seven sampling events although the last sampling event was excluded from the analysis (see Section 2.2.6).

The water temperature at the study site was recorded every 30 min throughout the survey with a temperature logger with a precision of ±0.5°C (HOBO Pendant; Onset Computer Corporation) attached to one of the benchmark eyebolts. We followed the procedure established by Blain and Gagnon (2013) to quantify the wave environment. The pressure of the water column on the seabed was recorded every two minutes by a water level logger with a precision of ±0.5 cm (HOBO U20-001-01-Ti Water Level Logger; Onset Computer Corporation). The logger was secured to the seabed, next to the line of benchmarks. Raw pressure values (psi) were corrected for barometric pressure by subtracting the hourly atmospheric pressure (psi) at the date and time of measurement (http://www.climate.weather.gc.ca/, Station St. John's Intl A). Each corrected value was then converted into a raw water depth (m) by multiplying it by a conversion factor of 0.68 m psi^{-1} (NOAA 2001). Raw water depths were corrected for tidal elevation and logger depth by subtracting the elevation at the date and time of measurement (http://www.tides.gc.ca/eng, Station 905) and the exact depth of the logger, yielding wave height. Temperature and significant wave height (SWH, the average height of the highest one-third of the wave data) were aggregated into mean daily averages, which we used to (1) study relationships between environmental variability and urchin density in the four zones; and (2) test the validity of thermal tipping ranges and regression equations from Experiment 1.

As mentioned, we calculated SWH from water pressure data acquired every two minutes. We used this relatively low frequency to avoid saturating the instrument's data storage unit in between site visits (data content was downloaded every two to four weeks). To assess data quality, we measured, with the same instrument, water pressure every second for five hours on a day with moderate wave action. Raw pressure data were corrected and converted to SWH as per the procedure above. We then examined the correspondence among mean SWH calculated from data points taken: (1) every two minutes; (2) every minute; (3) every second during 10 min at 0.5-h intervals; and (4) every second during 10 min at 1-h intervals. The latter two sampling regimes, termed "burst sampling", are commonly used in oceanographic studies (Emery and Thomson 2001, Lowe et al. 2005). The positive and negative deviations of a particular wave were likely to cancel one another out in the high frequency (1 Hz) readings of the two burst sampling regimes. We eliminated this potential bias by using only the highest, positive heights of waves within each time interval. SWH was respectively (1) 0.227±0.049 [SD] m; (2) 0.232±0.052 m; (3) 0.233±0.054 m; and (4) 0.236±0.065 m. SWH from data acquired every two minutes was therefore ~4% lower than the largest estimate from data acquired every second during 10 min at 1-h intervals. Accordingly, we relied on data acquired every two minutes.

Pressure loggers similar to ours have been used to quantify wave regimes as an alternative to more accurate, yet costly devices such as acoustic current meters (Eckman et al. 2003, Chen et al. 2005, Lauzon-Guay and Scheibling 2007b). Yet, pressure signals from surface waves attenuate with depth in a frequency-dependent manner, with higher frequency wave signals attenuating more than lower frequency wave signals (Denny 1988). As a result, pressure sensors attached to the seabed (the present study) inevitably yield less accurate SWH estimates than pressure sensors at the sea surface. The three closest sources of SWH recorded at the sea surface during our study period are 100 to 470 km from CBC (Appendix B). These considerable distances, together with the offshore location of buoys and the obstruction to linear propagation of surface waves by land masses between buoys and CBC, could yield far less accurate estimates of SWH at CBC than those from our logger. Consequently, we chose not to construct the SWH climate at CBC with buoy data. We nevertheless used buoy data to provide a general indication of the ability of our pressure logger to detect changes in the magnitude of SWH. We found that SWH recorded at CBC correlated generally well with that recorded from the three buoys (Appendix B), and hence we used our SWH data to characterize the wave environment at CBC. Although this approach may underestimate SWH, it is arguably the most reliable we could use with the resources at hand.

2.2.6 Statistical analysis

Note: details of the model parameters from the statistical analyses described below are provided in Appendix C.

Experiment 1 (individual feeding in water baths): Inspection of raw data (see Section 2.3.1) suggested feeding rate increased with temperature up to a breakpoint of ~12°C beyond which it decreased markedly, especially in large urchins. We used multiple piecewise (broken stick) regression to statistically detect the presence of a threshold temperature (n=96). This type of regression is frequently employed to identify breakpoints in response variables with non-linear behaviours (Toms and Lesperance 2003). We applied the Gauss-Newton non-linear least-squares algorithm (with 100 iterations) with feeding rate as the response variable, and temperature (3, 6, 9, 12, 15, and 18°C) and urchin body size (t.d., mm) as independent, continuous variables. The model indeed converged at a temperature breakpoint of 12.0 (±1.1 SE) °C (see Results). Accordingly, we modeled feeding rate as a function of water temperature (°C) and urchin body size (t.d., mm) with multiple linear regression analyses (Sokal and Rohlf 2012), one with the observations at 3, 6, 9, and 12°C (n=63), and one with the observations at 12, 15, and 18°C (n=48). Both analyses were applied to the raw data.

Urchins used in the warmest temperature treatments, 15°C and 18°C, were exposed to potentially greater thermal shock than urchins in the colder temperature treatments. To test for potential biases in feeding rates due to thermal shock, we compared feeding rates of urchins exposed to the 15°C and 18°C treatments that had been maintained in the holding tanks at temperatures of no more than 6°C below their temperature treatment, to feeding rates of urchins exposed to the 15°C and 18°C treatments that had been maintained at temperatures >6°C below their temperature treatment. We used 6°C as the threshold temperature difference to form the two groups of comparison because (1) it is an accurate reflection of the average magnitude of sudden changes in sea temperature at BCC in early summer [see description of Experiment 1];

and (2) it captured the broadest range of feeding rates, from highest at 12°C to lowest at 18°C [see Section 2.3.1]. This procedure yielded 22 and 10 estimates of feeding rates for urchins that underwent a temperature difference of respectively >6°C and ≤6°C. We carried out a randomization (permutation) test (Sokal and Rohlf 2012) to test for a difference in feeding rates between both groups of urchins. We determined the probability of obtaining the observed difference between group means ($D_o = -23.99$ mg kelp urchin^{-1}day^{-1}) by calculating the proportion of values less than D_o (one-tailed test) in a frequency distribution of 1000 randomized differences. Randomized differences were generated by calculating the difference between means for two groups of data points (n=22 and 10) drawn randomly from the 32 original estimates of feeding rates. We preferred this statistical approach over a Student's t-test because it involves no assumption about the frequency distribution of the test statistic, and hence is a more robust approach to dealing with non-normal residuals and unequal sample sizes (Sokal and Rohlf 2012).

Experiment 2 (aggregative feeding in the wave tank): We used a two-way ANOVA with the factors Waves (null, low, intermediate, and high wave velocity) and Season (spring and summer) to examine temporal differences in the effect of wave action on the aggregative feeding rate of urchins on kelp (n=32 [spring] and 28 [summer]). No transformation corrected the heterogeneity of the residuals in the analysis on the raw data. Therefore, the ANOVA was also run with the rank-transformed data. Because both analyses gave similar conclusions about the significance of each factor, we presented the results from analyses on the raw data (Conover 1980). Prior to running this two-way ANOVA, we had used two one-way ANOVAs, one for each season, with the factor Block (each of the eight spring or seven summer blocks of four days during which one replicate of each treatment was done), to determine whether results differed among blocks of days in each season. There was no significant effect of the factor Block in spring ($F_{7,24}=0.47$; $p=0.85$) and summer ($F_{6,21}=1.91$; $p=0.11$), and hence we ran the two-way ANOVA on data pooled from all blocks. We used a two-way MANOVA (Scheiner and Gurevitch 2001) with the factors Waves (null, low, intermediate, and high wave velocity) and Season (spring and summer) to examine temporal differences in the effect of wave action on the proportion of urchins (out of 118) feeding on kelp, underneath the kelp canopy, on the tiles outside of the area swept by kelp, and on the tank walls at the end of trials (n=32 [spring] and 28 [summer]). The data were logit-transformed (Warton and Hui 2011) to correct for heterogeneity of the residuals in the analysis on the raw data.

Field observations: We used linear regression analysis to examine relationships between urchin density and mean sea temperature (Temp) and significant wave height (SWH) at CBC. We used temperature and SWH data averaged over the 48 hours preceding each sampling event because preliminary analysis showed stabilization of variation beyond 48 h. We began with a multiple regression model with the factors Temp, SWH, and Zone (a categorical variable representing the four sampling zones: Barrens, Pre-front, Front, and Bed) to determine if sea temperature and SWH had an effect on urchin density across the zones (n=24). Temperature was the only factor affecting density across the zones (see Section 2.3.3). We therefore used simple linear regression analysis with the factor Temp to determine the relationship between sea temperature and urchin density in each of the four zones separately. We excluded data acquired on 25 September, 2012 (14 days after the passage of the tail end of Hurricane Leslie) from all regression analyses because they differed markedly from the rest of the dataset (see Section 2.3.3). Sea temperature and SWH from 3 July to 25 September, 2012, were not correlated (Pearson's product-moment correlation, r=-0.169, p=0.087), which enabled testing effects of both environmental factors. Each data point in each regression was based on mean urchin density calculated from all quadrats in each zone on each of the six sampling events from 3 July to 13 September, 2012 (n=24 and 6 for multiple and simple regression analyses, respectively). All regressions were applied to the raw data. As mentioned previously, quadrats to measure urchin density in the Barrens zone were spatially fixed, whereas those in the three other zones shifted from one sampling event to the next. Inspection of residuals from the multiple linear regression analysis and four simple linear regression analyses confirmed that residuals were not autocorrelated.

We tested the hypothesis that water temperature can predict short-term kelp bed destruction by *S. droebachiensis* in calm hydrodynamic environments by comparing expected and observed rates of kelp loss (g kelp day^{-1}) at CBC. Expected rates were calculated with the equations derived from Experiment 1, whereas observed rates came from our observational dataset at CBC. The following procedure was used to determine the expected daily rate of kelp loss for each of the six time intervals available from 3 July to 25 September, 2012. We calculated mean sea temperature for the time interval to determine which of the two regression equations (see Section 2.3.1 and 2.3.3) to use to calculate the daily feeding rate per urchin. We applied the appropriate equation a first time by assigning mean sea temperature and 25 mm to the temperature (T) and urchin size (S) terms, respectively. We ran it again with mean sea temperature and 45 mm, therefore providing one rate for small and one rate for large, urchins. For consistency, we used the lowest urchin size in each size category permitted by the limits of inference of the equation. Logistical considerations precluded measuring the size of urchins at CBC. The only data of urchin abundance and size structure in fronts for the region of Newfoundland that we are aware of had insufficient resolution to serve our goal (Himmelman 1969, 1986). We therefore determined the likely numbers of small and large urchins that together made up the total number of urchins at the front. This was done by multiplying mean urchin density at the front by the proportion of small (0.65) and large (0.35) urchins in fronts at the lower limit of *A. esculenta* beds at a similar time of the year in the Mingan Islands in the northern Gulf of St. Lawrence (Gagnon et al. 2004). We used published data from the Mingan Islands because this is the nearest system with comparable urchin densities and drivers of urchin-kelp bed dynamics (Gagnon et al. 2004). Resulting numbers of small and large urchins were then multiplied by corresponding feeding rates obtained from the regression equations (Experiment 1) and summed to obtain the expected total daily rate of kelp loss for the interval. The following procedure was used to determine the observed daily rate of kelp loss in each of the six intervals. We multiplied the mean surface area over which the lower edge of the kelp bed shifted during the interval along a 1-m swath of seabed by the kelp biomass averaged from measurements on the two sampling days that formed the interval. The resulting value was then divided by the number of days in the interval. We used simple linear regression analysis to measure the fit between expected and observed daily rates of kelp loss. The analysis was applied to the raw data (n=6). We did not attempt to correct the expected daily rates of kelp loss with the equations from Experiment 2 because of data incompatibility from the different approaches used to quantify the wave environment: horizontal wave velocity (in m s^{-1}) in the lab and amplitude of the vertical displacement of the sea surface (SWH, in metres) at CBC.

In all ANOVAs, MANOVA, and regression analyses, homogeneity of the variance was verified by examining the distribution of the residuals. Normality of the residuals was verified by examining the normal probability plot of the residuals (Snedecor and Cochran 1989). All MANOVAs met all the customary assumptions, including multivariate normality, homogeneity of variance-covariance matrices, and absence of multicollinearity (Scheiner and Gurevitch 2001). To detect differences among levels within a factor (ANOVAs and MANOVA), we used Tukey HSD multiple comparison tests (comparisons based on least-square means) (Sokal and Rohlf 2012). When a factor, or interaction between factors, was significant in the MANOVA, we examined the univariate model for the response variable to identify which one(s) contributed to the multivariate effect. This was done by conducting an ANOVA for the response variable with the same factors as in the MANOVA. The Pillai's trace multivariate statistic was used in the MANOVAs to determine which factor(s) were statistically significant (Scheiner and Gurevitch 2001). Because we could not presume the absence or presence of synergistic effects between explanatory variables, all multiple linear regression analyses were conducted using the multiplicative error model approach, which tests for individual and interactive effects of the explanatory variables (Kleinbaum et al. 2008). Accordingly, when interactive effects were not significant, we presented models with individual effects of only those explanatory variables that were significant in the truncated model. A significance level of 0.05 was used. All analyses were conducted with JMP 7.0 and Minitab 16.2.4.

2.3 RESULTS

2.3.1 Experiment 1

Inspection of data from Experiment 1 suggested that individual urchin feeding on kelp varied with body size among the six temperature treatments (Fig. 2.2). Feeding generally increased across the 3-12°C range in both small and large urchins. However, it was 2.5 (9°C) to 3.3 (12°C) times higher in large than small urchins for a given temperature, and peaked to 1424 (±120, SE) mg kelp urchin^{-1} day^{-1} in large urchins at 12°C (Fig. 2.2). Increasing temperature above 12°C negatively affected large urchins as shown by the 62% and 91% drops in feeding from 12°C to 15°C, and from 15°C to 18°C, respectively, i.e. a difference of two orders of magnitude between 12°C and 18°C (Fig. 2.2). Feeding in small urchins at 15 and 18°C was comparable to that in large urchins, while remaining as low (<432 [±59] mg kelp urchin^{-1} day^{-1}) as that in small urchins at any of the other temperatures (Fig. 2.2). Piecewise and multiple linear regressions revealed a temperature breakpoint of 12.0 (±1.1) °C, below and above which urchin feeding was respectively positively and negatively correlated with temperature and body size (Table 2.1). The mean feeding rate of urchins exposed to the warmest temperature treatments, 15°C and 18°C, and previously maintained in the holding tanks at temperatures ≤6°C below their temperature treatment (242.3±51.1 mg kelp urchin^{-1} day^{-1}),

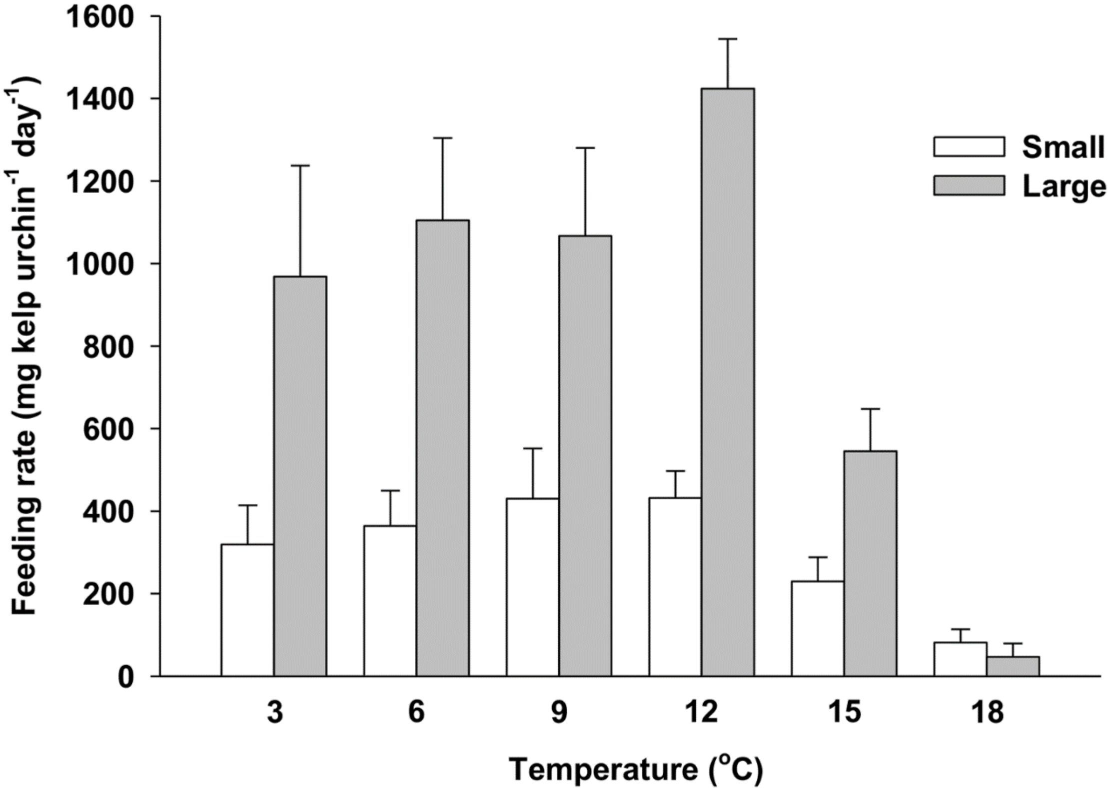


Fig. 2.2. Mean (+SE) feeding rate of small (25-35 mm t.d.) and large (45-60 mm t.d.) green sea urchins (*Strongylocentrotus droebachiensis*) on kelp (*Alaria esculenta*) in seawater at 3, 6, 9, 12, 15, and 18°C (Experiment 1).

Table 2.1. Results of multiple linear regression analyses examining relationships between feeding rate of green sea urchins (*Strongylocentrotus droebachiensis*) on kelp (*Alaria esculenta*), and water temperature (T) and urchin body size (S) (test diameter [t.d.], which can take on values from 25 to 60 mm) in each of two temperature ranges in Experiment 1 (see Section 2.2.6 for determination of the temperature breakpoint [12°C] delimiting the temperature ranges).

Temperature range	**Equation for feeding rate (mg kelp urchin^{-1} day^{-1})**	**r^2**	**F $_{(df)}$**	***p***
[3-12] °C	-814.9 +36.8*T + 31.6*S	0.513	31.66 $_{(2,60)}$	<0.001
]12-18] °C	-2363.9 + 140.9*T + 122.0*S – 7.0*T*S	0.840	77.25 $_{(3,44)}$	<0.001

was similar to that of urchins exposed to the 15°C and 18°C treatments and previously maintained at temperatures >6°C below their temperature treatment, 218.3±101.9 mg kelp urchin^{-1} day^{-1} (randomization test; $p=0.365$). Thermal shock, if present, was therefore unlikely to cause the drop in feeding rates above 12°C.

2.3.2 Experiment 2

Analysis of data from Experiment 2 indicated that aggregative urchin feeding on kelp varied among the four wave velocities independently of season (Table 2.2). Feeding rate peaked to 482 (±72) mg kelp urchin^{-1} day^{-1} in the absence of waves, being at least 2.5 times higher than at intermediate (0.2 m s^{-1}) and high (0.3 m s^{-1}) velocities (Fig. 2.3). Increasing velocity from null to low (0.1 m s^{-1}) had no perceptible effect on feeding as shown by a non-significant drop of 26% (Fig. 2.3). The overall (pooled across wave velocities) feeding rate during summer (362 [±59] mg kelp urchin^{-1} day^{-1}), when water temperature averaged 13.9±0.4 °C, was 1.7 times higher than during spring (215 [±34] mg kelp urchin^{-1} day^{-1}), when temperature was 5.1±0.2 °C (a significant difference, Table 2.2).

The MANOVA examination showed that wave velocity and season independently affected the proportion of urchins feeding on kelp and displacing in the wave tank (Table 2.3). The proportion of urchins feeding decreased steadily with an increase in wave velocity, from null (43%) to high (8%) (i.e. a fivefold decrease; LS means, $p<0.001$), while being similar in spring (21%) and summer (26%) (LS means, $p=0.136$) (Table 2.4, Fig. 2.4). Conversely, wave velocity had no perceptible effect on the number

Table 2.2. Summary of two-way ANOVA (applied to raw data) examining the effect of Waves (null, low, intermediate, and high wave velocity) and Season (spring and summer) on feeding rate of green sea urchins (*Strongylocentrotus droebachiensis*) on kelp (*Alaria esculenta*) in Experiment 2 (see Section 2.2.4 for a description of the experiment).

Source of variation	***df***	**MS**	***F*-value**	***p***
Waves	3	4.24×10^5	8.90	<0.001
Season	1	3.23×10^5	6.79	0.012
Waves × Season	3	1.25×10^4	0.26	0.852
Error	52	4.50×10^4		
Corrected total	59			

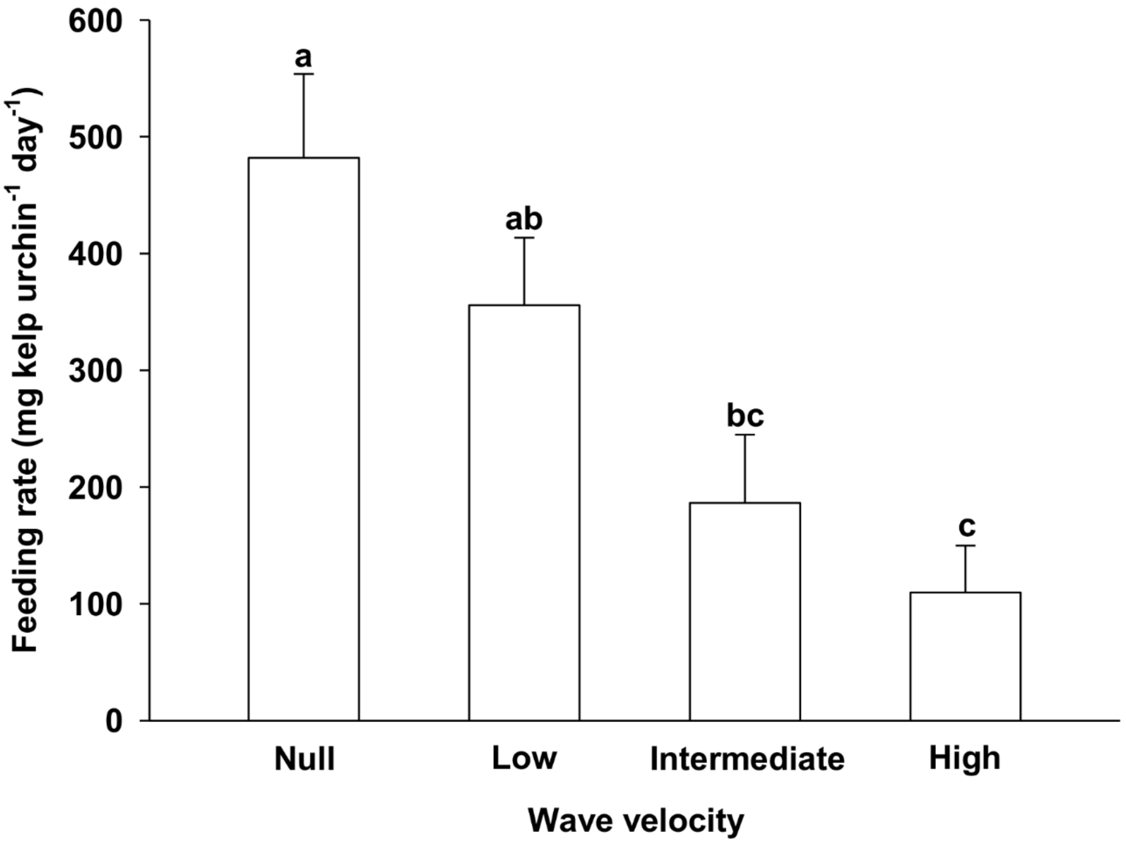


Fig. 2.3. Mean (+SE) feeding rate of large (40-60 mm t.d.) green sea urchins (*Strongylocentrotus droebachiensis*) on kelp (*Alaria esculenta*) at null, low, intermediate, and high wave velocity (0.0, 0.1, 0.2, and 0.3 m s^{-1}, respectively) (Experiment 2). Data were pooled across Season (spring and summer) treatments. Bars not sharing the same letter are different (LS means tests, $p<0.05$; n=15 for each velocity).

Table 2.3. Summary of two-way MANOVA (applied to logit-transformed data) examining the effect of Waves (null, low, intermediate, and high wave velocity) and Season (spring and summer) on the proportion of green sea urchins (*Strongylocentrotus droebachiensis*) feeding on kelp (*Alaria esculenta*), underneath the kelp canopy, on the tiles outside of the area swept by kelp, and on the tank walls, at the end of trials in Experiment 2 (see Section 2.2.4 for a description of the experiment).

Source of variation	**Test**	**Value**	***F*-value**	**NumDF**	**DenDF**	***p***
Waves	Pillai's Trace	1.27	9.36	12	153	<0.001
Season	F Test	0.27	3.30	4	49	0.018
Waves × Season	Pillai's Trace	0.28	1.31	12	153	0.217

Table 2.4. Summary of two-way ANOVAs (applied to logit-transformed data) examining the effect of Waves (null, low, intermediate, and high wave velocity) and Season (spring and summer) on the proportion of green sea urchins (*Strongylocentrotus droebachiensis*) feeding on kelp (*Alaria esculenta*), underneath the kelp canopy, on the tiles outside of the area swept by kelp, and on the tank walls, at the end of trials in Experiment 2 (see Section 2.2.4 for a description of the experiment).

Activity or location	**Source of variation**	***df***	**MS**	***F*-value**	***p***
Feeding	Waves	3	3.12	22.18	<0.001
	Season	1	0.35	2.42	0.126
	Waves × Season	3	0.18	1.28	0.290
	Error	52	0.14		
	Corrected total	59			
Underneath the kelp canopy	Waves	3	0.08	1.55	0.214
	Season	1	0.21	4.09	0.048
	Waves × Season	3	0.10	1.97	0.130
	Error	52	0.05		
	Corrected total	59			
On the tiles outside of the area swept by kelp	Waves	3	4.83	51.51	<0.001
	Season	1	0.73	7.81	0.007
	Waves × Season	3	0.01	0.12	0.949
	Error	52	0.09		
	Corrected total	59			
On the tank walls	Waves	3	2.29	26.32	<0.001
	Season	1	0.08	0.92	0.343
	Waves × Season	3	0.06	0.68	0.566
	Error	52	0.09		
	Corrected total	59			

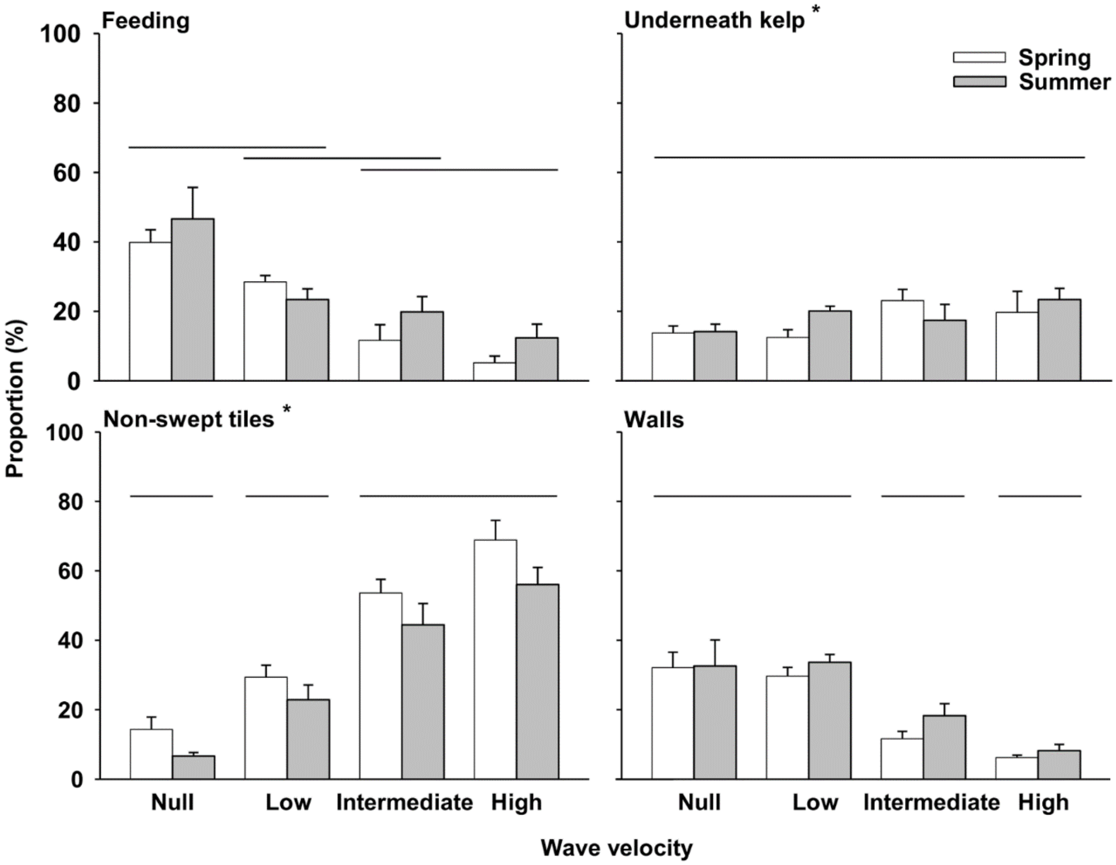

Feeding
Underneath kelp *
Non-swept tiles *
Walls
Spring
Summer
100
80
60
40
20
0
Proportion (%)
Null
Low
Intermediate
High
Wave velocity

Fig. 2.4. Proportion (+SE) of large (40-60 mm t.d.) green sea urchins (*Strongylocentrotus droebachiensis*) feeding on kelp (*Alaria esculenta*), underneath the kelp canopy, on the tiles outside of the area swept by kelp, and on the tank walls, at the end of trials at null, low, intermediate, and high wave velocity (0.0, 0.1, 0.2, and 0.3 m s^{-1}, respectively) in two seasons (Spring and Summer) (Experiment 2). Wave treatments not bracketed by the same horizontal line are different (data pooled across seasons, LS means, $p<0.05$, n=15 for each velocity). Panels with an asterisk indicate a significant difference in proportions between seasons (Summer > Spring for urchins underneath the kelp canopy and Spring>Summer for urchins on non-swept tiles) (data pooled across wave velocities, LS means, $p<0.05$, n=32 and n=28 for Spring and Summer, respectively).

of urchins that had moved underneath the kelp canopy and urchins that did so were significantly more numerous in summer (19%) than spring (17%) (Table 2.4, Fig. 2.4). Wave velocity and season independently affected the proportion of urchins that remained on the tiles outside of the area swept by kelp, with as little as 11% in the absence of waves to up to 63% at high velocity, and 42% and 33% in spring and summer, respectively (Table 2.4, Fig. 2.4). The proportion of urchins that climbed on the tank walls varied with wave velocity only, being similar (~32%) at null and low velocities (LS means, p=0.701), and decreasing to 7% with increasing velocity above 0.1 m s^{-1} (Table 2.4, Fig. 2.4).

2.3.3 Field observations

The lower limit of the kelp bed at CBC retreated on average by 0.43 m $week^{-1}$ (1.84 m $month^{-1}$) from 3 July to 25 September, 2012, and by the end had been pushed back by ~5.2 m (Fig. 2.5). The urchin front moved from a depth of ~7.5 m at the beginning of July to a depth of ~4.9 m in late September (Fig. 2.5). Kelp biomass within the first 2 m above the lower edge of the bed was relatively constant at 3.1 ± 0.3 kg m^{-2} from 3 July to 13 September. It was largely dominated (>90%) by *A. esculenta*. On 25 September (the last sampling day), we noted a shift in dominance from *A. esculenta* to larger and heavier *Laminaria digitata* sporophytes (~60%). Kelp biomass then peaked at 5.4±1.3 kg m^{-2} and urchins had grazed through much of the lower portion of the bed dominated by *A. esculenta*. The passage of the tail end of Hurricane Leslie on 11 September coincided with a sudden drop in sea temperature from ~15°C to ~6°C, as well

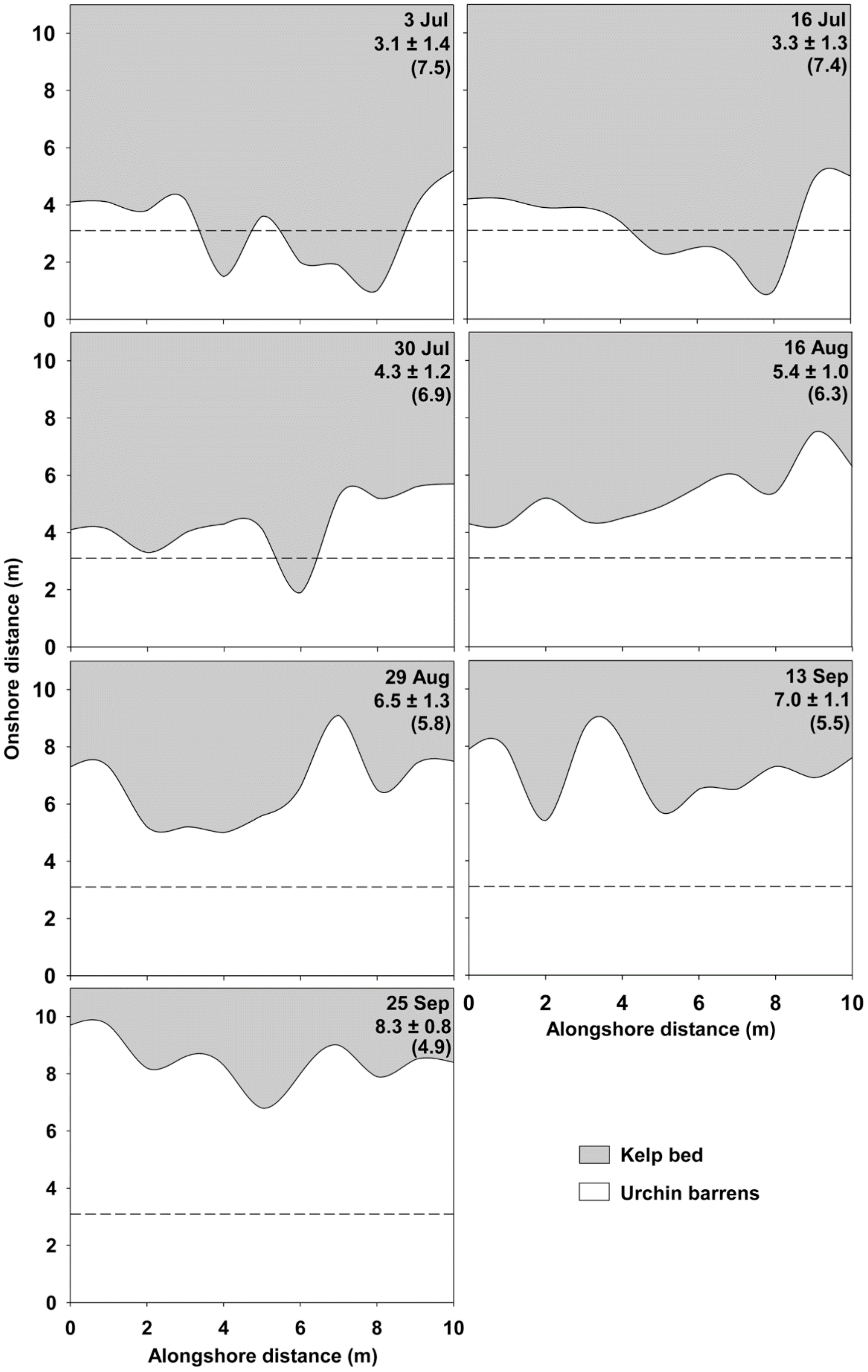

3 Jul
3.1 ± 1.4
(7.5)
16 Jul
3.3 ± 1.3
(7.4)
30 Jul
4.3 ± 1.2
(6.9)
16 Aug
5.4 ± 1.0
(6.3)
29 Aug
6.5 ± 1.3
(5.8)
13 Sep
7.0 ± 1.1
(5.5)
25 Sep
8.3 ± 0.8
(4.9)
Onshore distance (m)
Alongshore distance (m)
0
2
4
6
8
10
Kelp bed
Urchin barrens

Fig. 2.5. Change in the position of the kelp-barrens interface at Cape Boone Cove from 3 July to 25 September, 2012. Values directly below sampling dates are the mean distance (±SE) of the kelp-barrens interface relative to benchmark eyebolts in the urchin barrens (0 m). The depth across the grid (from 10 to 0 m along the y-axis) is from 4 to 9 m. Values in parentheses are the approximate depth (in m) of the kelp-barrens interface. Horizontal dashed lines indicate the mean distance of the kelp-barrens interface on the first sampling event (3 July).

as a twofold increase in SWH that did not exceed 0.51 m (Fig. 2.6). Temperature remained relatively low, below ~9°C, until the end of the survey, whereas SWH returned to the general pattern of variation between ~0.2 and ~0.4 m seen before Leslie (Fig. 2.6). That SWH did not exceed ~0.5 m even during the passage of the tail end of Leslie speaks to the relatively mild wave environment at CBC throughout the survey (Leslie had considerably weakened by the time it reached our site). Nevertheless, the sudden changes in sea temperature and state that accompanied Leslie seemed to adversely affect *A. esculenta*, which was already showing signs of tissue damage prior to the storm. We saw large pieces of *A. esculenta* blades covering the higher end of the barrens two days after the hurricane, as well as broken stipes of *A. esculenta* without blades two and 14 days after the hurricane. In contrast, *L. digitata* sporophytes remained generally healthy throughout the survey.

Urchin density was consistently higher at the front (Front zone) than in any of the three other zones (Barrens, Pre-front, and Bed). It peaked at 162.0 ± 22.7 individuals m^{-2} on 16 August, when mean sea temperature also peaked at 16.7°C (Fig. 2.6). Multiple linear regression analysis showed that urchin density across zones from 3 July to 13 September, 2012, was affected by sea temperature but not significant wave height (SWH) (Table 2.5). Simple linear regression analysis indicated that density in the Front and Bed was positively and negatively related to sea temperature, respectively (Table 2.6, Fig. 2.7). The magnitude of the effect of sea temperature on urchin density was greatest in the Front: density increased by a factor of 6.6 for every degree increase in temperature (Table 2.6). This effect was twice more pronounced than that observed in the bed, where

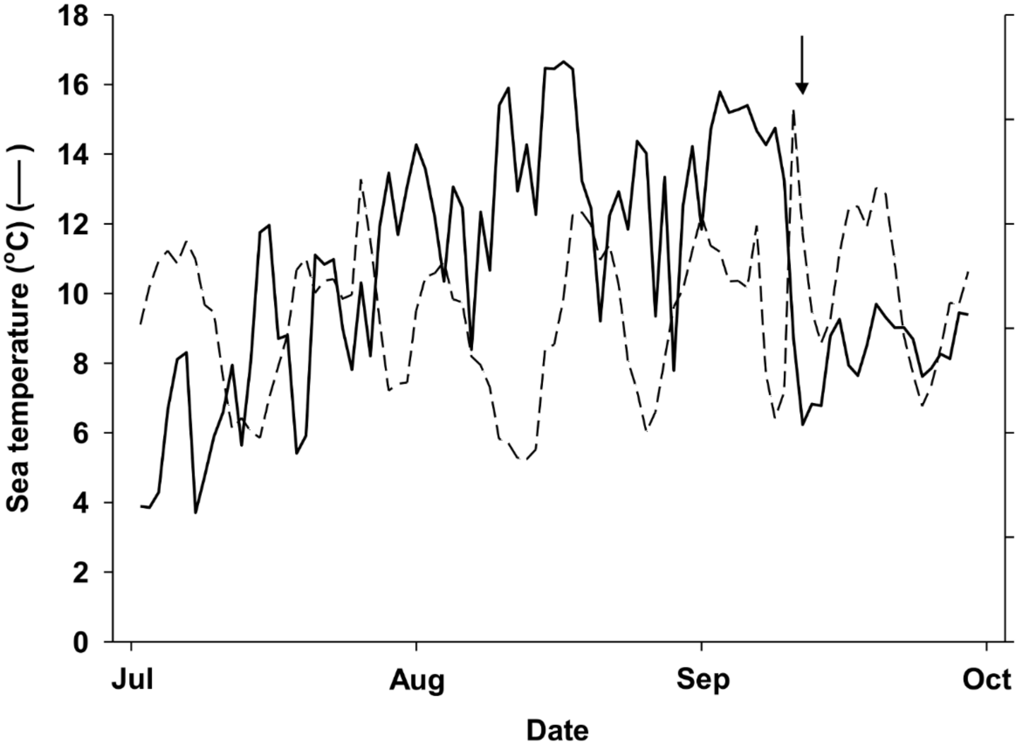


Fig. 2.6. Change in mean daily sea temperature and significant wave height (SWH) at Cape Boone Cove from 1 July to 30 September, 2012. Sea temperature and wave height data were acquired every 30 and 2 minutes, respectively, with one temperature logger and one water level logger secured to the seabed at a depth of 9 m. The arrow indicates the date (11 September) that the tail end of Hurricane Leslie reached the southeastern tip of Newfoundland (note the sharp decline in sea temperature and slight increase in SWH associated with this event).

Table 2.5. Summary of multiple linear regression analysis (applied to raw data) examining the effect of sea temperature (Temp) and significant wave height (SWH) on the density of green sea urchins (*Strongylocentrotus droebachiensis*) in the four zones (Zone, a categorical variable: Barrens, Pre-front, Front, and Bed) sampled at Cape Boone Cove from 3 July to 13 September, 2012.

Source of variation	***df***	**MS**	***F*-value**	***p***
Temp	1	39.50	0.17	0.689
SWH	1	154.92	0.66	0.433
Zone	3	358.39	1.52	0.260
SWH*Zone	3	394.25	1.67	0.225
Temp*Zone	3	1368.46	5.81	0.011
Error	12	235.68		
Corrected total	23			

Table 2.6. Summary of simple linear regression analyses (applied to raw data) examining the relationship between the density of green sea urchins (*Strongylocentrotus droebachiensis*) and sea temperature (Temp [in °C], the slope parameter) in each of the four zones sampled at Cape Boone Cove from 3 July to 13 September, 2012. Barrens: 0.2 m from benchmark eyebolts in the urchin barrens; Pre-front: 2 m from the lower edge of the kelp bed; Front: at the leading edge of the urchin front; and Bed: 2 m into the kelp bed. Model coefficients are shown with corresponding 95% confidence limits (CL).

Zone	**Intercept (95% CL)**	**Temp (95% CL)**	**r^2**	**$F_{(df)}$**	***p***
Barrens	78.6 (6.6, 150.6)	-0.1 (-6.9, 6.8)	0.0002	$0.001_{(1,4)}$	0.981
Pre-front	95.3 (30.1, 160.4)	-3.5 (-9.7, 2.7)	0.381	$2.46_{(1,4)}$	0.192
Front	51.7 (3.4, 100.0)	6.6 (2.0, 11.2)	0.799	$15.93_{(1,4)}$	0.016
Bed	72.6 (54.1, 91.1)	-3.0 (-4.7, -1.2)	0.844	$21.70_{(1,4)}$	0.010

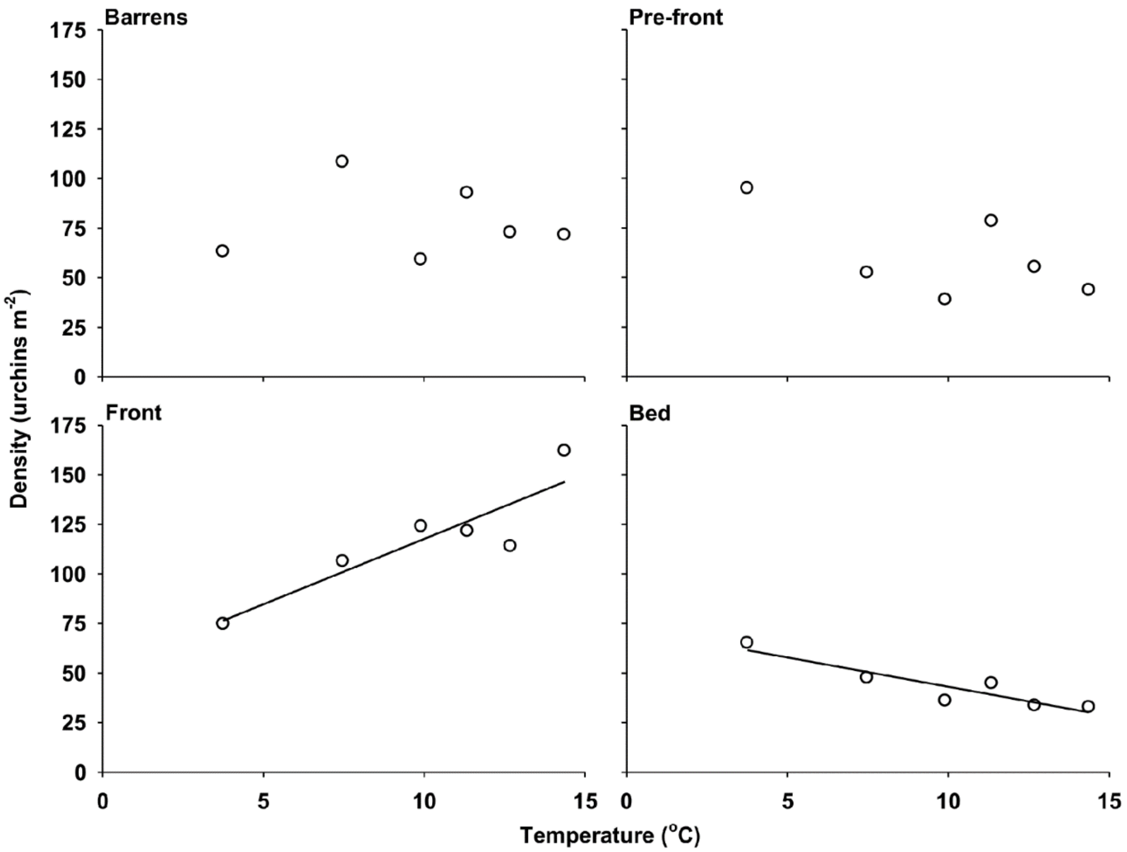


Fig. 2.7. Relationship between the density of green sea urchins (*Strongylocentrotus droebachiensis*) and sea temperature in each of the four zones sampled at Cape Boone Cove from 3 July to 13 September, 2012. Barrens: 0.2 m from benchmark eyebolts in the urchin barrens; Pre-front: 2 m from the lower edge of the kelp bed; Front: at the leading edge of the urchin front; and Bed: 2 m into the kelp bed (see Table 2.6 for details of the regression analyses).

density decreased in a 3:1 ratio with temperature (Table 2.6). Temperature had no detectable effect on urchin density in the Barrens and Pre-front (Table 2.6, Fig. 2.7).

There was a strong (r^2=0.878) positive relationship between observed and expected daily rates of kelp loss at CBC from 3 July to 13 September, 2012 (Table 2.7, Fig. 2.8). Yet, the slope of this relationship, 8.8 (Table 2.7), was similar to that of a theoretical relationship in which observed rates increase 10 times faster than expected rates (paired t-test, t_3=-0.75, p=0.510; Fig. 2.8), therefore indicating that the observed rates of kelp loss were one order of magnitude greater than those expected. Including data from 25 September, the last sampling event (14 days after Hurricane Leslie), only marginally affected the slope (9.9) of the relationship, which, however, was not significant (Table 2.7). Observed rates of kelp loss increased with mean sea temperature in July, but leveled off in August and decreased during the first part of September when temperature reached and remained within the 12-15°C tipping range found in Experiment 1 (Fig. 2.9).

2.4 DISCUSSION

Our study demonstrates that sea temperature, and not only hydrodynamic forces as found in other studies (Lauzon-Guay and Scheibling 2007a, b, Feehan et al. 2012), can predict short-term kelp bed destruction by urchin fronts in shallow reef communities. We experimentally determined that individual feeding in the green sea urchin, *Strongylocentrotus droebachiensis,* during early summer (June-July) obeyed a non-linear, size- and temperature-dependent relationship. Feeding in large (45-60 mm t.d.) urchins

Table 2.7. Summary of simple linear regression analyses (applied to raw data) examining relationships between observed and expected daily rates of kelp loss during the summer 2012 survey at Cape Boone Cove with and without data from 25 September (the last sampling event). Model coefficients are shown with corresponding 95% confidence limits (CL).

Data	**Intercept (95% CL)**	**Slope (95% CL)**	**r^2**	**$F_{(df)}$**	**p**
25 Sep in	-374.1 (-1688.0, 940.0)	9.9 (-12.1, 31.8)	0.281	$1.56_{(1,4)}$	0.279
25 Sep out	-361.2 (-667.8, -54.7)	8.8 (3.7, 13.9)	0.878	$29.85_{(1,3)}$	0.012

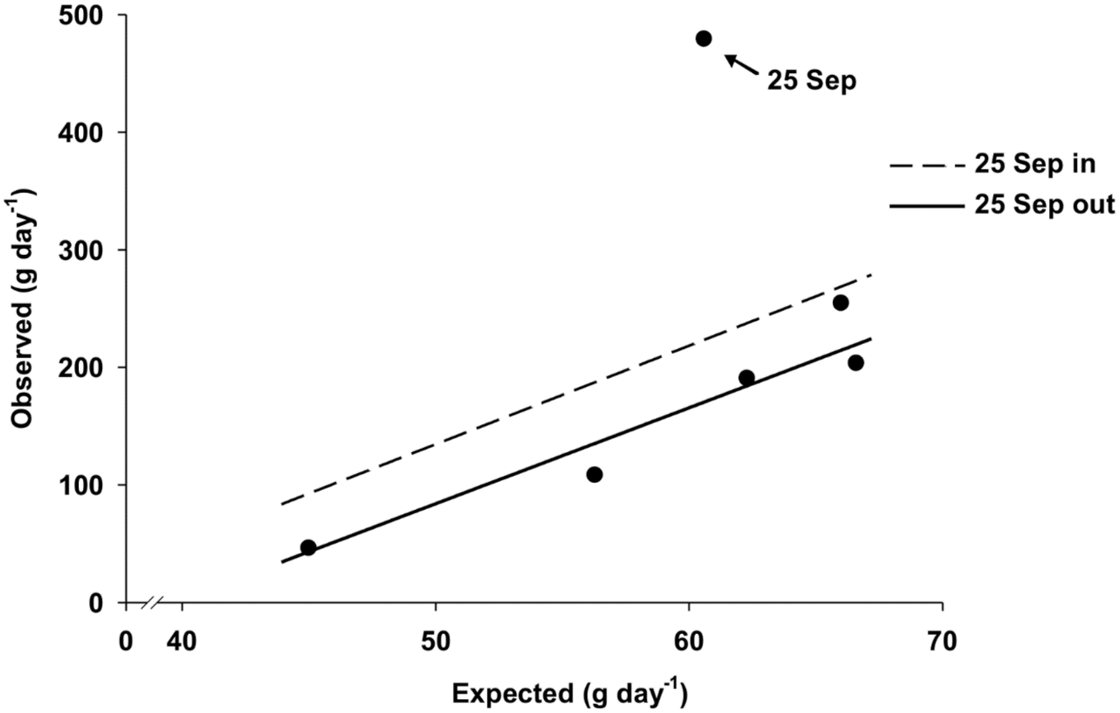


Fig. 2.8. Relationship between observed and expected daily rates of kelp loss during the summer 2012 survey at Cape Boone Cove (CBC) with and without data from 25 September, the last sampling event, which was 14 days after the passage of the tail end of Hurricane Leslie. Observed rates were calculated from our observational dataset at CBC, whereas expected rates were calculated with the equations derived from Experiment 1 (see Statistical analysis and Table 2.1 for details of the observational dataset and equations used and Table 2.7 for details of the two regression lines shown).

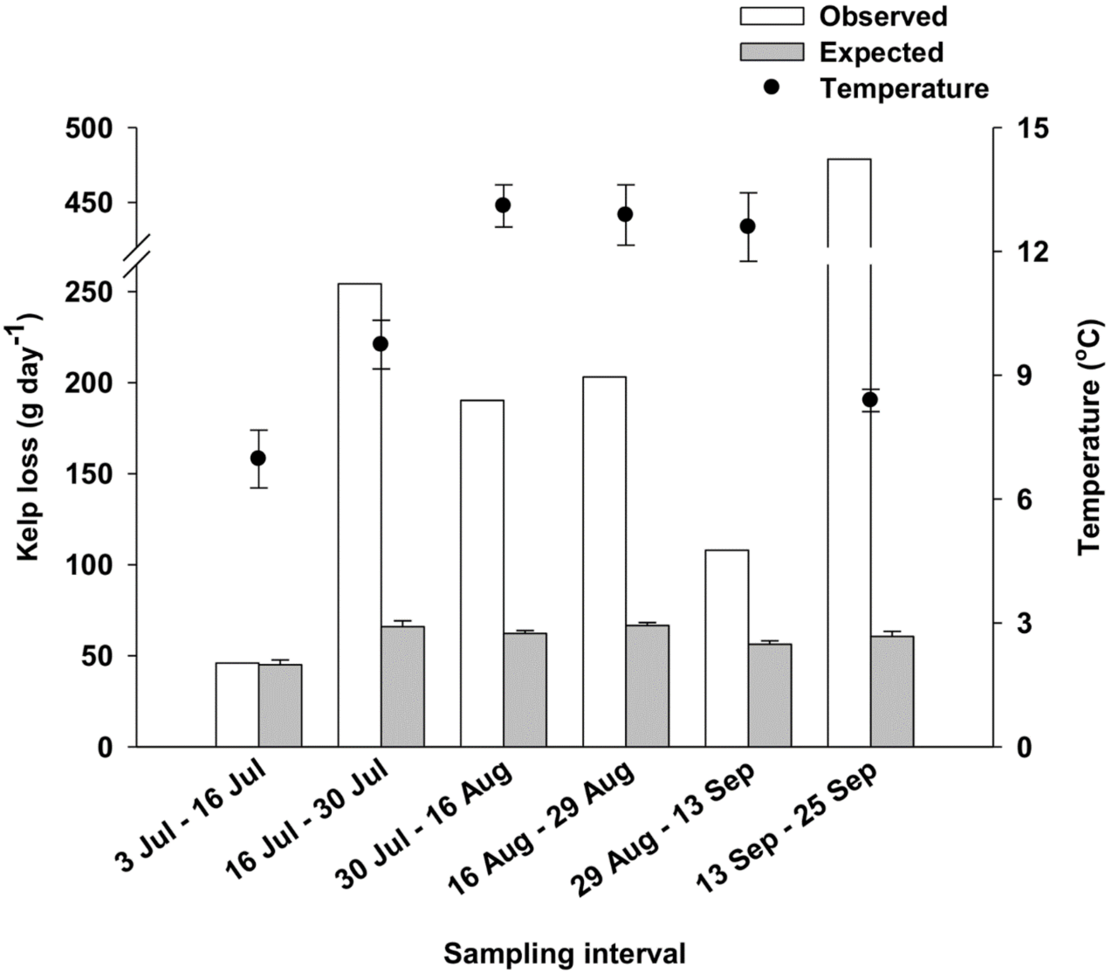


Fig. 2.9. Observed and expected (+SE) daily rates of kelp loss and mean (±SE) sea temperature for each of the six sampling intervals during the summer 2012 survey at Cape Boone Cove. Sampling intervals 5 (29 Aug - 13 Sep) and 6 (13 Sep - 25 Sep) include data acquired two and 14 days (on 13 and 25 September) after the passage of the tail end of Hurricane Leslie.

was consistently highest at temperatures <12°C and dropped sharply within and above the 12-15°C range (Experiment 1). We also found that daily rates of kelp loss over ~3 months at the Cape Boone Cove (CBC) site were highly correlated (88%) with those calculated from sea temperature at the site and regression equations derived from results of the latter experiment. These findings speak to the importance of considering body size and natural variation in sea temperature in studies of urchin-kelp interactions. They also provide a mechanistic explanation for temporal variation in urchin-kelp interfaces in environments dominated by low hydrodynamic forces.

Most studies of kelp-bed boundary dynamics in the northwestern Atlantic (NWA) establish statistical relationships among rates of kelp retreat, urchin density or biomass at fronts, sea temperature, and significant wave height (SWH) (Breen and Mann 1976, Himmelman 1984, Scheibling et al. 1999, Gagnon et al. 2004, Lauzon-Guay and Scheibling 2007a, b, Feehan et al. 2012). These studies have yielded inconsistent outcomes from strong correlations to contradictory results. Use of urchin density or biomass as proxies of the destructive potential of urchin fronts may partly account for discrepancies among studies. Certainly, the amount of kelp a front eradicates is fundamentally determined by the ability of each individual in the front to consume kelp. Seminal studies of ecological energetics in green sea urchins (Percy 1972, Miller and Mann 1973, Vadas 1977, Larson et al. 1980), together with more recent studies of gonadic growth and feed intake in aquaculture settings (Siikavuopio et al. 2006, Siikavuopio et al. 2008), support the notion that feeding increases with body size and temperature under conditions of low water motion. Predicting kelp bed destruction from urchin density or biomass without considering the size structure of urchins at the front and sea temperature may therefore overlook per capita aspects of urchin-kelp interactions that ultimately drive a front's performance.

Metabolic rate in most animals and plants, including sea urchins, is governed largely by two interacting processes: (1) the temperature dependence of biochemical processes by which metabolic rate accelerates with increasing temperature within a biologically relevant temperature range; and (2) the quarter-power allometric relation by which biological rate processes scale with body size (Gillooly et al. 2001). As per the emerging conceptual foundations of the metabolic theory of ecology (MTE), these organismal processes dictate physiological performance, rates of resource acquisition, growth, reproduction, and survival, which in turn affect processes at the species, population, community, and ecosystem levels (Brown et al. 2004, O'Connor et al. 2009, O'Connor et al. 2011, Harley 2013). Recent studies suggest that some marine herbivore-plant interactions strengthen with warming. For example, Poore et al. (2013) found that increasing temperature reduced survival and growth of the amphipod *Peramphithoe parmerong*, while affecting the palatability of its algal food, *Sargassum linearifolium*. O'Connor (2009) showed that increasing temperature increased per capita interaction strength between the amphipod *Ampithoe longimana* and seaweed *Sargassum fillipendula*, while reversing a positive effect of temperature on growth in the latter.

Our results generally support the tenets of the MTE by showing that individual and aggregative feeding in *S. droebachiensis*, and ultimately urchin-kelp interactions in a natural habitat, are influenced by water temperature and urchin body size (see details below). They also provide new insights into the biologically relevant temperature range for *S. droebachiensis* during summer at our study site, when sea temperature typically drops and rises by up to 10°C over the course of only a few hours to days (Caines and Gagnon 2012, Blain and Gagnon 2013). Experiment 1 established that kelp consumption by urchins in the laboratory increased linearly with temperature across the 3-12°C range and dropped markedly within and above the 12-15°C range. This relationship was more apparent in large than small urchins, which has three important conceptual implications. Firstly, it suggests that below ~12°C, the rate of kelp loss to a front should be partly driven by differences in the size structure of urchins, with an overriding influence, per capita, of large urchins. This means, for example, that small (≤4 cm t.d.) urchins, which represent on average ~65% of urchins at fronts advancing over *A. esculenta* beds during summer in the northern Gulf of St. Lawrence (Gagnon et al. 2004), may cause ~43% of the kelp loss, compared to ~57% of the loss by ~53% fewer, albeit larger (>4 cm t.d.), urchins. Secondly, it shows that feeding is more sensitive to increases in temperature above ~12°C in large than small urchins. Accordingly, the rate of kelp loss to a front within and above the 12-15°C range should be negatively related to sea temperature at sites with low hydrodynamic forces. It should also be increasingly predictable upon strict knowledge of the number of urchins (density) at the front, i.e. regardless of size structure. Thirdly, it establishes that feeding in *S. droebachiensis* is much reduced at temperatures above 15°C, a drop that we showed was unlikely to be caused by thermal shock as urchins were introduced to their experimental temperatures. Kelp loss to a front should therefore slow down as temperature approaches 18°C, although such relatively high temperatures (and other factors) may also increase kelp mortality, yielding similar or higher overall rates of kelp loss (see below). The 12-15°C feeding discontinuity documented herein is based on urchins that were not pre-acclimated to their respective experimental temperature treatments. This procedure was used to account for effects of natural variability in sea temperature at CBC on urchin feeding. It is therefore a good representation of the ability of urchins to adapt feeding to relatively sharp temperature changes (in the present study up to ~10°C) during a specific period (June-September). Longer-term studies are required to determine if the 12-15°C feeding discontinuity changes in space and time. Such a discontinuity was nevertheless useful in predicting patterns of kelp loss at CBC (see below). Certain marine invertebrates such as limpets and mussels physiologically adapt, to various degrees, to acute and long-term rises in temperature by adjusting the expression of protein-coding genes (Gracey et al. 2008, Dong and Somero 2009, Somero 2010). Addressing the extent to which the green sea urchin may physiologically adapt to acute and long-term changes in sea temperature is critical to define the thermal boundaries within which destructive grazing of kelp communities is likely to occur as the global ocean continues to warm (Halpern et al. 2008, Burrows et al. 2011). It would also help further test the limits of prediction of the MTE by incorporating effects of short-term variability (in addition to long-term mean changes) in sea temperature on urchin feeding and the ecological cascades which may result from it.

Results of Experiment 1 were consistent with patterns in the field as shown by the high statistical fit between observed and expected daily rates of kelp loss at CBC from 3 July to 13 September, 2012, when sea temperature varied between 3.7 and 16.7°C and

SWH was consistently low, <0.51 m. Observed rates of kelp loss increased with mean sea temperature in July, but leveled off in August and decreased during the first part of September when temperature reached and remained within the 12-15°C tipping range found in Experiment 1. Interestingly, the observed rates of kelp loss were approximately one order of magnitude greater than those expected. The latter result is surprising given that the expected rates were obtained from results of Experiment 1, in which urchin feeding was not impeded by factors such as water turbulence and competition. Expected rates should therefore have been equal or higher than the observed rates. The lower portion of the kelp bed at CBC was composed mainly of *Alaria esculenta*, which started to erode in the first two weeks of August, when sea temperature on many days exceeded 12°C and hovered around the proposed lethal 16°C for the species (Munda and Lüning 1977). We think that the observed rates of kelp loss from mid-August to mid-September (prior to Hurricane Leslie) originated from a temperature-induced decline in urchin feeding offset by increasing kelp loss through natural senescence. The sudden 4-fold increase in the rate of kelp loss over the two weeks that followed Leslie was largely driven by fragmentation and detachment of the weakened *A. esculenta* sporophytes. The urchin front progressively moved into shallower water as it grazed down the lower margin of the kelp bed, and hence it may have been exposed to increasingly greater hydrodynamic forces resulting from lesser attenuation of wave motion at shallower depths (Denny 1988). As a result, it is possible that the stabilization and subsequent decline in rates of kelp loss from early August to mid-September was caused by a combination of the temperature effect explained above and a gradual decline in urchin displacement and feeding under increasingly high bottom flows as shown by Experiment 2 (see below). The relatively small change in depth (2.6 m) of the front between the onset and end of the field survey, and the strong agreement between observed and expected rates of kelp loss, suggest that temperature had the greatest influence on the urchin front.

Overall, our findings indicate that in habitats with relatively low wave energy, such as CBC, rates of kelp bed destruction by urchin fronts can be predicted from basic knowledge of (1) relationships among individual feeding, temperature, and body size, which we established herein for early summer (June and July) in eastern Newfoundland. These relationships should also be determined for other kelp species and times of the year to incorporate likely temporal variation in urchin-kelp interactions; (2) mean kelp biomass in the bed as well as the number and size structure of urchins at the front, which can be determined accurately by way of a few hours of field work; and (3) sea temperature at the site, which can be obtained for long periods of time from inexpensive and easy-to-install temperature loggers. Continuous records of temperature over months and years should help anticipate times when temperature is likely to reach thermal tipping ranges (12-15°C in the present study) in urchin feeding, which is critical information for marine resource management purposes.

In Nova Scotia (NS), Lauzon-Guay and Scheibling (2007b) found no statistical relationships between water temperature and the rate of advance of, or urchin density at, a front at temperatures between 0.8 and 17°C. However, the rate of front advance at their site decreased substantially beyond 17°C, with a few instances where the front retreated away from the kelp (Lauzon-Guay and Scheibling 2007b). The sharp drop in urchin feeding around 15°C and above in our Experiment 1 is consistent with the latter result. Lauzon-Guay and Scheibling (2007b) also found negative relationships between SWH across the 0.5-2 m range, and urchin movement or density at the front. In another study at the same site, variation in urchin density at the front over 24 d was negatively correlated with SWH across the 0.5-1.5 m range (Lauzon-Guay and Scheibling 2007a). That in NS temperatures <17°C did not seem to influence urchin-kelp interactions, while the wave environment markedly affected urchin abundance at the front (Lauzon-Guay and Scheibling 2007a, b), suggests that effects of wave action can override those of temperature when SWH is consistently >0.5 m. In the present study, SWH never exceeded 0.51 m, indicating that the wave environment was generally too mild to overcome the influence of temperature. Our study of the relationship between wave velocity and grazing of kelp lines by urchins in a controlled wave environment (Experiment 2) provides the first experimental demonstration of the mechanistic underpinnings for the latter findings.

We found that aggregative feeding rates were: (1) >2.5 times higher in the absence of waves than at intermediate [0.2 m s^{-1}] and high [0.3 m s^{-1}] wave velocities [no perceptible difference with low, 0.1 m s^{-1}, velocity]; and (2) >1.5 times higher in summer [late August to early October] when temperature was within the 12-15°C tipping range of Experiment 1, than spring [April-May] when temperature was lower, ~5°C. These findings, together with significant decreases in both seasons in the proportion of urchins feeding and climbing on the tank walls as wave velocity increased, demonstrate the pervasive effect that wave action can have on feeding and displacement in *S. droebachiensis*. That significantly more urchins remained stationary outside of the area swept by kelp in spring than summer suggests that rising temperature may affect specific components of the behavioural repertoire of the green sea urchin. However, this effect was confounded with season in our experiment, which was designed to explore temporal differences as opposed to the strict effect of temperature on these relationships. These results must therefore be interpreted cautiously because factors other than temperature, including reproductive stage of urchins, food availability, and the frequency and intensity of wave storms, change with season and may also affect movement and foraging in *S. droebachiensis* (Scheibling and Hatcher 2007). Kawamata (1998) documented a similar effect in the urchin *Mesocentrotus nudus* (formerly *Strongylocentrotus nudus*): displacement decreased with increasing wave velocity and ceased at ~0.7 m s^{-1}. The latter stopping velocity is more than twice the 0.3 m s^{-1} reported herein and in a study of the ability of *S. droebachiensis* to contact the seaweed *Desmarestia viridis* (Gagnon et al. 2006). Altogether, these findings reinforce the notion that urchins are sensitive to changes in the hydrodynamic environment, and that tolerance limits are species-specific.

Our study of the relationships among urchin density, sea temperature, and SWH at CBC yielded foundational results for the largely unstudied region of Newfoundland. Urchin density was affected by variation in sea temperature, but not SWH. Density in the front and within the first 2 m of kelp ahead of the front was positively and negatively correlated to sea temperature, respectively. These results suggest that as sea temperature increases, urchins in the lower bed migrate to the front, therefore increasing the destructive potential of urchins on kelp. That urchin density several metres below the front did not vary with temperature and SWH, further supports the notion that the typical increase in urchin density in fronts during summer (Scheibling et al. 1999, Gagnon et al. 2004, Lauzon-Guay and Scheibling 2007b) is mainly a result of urchins in the bed accumulating in the front as the latter advances through kelp. Further studies are required to test the suggestion that urchins in the lower bed are generally attracted by kelp fragments and associated waterborne chemicals that may settle and diffuse ahead of the plowing front as kelp are being grazed down.

Our integrated approach to the study of individual and aggregative feeding in the green sea urchin, *Strongylocentrotus droebachiensis*, provides the first compelling evidence that water temperature, and not only hydrodynamic forces, can predict kelp bed destruction by urchin fronts in shallow reef communities. By contrast with other systems (Lauzon-Guay and Scheibling 2007a, b), the hydrodynamic environment at our study site was generally too calm to overcome the effects of temperature on urchin feeding. This finding speaks to the importance of making accurate climate change predictions if we are to anticipate which of the thermal and hydrodynamic environments will be a more important driving force of urchin-kelp dynamics at local and regional scales. The identification of thermal and hydrodynamic thresholds and gradients that trigger shifts in individual and aggregative feeding also has several important conceptual and operational ramifications. Firstly, it highlights the importance of considering thermal regimes in studies of urchin-kelp interactions and kelp-bed boundary dynamics, especially in environments dominated by low hydrodynamic forces where urchins can displace, aggregate, and feed upon kelp more readily. Secondly, it provides novel and vital information, which can feed mathematical models aimed at predicting the timing and magnitude of community phase shifts, with potential applications for the development of a sustainable urchin fishery in Newfoundland (Lauzon-Guay et al. 2009, Lauzon-Guay and Scheibling 2010). Longer-term experimental and mensurative studies of urchin-kelp interactions at multiple sites spanning broader geographical, thermal, and hydrodynamic ranges are required to test the generality of our findings. Our results support the notion that urchin feeding generally conforms to the basic predictions of the rising MTE. Given (1) the functional importance of urchins in shallow rocky reefs (Scheibling and Hatcher 2007); (2) the influence of sea temperature on their ability to feed [as demonstrated by the present study]; and (3) ongoing global shifts in sea temperature and state induced by climate change (Halpern et al. 2008, Burrows et al. 2011), studying urchin-seaweed-predator interactions within the conceptual foundations of the MTE holds high potential for improving capacity to predict and manage shifts in marine food web structure and productivity.

CHAPTER III

Spatial dynamics of the green sea urchin, *Strongylocentrotus droebachiensis*, in food-depleted habitats

3.1 INTRODUCTION

As climate-driven alterations to sea state (waves and currents) accelerate on a global scale, there is a growing concern about their potential effects on the structure and function of intertidal and shallow subtidal communities (Halpern et al. 2008, Burrows et al. 2011, Young et al. 2011). Studies of marine coastal community responses to waves and currents have focused largely on documenting the consequences of extreme low or high hydrodynamic forces on distribution, abundance, mortality, and population recovery of numerically dominant organisms (e.g. Harris et al. 1984, Ebeling et al. 1985, Seymour et al. 1989, Underwood 1999, Siddon and Witman 2003). Rigorous experimental testing of the effects of non-lethal waves and currents on the ability of consumers to exert top-down community control has lagged behind observational studies of pattern (but see Kawamata 1998, Gagnon et al. 2006, St-Pierre and Gagnon 2015). The general lack of experimental demonstrations of wave-induced behavioural shifts in functionally important consumers limits the ability to formulate accurate predictions about the frequency and magnitude of changes in marine communities resulting from shifts in sea state (Scheffer et al. 2001, Wang et al. 2004, deYoung et al. 2008, Lauzon-Guay et al. 2009, Young et al. 2011).

With a circumpolar distribution (Scheibling and Hatcher 2007), the omnivorous green sea urchin, *Strongylocentrotus droebachiensis*, presents a striking example of a widespread consumer that exerts strong top-down community control, by removal of foundational (*sensu* Bruno and Bertness 2001) kelp species (Chapter II, Scheibling et al. 1999, Gagnon et al. 2004, Lauzon-Guay and Scheibling 2007b). A few correlational field studies indicate that individual displacement, the formation of grazing fronts, and rates of kelp bed destruction by fronts are negatively related to wave height or current speed (Dumont et al. 2006, Lauzon-Guay and Scheibling 2007a, b). Although informative, such studies do not allow for proper testing and partitioning of causal links between the hydrodynamic environment, other environmental factors, and various behavioural aspects that ultimately determine the species' fitness and destructive potential. More recently, attention has been directed towards experimental quantification of the effects of varying hydrodynamic forces on displacement and feeding of green sea urchins. Using flume tank experiments, Morse and Hunt (2013) found that urchin displacement speed was negatively related to current speed in the 0.12 to 0.47 m s^{-1} range. A change in current speed from 0.3 to 0.36 m s^{-1} also triggered a directional switch of >90° in cross-current urchin displacement (Morse and Hunt 2013). Using oscillatory wave tank experiments, Chapter II showed that feeding of aggregated urchins on kelp (*Alaria esculenta*) at a peak wave velocity of 0.1 m s^{-1} can be more than three times higher than at 0.3 m s^{-1}.

Studies of alternation between "kelp bed" and "barrens" community states initiated by changes in abundance and activity of urchins in grazing fronts at the kelp-barrens interface have provided a clear understanding of the functional importance of *S. droebachiensis* (reviewed by Filbee-Dexter and Scheibling 2014, Ling et al. 2015). Comparatively less effort has been devoted to examining urchin displacement, distribution, and aggregation in barrens (but see Garnick 1978, Hagen and Mann 1994, Dumont et al. 2004, 2006, Lauzon-Guay et al. 2006), where urchin food including kelp is scarce and less likely to influence urchin activity. It is well recognized that benthic marine consumers can take advantage of seabed topography and its influence on water flow in ways that ultimately increase fitness (Denny 1988, Barry and Dayton 1991, Guichard and Bourget 1998, St-Pierre and Gagnon 2015). One poorly studied, but important aspect of green sea urchin ecology, is the ability to associate with different seabed topographies in barrens in response to shifts in hydrodynamic conditions. Gagnon et al. (2006) experimentally determined that in the absence of food, up to four times more urchins moved from horizontal to vertical surfaces in the absence of waves than under moderate wave action. Casual field observations also suggest that green sea urchins largely cluster in crevices and along the base of rocky outcrops during periods of strong wave action, especially during winter when sea temperature is low and metabolic activity is presumably reduced (Chapter II, Garnick 1978, Vadas et al. 1986, Scheibling et al. 1999). Such ability to switch microhabitats (defined herein as areas of seabed with characteristic topographies and water flows) can be beneficial if, for example, it helps reduce the risk of dislodgement when hydrodynamic forces exceed the biomechanical tolerance limits of an organism (Denny 1987, Denny 1988, Lau and Martinez 2003, St-Pierre and Gagnon 2015).

Another important aspect that deserves more attention is how population density and wave action may interact in shaping patterns of urchin distribution and aggregation in barrens. Hagen and Mann (1994) found that mean aggregation size and degree of crowding and patchiness of green sea urchins in laboratory tanks more than doubled with a six-fold increase in urchin numbers from five to 30. Bernstein et al. (1983) found that the degree of aggregation of caged green sea urchins in a wave-exposed subtidal habitat was higher at high (20 individuals m^{-2}) than at low (4 individuals m^{-2}) urchin density. The latter two studies did not evaluate the influence of the hydrodynamic environment on patterns of urchin aggregation and distribution. The interaction between urchin density and wave action would be particularly worth testing during summer, when urchin activity typically peaks (Chapter II, Scheibling et al. 1999, Gagnon et al. 2004, Lauzon-Guay and Scheibling 2007b). Current evidence suggests that shoreward migration of green sea urchins across barrens is the primary mechanism of repopulation of grazing fronts following disturbance (Scheibling et al. 1999, Brady and Scheibling 2005). Clearly, a better understanding of the factors that regulate urchin displacement, microhabitat use, distribution, and aggregation in barrens is necessary to improve capacity to predict and manage shifts in urchin abundance in barrens, and by extension grazing fronts, the primary target of the green sea urchin fishery (Andrew et al. 2002, Botsford et al. 2004, Miller and Nolan 2008, DFO 2012).

In the present study, we report on the results of two complementary experiments in an oscillatory wave tank, and observations over six months at two barrens sites in southeastern Newfoundland, to examine effects of varying hydrodynamic conditions on displacement, microhabitat use, distribution, and aggregation in *S. droebachiensis*. The two experiments mimic barrens conditions, including the back-and-forth flow of waves, to identify velocities and urchin densities triggering shifts in displacement, microhabitat use, distribution, and aggregation. Field observations test the generality of the results from the laboratory experiments by examining variation in wave height and sea temperature, and associated changes in microhabitat use and distribution.

3.2 MATERIALS AND METHODS

3.2.1 Study and collection site

The present study was carried out with *Strongylocentrotus droebachiensis* at, or collected from, Bread and Cheese Cove (BCC, 47°18' 30.8" N, 52°47' 19.1" W), a semi-protected cove on the north shore of Bay Bulls in Newfoundland, Canada. The seabed at BCC is composed of gently sloping bedrock to a depth of ~15 m (chart datum) with scattered boulders between 3 and 5 m. Kelp beds, mainly *Alaria esculenta* and *Laminaria digitata*, dominate the 0-2 m depth range, followed by an extensive urchin (*S. droebachiensis*) barrens to a depth of ~15 m. Transient beds of the annual, acidic, brown seaweed *Desmarestia viridis* establish every year in this barrens (Blain and Gagnon 2014) and are interspersed with a few stands of the grazing-resistant kelp *Agarum clathratum* (Gagnon et al. 2005).

3.2.2 Collection and acclimation of urchins prior to experimentation

Urchins used in Experiment 1 and Experiment 2 (see Sections 3.2.3 and 3.2.4) were hand-collected by divers at depths of 3 to 6 m in the barrens at BCC in January, June, and July, 2012. They were transported in large containers filled with seawater to the Ocean Sciences Centre (OSC) of Memorial University of Newfoundland. Upon arrival at the OSC (<5 hours after collection), urchins were transferred to 330-L holding tanks supplied with ambient flow-through seawater pumped in from a depth of ~5 m in the adjacent embayment, Logy Bay, and sorted by size. All individuals with a test diameter of 40 to 60 mm that clung or displaced readily in the tanks, indicating that the podia functioned normally, were kept for the experiments. This size class was chosen because individuals of this size are sexually mature (Himmelman 1986, Raymond and Scheibling 1987, Munk 1992), therefore eliminating potential behavioural differences between mature and non-mature individuals, and it was the most frequent size class at times of collection. Each holding tank contained 200 urchins. Urchins used in Experiment 1 spent three to 15 days in the holding tanks prior to being used in trials. They were not fed because urchin feeding in eastern Canada at the time the experiment was conducted (January) is typically low (Scheibling and Hatcher 2007, P. Gagnon, personal observations) and feeding them could have altered metabolic activity and behaviour. Urchins used in Experiment 2 spent three to 14 days in the holding tanks. They were fed every two days with 25 g (wet weight) of freshly collected *Alaria esculenta* blades (including midribs) cut into pieces of ~2.5 x 2.5 cm to standardize hunger levels at a time of year (June and July) when feeding in eastern Canada markedly increases (Chapter II, Scheibling et al. 1999, Gagnon et al. 2004, Lauzon-Guay and Scheibling 2007b). Urchin feces and unconsumed kelp were removed from the holding tanks every two days. Water temperature in the holding tanks prior to trials in Experiment 1 and Experiment 2 was measured with a temperature logger with a precision of ±0.5 °C (HOBO Pendant; Onset Computer Corporation). It averaged 4.1 °C (±0.2) and 10.0 °C (±0.9), respectively.

3.2.3 Experiment 1: displacement and microhabitat use

To test the effects of wave action on displacement and microhabitat use by *Strongylocentrotus droebachiensis*, a microcosm experiment, Experiment 1, was carried out in an oscillatory wave tank. The tank mimicked the back-and-forth flow caused by waves in shallow subtidal habitats (Fig. 2.1; Appendix A; St-Pierre and Gagnon 2015). The experiment was conducted at the end of January 2012 to test the prediction that in the cold waters of winter, the displacement of urchins and frequency of association with topographically uneven microhabitats are respectively lower and higher at high than low wave velocities. This prediction stems from the argument that urchins at that time of year should be less active and more inclined to cling to uneven surfaces that provide a good purchase to avoid dislodgement. This effect should exacerbate with increasing wave action because displacement in benthic mobile organisms generally decreases as hydrodynamic forces increase (Chapter II, Denny 1988, Siddon and Witman 2003, Gagnon et al. 2006, St-Pierre and Gagnon 2015).

Forty eight (48) urchins were allowed to displace and make contact with six microhabitats (see below) at four wave velocities: 0.0 m s^{-1} (null), 0.1 m s^{-1} (low), 0.2 m s^{-1} (intermediate), and 0.3 m s^{-1} (high) (peak longitudinal velocity measured with a Doppler current meter [Vector Current Meter; Nortek] at ~5 cm above the centre of the experimental area). Wave velocity was changed by adjusting water depth in the tank (see Appendix A for water depth at each velocity). The corresponding urchin density, 44 individuals m^{-2}, was similar to that in urchin barrens in the northern Gulf of St. Lawrence and southeastern Newfoundland (Chapter II, Himmelman 1986, Gagnon et al. 2004). Wave velocity included the maximum value of ~0.3 m s^{-1} above which the mobility of most urchins was greatly reduced as determined from preliminary trials and other studies (Chapter II, Gagnon et al. 2006). A fixed frequency of 14 wave cycles min^{-1}

was used in treatments with waves because (1) the present study focuses on the effects of water velocity on displacement and microhabitat use, rather than the effects of wave frequency; and (2) it reflects the general wave frequency under moderate winds at the study and collection site [Chapter II, St-Pierre and Gagnon 2015].

Trials were conducted on a 3 x 4 grid arrangement of concrete tiles (12 tiles, 0.27 x 0.27 x 0.05 m [L, W, H] each) (Fig. 3.1). The grid was located in the centre of the tank. It was delimited longitudinally by the tank walls and transversally by nylon netting with 2.5-cm mesh to restrict urchins to the experimental area. Preliminary trials showed no effect of netting on flow direction and speed. The upper surface of the tiles was sculpted with small holes and cracks to simulate natural bedrock heterogeneity and rugosity. Urchins had access to six microhabitats: (1) flat; (2) protrusion; (3) depression; (4) ledge; (5) crevice; and (6) wall. The surface areas of these microhabitats were (respectively) 0.64, 0.06, 0.13, 0.04, 0.14, and 0.73 m^2, yielding an experimental area of 1.74 m^2. The free surface of the 12 tiles formed the flat microhabitat. Topographical features were added to nine tiles to create the protrusion, depression, and ledge microhabitats, with three tiles per habitat. Protrusion tiles had one concrete brick (0.2 x 0.1 x 0.05 m [L, W, H]) in the centre (Fig. 3.1). Depression tiles had one gently sloping depression (0.21 m in diameter, 0.04 m deep) in the centre surrounded by a flat, horizontal rim (0.03 m at the narrowest points, Fig. 3.1). Ledge tiles had one rectangular (0.2 x 0.1 x 0.003 m [L, W, H]) piece of acrylic in the centre fastened at an angle of 45° relative to the tile (Fig. 3.1). Bricks and acrylic pieces in the protrusion and ledge microhabitats were oriented perpendicularly to the longitudinal walls of the tank to create

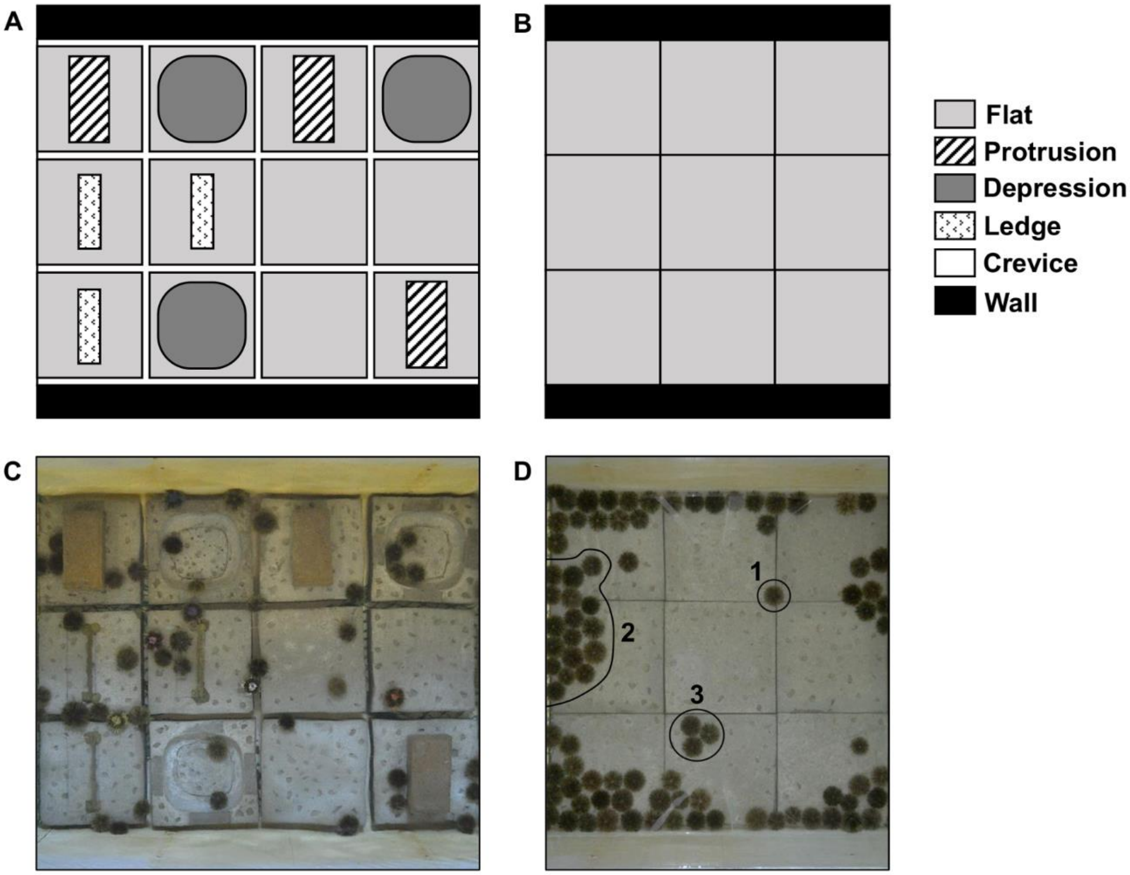


Fig. 3.1. Set-up of the experimental area (3 x 4 or 3 x 3 grid of concrete tiles and two longitudinal tank walls) and urchins at the end of a trial at a wave velocity of 0.2 m s^{-1} in (A, C) Experiment 1 [44 individuals m^{-2}; each tile is 0.27 x 0.27 x 0.05 (L, W, H) m] and (B, D) Experiment 2 [110 individuals m^{-2}; each tile is 0.30 x 0.30 x 0.05 m]. (C) Urchins [six individuals] with a colored spot on the aboral side were used to quantify displacement in Experiment 1 [see Section 3.2.3 for details]. (D) Examples of [1] solitary urchin, [2] bounded aggregation, and [3] unbounded aggregation (see Section 3.2.4 for details).

similar water flows among trials of the same wave velocity. Grooves (0.02 m wide, 0.05 m deep) between the 12 adjacent tiles formed the crevice microhabitat. The longitudinal tank walls flanking the tiles formed the wall microhabitat. Urchins in these microhabitats provided an indication of the inclination and ability to: (1) remain on bare, horizontal surfaces [flat]; (2) associate with steeply sloping, low-profile points such as small and abrupt rocks and rocky outcrops [protrusion]; (3) move to the bottom of shallow troughs like on irregular bedrock platforms [depression]; (4) associate with the base of jagged, low-profile surfaces such as the base of serrated boulders or rocky cliffs [ledge]; (5) move to tight spaces such as grooves in bedrock or gaps between adjacent rocks [crevice]; and (6) associate with steeply sloping, vertical surfaces like large rocky cliffs [wall]. Urchins were in the depression, ledge, or wall microhabitats if >50% of the test overlapped with the habitat, in the protrusion microhabitat if touching a brick, in the crevice microhabitat if partially inserted in or extending across grooves between tiles, and in the flat microhabitat if anywhere else. Water velocity differed among microhabitats, ranging from 0.083 m s^{-1} (depression) to 0.131 m s^{-1} (wall) at low wave velocity, 0.191 m s^{-1} (depression) to 0.254 m s^{-1} (wall) at intermediate velocity, and 0.277 m s^{-1} (depression) to 0.326 m s^{-1} (wall) at high velocity (Table 3.1). While in using this approach effects of microhabitats are confounded by those of water velocity, it is an accurate representation of the conditions to which urchins are exposed in natural habitats. The experiment aimed to quantify the combined effect of both factors, as opposed to their individual effects.

Each trial lasted 45 min to allow sufficient time for urchins to contact at least one "non-flat" microhabitat at all wave velocities as determined from preliminary trials. Urchins were introduced, oral surface down, to the flat sections of the 12 tiles, with four

Table 3.1. Mean (±SE) peak longitudinal water velocity (m s^{-1}) in each microhabitat in Experiment 1 and Experiment 2 for the low (0.1 m s^{-1}), intermediate (0.2 m s^{-1}), and high (0.3 m s^{-1}) wave velocity treatments (see Sections 3.2.3 and 3.2.4 for a description of the experiments).

		Wave velocity treatment		
Experiment	Microhabitat	Low	Intermediate	High
1, 2	flat	0.102 (0.001)	0.230 (0.005)	0.325 (0.003)
1	protrusion	0.099 (0.001)	0.226 (0.002)	0.323 (0.003)
1	depression	0.083 (0.001)	0.191 (0.002)	0.277 (0.002)
1	ledge	0.097 (0.001)	0.202 (0.005)	0.292 (0.007)
1	crevice	0.106 (0.001)	0.215 (0.001)	0.299 (0.003)
1, 2	wall	0.131 (0.001)	0.254 (0.002)	0.326 (0.002)

urchins per tile. They were allowed to explore the experimental area in the absence of waves for one minute following the placement of the last individual. In trials with waves, the motor was then turned on to create an initial wave velocity of 0.1 m s^{-1}. The velocity was gradually increased over the following two and five minutes in the 0.2 and 0.3 m s^{-1} treatments, respectively. This gradual increase was necessary to allow urchins to adapt to the increasing hydrodynamic forces and avoid dislodgement. However, it yielded different acclimation times among wave velocities, with 1 min at 0.0 and 0.1 m s^{-1}, 3 min at 0.2 m s^{-1}, and 6 min at 0.3 m s^{-1}. Because urchins moved more rapidly at low than high wave velocities, but acclimation time increased with wave velocity, the proportion of urchins in contact with each of the six microhabitats at the end of the acclimation was similar among velocity treatments (see Section 3.2.6). Patterns of urchin-microhabitat associations beyond acclimation were therefore caused by the sole effects of wave velocity. The end of the acclimation marked the onset of trials. The experimental area was photographed at the beginning of each trial and every five minutes thereafter with a digital camera (D5000; Nikon) located 1.3 m above the water surface.

The images of the experimental area were analyzed with PhotoImpact v6.0 (Ulead Systems, Inc.) and SigmaScan Pro v5.0.0 (Systat Software). They were used to calculate, for each trial, the mean displacement of six urchins marked with a few drops of colored lacquer (Fig. 3.1), as well as the proportion of urchins in each of the six microhabitats. The displacement of each urchin, defined by the sum of the linear distances moved from one image to the next, was calculated from the nine 5-min intervals available for each trial. The proportion of urchins in microhabitats was calculated from urchin counts at 15, 30, and 45 min. Urchins in contact with at least one individual were not included in these calculations. They were instead considered as being part of an aggregation. This distinction was necessary because the ability of aggregated urchins to displace and select a given microhabitat was reduced compared to solitary (non-aggregated) urchins, which were not physically obstructed by other individuals. The number of urchins in each microhabitat was corrected for differences in surface area among microhabitats. This was done by multiplying the number of urchins in the microhabitat by the ratio of the surface area of the largest microhabitat (wall, 0.73 m^2) to the surface area of the microhabitat. Ratios were: 1.1 (flat), 12.2 (protrusion), 5.5 (depression), 18.3 (ledge), 5.2 (crevice), and 1.0 (wall). The standardized proportion of urchins in each microhabitat was then obtained by dividing the average of corrected numbers of urchins at 15, 30, and 45 min by the sum of averages of corrected numbers of urchins in the six microhabitats.

Each wave velocity treatment was replicated 10 times between 20 January and 1 February, 2012. Trials were blocked over time by carrying out one replicate of each treatment on each day (four trials per day). The order of the treatments was randomized within each day. Tiles in the grid were reshuffled randomly between trials. Each trial was run with urchins not used previously. The relatively long (~2 h) flushing time of the wave tank prevented running each trial with new seawater. The tank was therefore filled with new seawater in the minutes preceding the first trial of each day and emptied after the last trial. Water temperature was recorded in each trial. It averaged 4.5 °C (±0.2).

3.2.4 Experiment 2: distribution and aggregation

In the present study, “urchin aggregation” refers to any group of two or more urchins in contact with one another. To test the effects of wave action and urchin density on urchin distribution and aggregation, a microcosm experiment, Experiment 2, was carried out in the oscillatory wave tank described in Experiment 1. The experiment was conducted in June, July, and August (summer) 2012, when sea surface temperature in Newfoundland, including BCC, typically rises and peaks (Chapter II, Caines and Gagnon 2012, Blain and Gagnon 2013) and urchins readily displace and aggregate (Chapter II). The experiment tested the prediction that the degree of aggregation and size of aggregations increase with wave action and urchin density.

Forty one (41), 89, and 140 urchins were allowed to displace and aggregate at wave velocities of 0.0 m s^{-1} (null), 0.1 m s^{-1} (low), 0.2 m s^{-1} (intermediate), and 0.3 m s^{-1} (high). These wave velocities and a frequency of 14 wave cycles min^{-1} were used in treatments with waves for reasons given in Experiment 1. Corresponding urchin densities, 51 (low), 110 (intermediate), and 173 (high) individuals m^{-2}, were similar to those in urchin barrens at a distance of 5 m or more from the lower edge of *Alaria esculenta* beds in the northern Gulf of St. Lawrence and eastern Newfoundland (Chapter II, Himmelman 1986, Gagnon et al. 2004).

Trials were conducted on a 3 x 3 grid arrangement of concrete tiles (nine tiles, 0.3 x 0.3 x 0.05 m [L, W, H] each) (Fig. 3.1). The grid was located in the centre of the tank. It was delimited longitudinally by the tank walls and transversally by nylon netting with 2.5-cm mesh to restrict urchins to the experimental area. The upper surface of the tiles was sculpted with small holes and cracks to simulate natural bedrock heterogeneity and rugosity. Contrary to Experiment 1, no topographical features were added to the tiles and there was no space (grooves) between them (Fig. 3.1). Urchins therefore had access to two microhabitats, flat (the nine tiles) and wall (the two longitudinal tank walls), which had different water velocities (Table 3.1) and together formed an experimental area of 1.37 m^2.

Each trial lasted 90 min to allow sufficient time for urchins to displace and form aggregations at all wave velocities and urchin densities as determined from preliminary trials. Urchins were introduced, oral surface down, to the tiles and spaced evenly across them. Like in Experiment 1, they were allowed to explore the experimental area in the absence of waves for one minute following the placement of the last individual. In trials with waves, the wave tank motor was then turned on to create an initial wave velocity of 0.1 m s^{-1}. The velocity was gradually increased over the following two and five minutes in the 0.2 and 0.3 m s^{-1} treatments, respectively, to allow urchins to adapt to the increasing hydrodynamic forces and avoid dislodgement. Urchin distribution (R, see below) at the onset of trials was similar among velocity treatments (see Section 3.2.6). Patterns of urchin distribution at the end of trials were therefore caused by the sole effects of wave velocity and urchin density. The experimental area was photographed at the beginning and end of each trial with a digital camera (D5000; Nikon) located 1.3 m above the water surface.

The nearest neighbour R-ratio (Clark and Evans 1954) was calculated from each image with PhotoImpact v6.0 (Ulead Systems, Inc.) and ImageJ v1.44p (National Institutes of Health, USA). This ratio is frequently used to characterize the distribution of organisms, in this case urchins on the tiles, from clumped (R=0), to random (R=1), to uniform (R=2.15) (Krebs 1999). It is obtained from the equation $R = (r_a / r_e)$, where r_a is the mean nearest neighbour distance (NND; the linear distance between the centre of each individual and the centre of its closest neighbour) in the observed population, and r_e is the mean NND expected under a random distribution for a given population density, ρ, obtained from the equation $r_e = 0.5\rho^{-0.5}$. The R-ratio for an area with no boundary strip can artificially yield an uniform distribution because organisms near the edges of the area tend to have higher NNDs than those near the centre (Sinclair 1985, Krebs 1999). To minimize this bias, NNDs of individuals with >50% of the test inside of a 5-cm boundary strip bordering the four sides of the 3 x 3 grid of tiles were omitted. This strip was sufficiently large to contain entire urchins and it minimized area loss. Urchins in the strip that were the nearest neighbours of urchins in the inner area (0.64 m^2) were nevertheless used to calculate NNDs for the latter individuals (Krebs 1999). As noted by Clarke and Evans (1954), if the area sampled is relatively small there can be individuals as close to each other as their physical size permits and that simultaneously have uniformly distributed body centres. To avoid a potential bias towards a uniform distribution, every NND was corrected for the minimum spatial requirement of urchins. This was done by subtracting the mean test diameter of 10 haphazardly chosen urchins from every NND in each trial. Urchins that were smaller than the mean test diameter and in contact with another urchin had negative NNDs. Negative NNDs were illogical, and hence were replaced by the value of zero. Urchins on the tank walls were not included in calculations because the factors that affect the distribution of urchins may differ between vertical and horizontal surfaces.

Preliminary inspection of images indicated that urchin aggregations formed around individuals in contact with the base of the tank walls and transverse nettings or around individuals on the tiles away from the walls (Fig. 3.1). Aggregations of the former type, termed “bounded aggregations”, were bound on one side (walls or nettings) and could expand only laterally or towards the inner tile, like aggregations in barrens that form around the base of boulders and rocky cliffs. Aggregations of the latter type, termed “unbounded aggregations”, were not bound on any side and could expand in any direction until contacting another aggregation or vertical surface, like aggregations in barrens that form on bare bedrock platforms. The proportion of bounded and unbounded aggregations was calculated for each trial by dividing the number of aggregations of each type by the total number of aggregations. The mean number of urchins per bounded and unbounded aggregation was also calculated for each trial by dividing the total number of urchins in each type of aggregation by the corresponding number of aggregations. Solitary (non-aggregated) urchins on the tiles and tank walls were also counted. Solitary urchins on the tank walls provided an indication of the tendency to displace within the tank: the higher the number on the walls, the higher the displacement. Urchins aggregated on the tank walls were dismissed because the factors that affect urchin aggregation may differ between vertical and horizontal surfaces.

Each of the 12 combinations of wave velocity and urchin density was replicated 10 times from 15 June to 13 August, 2012. Trials were blocked over time by conducting one replicate of each urchin density at the same wave velocity within the same day (three trials per day) over four consecutive days (12 trials per block of four days). The order of density treatments within each day and of wave treatments within each block of days was randomized. Each trial was run with urchins not used previously. The tank was filled and drained once a day as explained in Experiment 1. Water temperature during trials averaged 11.9 °C (±1.1).

3.2.5 Field observations: microhabitat use and distribution in the barrens

Microhabitat use and distribution of urchins and their relationship with thermal and wave environments were assessed by tracking changes over six months in sea temperature, wave conditions, and the number and location of urchins on two bedrock platforms separated by ~50 m at a depth of 5 m in the barrens at Bread and Cheese Cove (BCC). Both platforms, hereafter termed “inner” and “outer” with respect to their relative seaward alignment, were virtually horizontal and dominated by flat surfaces. They contained scattered grooves (crevices), as well as a few shallow troughs and jagged boulders similar to depressions and ledges in Experiment 1. Troughs and boulders were not sampled because the effects of their different shapes and sizes on local hydrodynamic conditions could not be controlled for. Logistical considerations precluded installing artificial depressions, ledges, and walls on the platforms. Results of Experiment 1 (see Section 3.3.1) and preliminary surveys in the barrens suggested that urchins readily associated with flat, crevice, and protrusion microhabitats. The present survey therefore focused on urchins on flat bedrock, in crevices, and on artificial protrusions (identical in shape and size to one another, see below).

Microhabitat use was quantified in 10 plots of 0.5 x 0.5 m on the inner bedrock platform. The position and orientation of all plots, which were spaced by at least 5 m from one another, were marked permanently by embossing one corner of a square frame in marine epoxy (Z-Spar A-77 Splash Zone Compound; Kop-Coat Inc.) affixed to the bedrock. Plots were haphazardly placed on the platform to contain comparable amounts of flat and crevice microhabitats, with no crevice deeper than 5 cm and wider than 2 cm. One concrete brick (0.2 x 0.1 x 0.05 m) fastened to the bedrock with marine epoxy at ~0.5 m from the marked corner of each plot was used to create the same protrusion microhabitat as in Experiment 1. Bricks were used instead of naturally occurring boulders because the former had identical shape and size, therefore similarly affecting near-bottom water flows. All plots and bricks were photographed with a submersible digital camera system (Nikon D5000 with an Ikelite SLR-DC housing) on 30 April, 2012, and every five to 16 days until 25 October, 2012 (22 times). The contour of each plot was made visible by inserting, before the photograph, one corner of a 0.5 x 0.5-m frame into the embossed portion of the marking marine epoxy.

Images of plots and bricks were analyzed with PhotoImpact v6.0 (Ulead Systems, Inc.). They were used to count urchins in each microhabitat. In images of plots, a 2.5-cm wide strip, corresponding to the radius of large urchins, was drawn along each side of each crevice. Urchins were assigned to the crevice microhabitat if >50% of the test overlapped with one of the 5-cm wide strips, else to the flat microhabitat. The number of urchins in the latter two microhabitats was corrected for differences in microhabitat surface areas among and within plots. This was done like in Experiment 1 by multiplying the number of urchins in each microhabitat in each plot by the ratio of the surface area of the largest microhabitat across plots (flat, plot 9, 0.22 m^2) to the surface area of the corresponding microhabitat in the plot (see Appendix D for plot-specific ratios). The standardized proportion of urchins in crevices in each plot was then obtained by dividing the corrected number of urchins in crevices by the corrected total number of urchins in the plot. The standardized proportion of urchins on flat bedrock was the difference between 100% and the standardized proportion of urchins in crevices. In images of bricks, a 10-cm wide strip, corresponding to two times the diameter of large urchins, was drawn on the flat bedrock along each side of each brick, yielding plots of 0.12 m^2 (0.4 x 0.3 m) centred on bricks. Urchins in these plots were assigned to the protrusion microhabitat if located on any surface of the brick or on the bedrock with spines touching the brick, else to the strip surrounding the brick. The proportion of urchins in the protrusion microhabitat in each plot was obtained by dividing the number of urchins in contact with the protrusion by the total number of urchins in the plot (protrusion + strip). Proportions of urchins in the flat, crevice, and protrusion microhabitats were used instead of raw numbers of urchins to account for likely variation in urchin abundance on the platform throughout the survey.

Urchin distribution and density were quantified in a square zone of 6×6 m (36 m^2) on the outer bedrock platform. The four corners of the zone were permanently marked with bolts set into the bedrock. The entire zone was filmed with a submersible video camera system (Sony HDV 1080i/MiniDV with an Amphibico Endeavor housing) propelled by a diver at a fixed distance (1.5 m) above the seabed on 8 May, 2012, and every five to 15 days until 25 October, 2012 (22 times). On each sampling event, two facing sides of the zone were delineated with 6-m benchmark lines tied to the bolts and marked at 0.5-m intervals with cable ties. A 1 x 6-m section of the zone was filmed along a transect line attached to the first pair of cable ties on the benchmark lines. The transect line was shifted to the next pair of cable ties until the entire area was filmed. This procedure yielded 11 video segments, which overlapped spatially. Segments were converted into individual images with PanoraGen.DV v1.0 and subsequently stitched into a single mosaic of the entire zone with PhotoImpact v6.0. The mosaic with the best image quality was used to draw as many plots of 0.5 x 0.5 m as possible with a minimum distance of 0.2 m from one another and that contained (1) <25% of flat bedrock and >75% of bedrock with crevices; or (2) >90% of flat bedrock and <10% of bedrock with crevices. These plots, which typified respectively the crevice and flat microhabitats, had no noticeable depression, protrusion, ledge, or wall. They were drawn at the same locations on the 21 other mosaics. Urchins with a test diameter ≥2 cm (smallest detectable size on the imagery) were counted in all plots of each mosaic. A few plots in some mosaics were discarded because of poor image quality or the presence of occasional seaweed (mainly kelp) debris, which could have hidden urchins from view or induced feeding aggregations. As a result, 10 to 15 plots of each microhabitat were used on each sampling event. The information from all plots of a same microhabitat was used to calculate the nearest neighbour R-ratio and mean urchin density on each sampling event (see Experiment 2 for meaning and calculations of R-ratio).

Sea temperature at BCC was recorded every 30 min throughout the study with a temperature logger (±0.5°C, HOBO Pendant; Onset Computer Corporation) attached to one eyebolt drilled into the seabed at a depth of 5 m. The wave environment was quantified by recording the pressure of the water column every minute with a water level logger (HOBO U20-001-01-Ti Water Level Logger; Onset Computer Corporation) secured to the seabed at a depth of 5 m (both loggers were located in between the two bedrock platforms). Raw pressure values (psi) were corrected for barometric pressure by subtracting the hourly atmospheric pressure (psi) at the date and time of measurement (http://www.climate.weather.gc.ca/, Station St. John's Intl A). Each corrected value was then converted into a raw water depth (m) by multiplying it by a conversion factor of 0.68 m psi^{-1} (NOAA 2001). Raw water depths were corrected for tidal elevation and logger depth by subtracting the elevation at the date and time of measurement (http://www.tides.gc.ca/eng, Station 905) and the exact depth of the logger, yielding wave height. Although this method may underestimate wave height, it is the most reliable we could use with the resources at hand (see Chapter II for data quality assessment using this method).

3.2.6 Statistical analysis

Experiment 1: A two-way ANOVA with the factors Waves (null, low, intermediate, and high wave velocity) and Block (each daily block of one replicate of each treatment) was used to examine the effects of wave action on the displacement of urchins during trials. The analysis was applied to the raw data (n=40).

A one-way MANOVA (Scheiner and Gurevitch 2001) with the factor Waves (null, low, intermediate, and high wave velocity) was used to examine the effects of wave action on standardized proportions of urchins in each of the six microhabitats (flat, protrusion, depression, ledge, crevice, and wall) during trials. Prior to running this analysis, a two-way MANOVA with the factors Waves (null, low, intermediate, and high wave velocity) and Block (each daily block of one replicate of each treatment) was run to determine if results differed among blocks. There was no significant effect of the factor Block ($F_{54,162}=1.078$; $p=0.353$) $\alpha=0.25$, the recommended significance level to make decisions about the removal or retention of block variables or block-by-factor interactions in general linear models (Quinn and Keough 2002, Sokal and Rohlf 2012). The one-way MANOVA was therefore run on data pooled from all blocks. The analysis was applied to the logit-transformed data (Warton and Hui 2011) to correct for heterogeneity of the residuals in the analysis on the raw data (n=240). A one-way MANOVA with the same structure showed that standardized proportions of urchins in each of the six microhabitats at the onset of trials (i.e. at the conclusion of the acclimation in the wave tank) did not differ among velocity treatments ($F_{18,72}$=1.206; p=0.280). Changes in patterns of urchin-microhabitat associations beyond acclimation were therefore assumed to be caused by the sole effects of wave velocity. The latter MANOVA was also applied to the logit-transformed data (n=240).

Experiment 2: A one-way ANOVA with the factor Waves (null, low, intermediate, and high wave velocity) showed that the nearest neighbour R-ratio (R) at the onset of trials did not differ among velocity treatments ($F_{3,116}$=1.32, p=0.272). Patterns of urchin distribution beyond acclimation were therefore assumed to be caused by the sole effects of wave velocity. The ANOVA was applied to the square-root transformed data (Zar 1999) to correct for non-normality of the residuals in the analysis on the raw data (n=120).

Patterns of urchin distribution at the end of trials were characterized by calculating, for each trial, a critical z-statistic with the equations $z = ((r_a - r_e) / s_r)$, and $s_r = 0.26136\,(N\rho)^{-0.5}$, where r_a is the mean NND for the trial, r_e is the mean NND expected under a random distribution, s_r is the standard error of r_e, N is the total number of urchins, and ρ is the urchin density (see Section 3.2.4 and Clark and Evans 1954). Urchins were randomly distributed (R=1) if $|z|$ was $\leq$ 1.96 (two-tailed test of significance at α=0.05), clumped if $|z|$ was >1.96 and R<1, or uniformly distributed if $|z|$ was >1.96 and R>1 (Krebs 1999).

A three-way ANOVA with the factors Waves (null, low, intermediate, and high wave velocity), Density (low, intermediate, and high urchin density), and Block (each block of four days during which one replicate of each treatment was done) was used to examine the effects of wave action and urchin density on the nearest neighbour R-ratio (R) of urchins in trials in which the latter was significantly lower than 1 (114 out of 120 trials; 95%). The ANOVA was applied to the square root-transformed data to correct for heterogeneity of the residuals in the analysis on the raw data (n=114). Because the factor Block was significant (see Section 3.3.2), the mean squares (MS) values of the Waves x Block and Density x Block terms were used as denominators to calculate the F-value for the factors Waves and Density, respectively. This procedure is recommended for factorial randomized complete block designs with sufficient degrees of freedom to include factor-by-block interactions in the model, and when such interactions are significant at α=0.25 (Quinn and Keough 2002, Sokal and Rohlf 2012).

A two-way ANOVA with the factors Waves (null, low, intermediate, and high wave velocity) and Density (low, intermediate, and high urchin density) was used to examine the effects of wave action and urchin density on the proportion of urchin aggregations that were bounded. Trials in which there was no urchin aggregation (2 out of

120 trials; <2%) were excluded from the analysis. Prior to running this analysis, a three-way ANOVA with the factors Waves (null, low, intermediate, and high wave velocity), Density (low, intermediate, and high urchin density), and Block (each block of four days during which one replicate of each treatment was done) was run to determine if results differed among blocks. There were no significant factor-by-block interactions (Waves x Block: $F_{27,52}=0.98$, $p=0.504$; Density x Block: $F_{18,52}=0.46$, $p=0.965$). The two-way ANOVA was therefore run on data pooled from all blocks. The analysis was applied to the logit-transformed data to correct for heterogeneity of the residuals in the analysis on the raw data (n=118).

Three two-way ANOVAs (one for each urchin density) with the factors Waves (null, low, intermediate, and high wave velocity) and Block (each block of four days during which one replicate of each treatment was done) were used to examine the effects of wave action on: (1) number of urchins per bounded aggregation; (2) number of urchins per unbounded aggregation; (3) number of solitary urchins on the tiles; and (4) number of solitary urchins on the tank walls, at the end of trials. Numbers of aggregated and solitary urchins were examined for each urchin density separately to avoid confounding effects of wave action and density had three-way ANOVAs (with the factors Waves, Density, and Block) been used. Effects of wave action and urchin density were not confounded in the analyses of R (see above) because calculations of R controlled for density effects (see Section 3.2.4). The factor Block was not significant at $\alpha=0.25$ in three of the twelve two-way ANOVAs (see Section 3.3.2). It was nevertheless retained in all models for consistency. Only those trials in which there were bounded aggregations (118 out of 120; 98%), unbounded aggregations (52 out of 120; 43%), and solitary urchins (120 out of

120; 100%) were used in the corresponding analyses. Analyses of the number of urchins per bounded (n=38 to 40) and unbounded (n=11 to 21) aggregations were applied to the log(x+1)-transformed data (Zar 1999) to correct for heterogeneity of the residuals in the analysis on the raw data, with the following exception. No transformation corrected the heterogeneity of the residuals in the analysis on the raw data for unbounded aggregations at low urchin density. The latter ANOVA was therefore also run with the rank-transformed data. Because both analyses yielded the same conclusions about the significance of each factor, we presented the results from the analysis on the raw data (Conover 1980). The ANOVAs on the number of solitary urchins on the tiles and walls were applied to the raw data (n=40).

Field observations: Multiple linear regression analysis was used to relate proportions of urchins in crevice, flat, and protrusion microhabitats to sea temperature and wave height on the inner bedrock platform at Bread and Cheese Cove (BCC). Each of the three regression models was based on 22 data points (n=22 for each microhabitat). Each point in the models for crevice and flat microhabitats was the mean proportion of urchins from the 10 plots for a given sampling event and corresponding mean sea temperature and significant wave height (SWH, the average height of the highest one-third of the wave data). As mentioned previously, the standardized proportion of urchins on flat bedrock was the difference between 100% and the standardized proportion of urchins in crevices. Accordingly, the latter two models yielded reciprocal results, which are nevertheless presented to discuss different perspectives. Three out of the 10 concrete bricks used to create the protrusion microhabitat were lost during the passage of the tail end of

Hurricane Leslie on 11 September, 2012. Accordingly, each point in the model for the protrusion microhabitat was the mean proportion of urchins from the 10 protrusions for the first 15 sampling events and from seven protrusions for the last six sampling events, and corresponding mean sea temperature and SWH. Mean sea temperature and SWH were calculated over the 48 h preceding each sampling event because preliminary analysis showed stabilization of variation beyond 48 h. Multiple regression analysis was also used to relate the distribution (R) and density of urchins in flat and crevice microhabitats to sea temperature and wave height on the outer bedrock platform at BCC. Each regression model (four in total) was also based on 22 data points (n=22 for each combination of response variable and microhabitat). Each point was the R-ratio or mean urchin density from 10 to 15 plots for a given sampling event and corresponding mean sea temperature and SWH over the preceding 48 h. All regressions were applied to the raw data. Sea temperature and SWH throughout the entire field survey were not correlated (Pearson's product-moment correlation, r=0.056, p=0.805), which enabled testing the effects of both environmental factors. As mentioned previously, sample plots on the two bedrock platforms were spatially fixed. Inspection of all regression analyses indicated that residuals were not autocorrelated. The absence or presence of synergistic effects between the two explanatory variables (temperature and SWH) was not known a priori. All analyses were therefore conducted using the multiplicative error model approach, whereby explanatory variables are tested for both individual and interactive effects (Kleinbaum et al. 2008). If interactive effects were not significant, models with individual effects of only those explanatory variables that were significant in the truncated models were presented.

In all ANOVAs, MANOVAs, and regression analyses, homogeneity of the variance was verified by examining the distribution of the residuals. Normality of the residuals was verified by examining the normal probability plots of the residuals (Snedecor and Cochran 1989). All MANOVAs met all the customary assumptions, including multivariate normality, homogeneity of variance-covariance matrices, and absence of multicollinearity (Scheiner and Gurevitch 2001). Tukey HSD multiple comparison tests (comparisons based on least-square means, Sokal and Rohlf 2012) were used to detect differences among levels within a factor (ANOVAs and MANOVAs). When a factor or interaction between factors was significant in the MANOVAs, the univariate model for the response variables was examined to identify which variables contributed to the multivariate effect. This was done by carrying out an ANOVA for the response variable with those factors that were significant in the MANOVA (Scheiner and Gurevitch 2001). The Pillai's trace multivariate statistic was used in the MANOVAs to determine which factor(s) were statistically significant (Scheiner and Gurevitch 2001). A significance level of 0.05 was used unless otherwise specified. All analyses were carried out with JMP 7.0 and Minitab 17.1.0.

3.3 RESULTS

3.3.1 Experiment 1

Analysis of data from Experiment 1 indicated that the distance moved by urchins over 45 min varied among the four wave velocities (Table 3.2). Displacement peaked to 54.5 (±7.3) cm in the absence of waves and dropped steadily by ~40% as wave velocity increased from null to high (32.4±2.1 cm) (Fig. 3.2). The MANOVA and associated

Table 3.2. Summary of two-way ANOVA (applied to raw data) examining the effect of Waves (null, low, intermediate, and high wave velocity) and Block (each daily block of one replicate of each treatment) on the displacement of green sea urchins (*Strongylocentrotus droebachiensis*) in Experiment 1 (see Section 3.2.3 for a description of the experiment).

Source of variation	***df***	**MS**	***F*-value**	***p***
Waves	3	1074.2	5.44	0.005
Block	9	452.9	2.29	0.046
Error	27	197.5		
Corrected total	39			

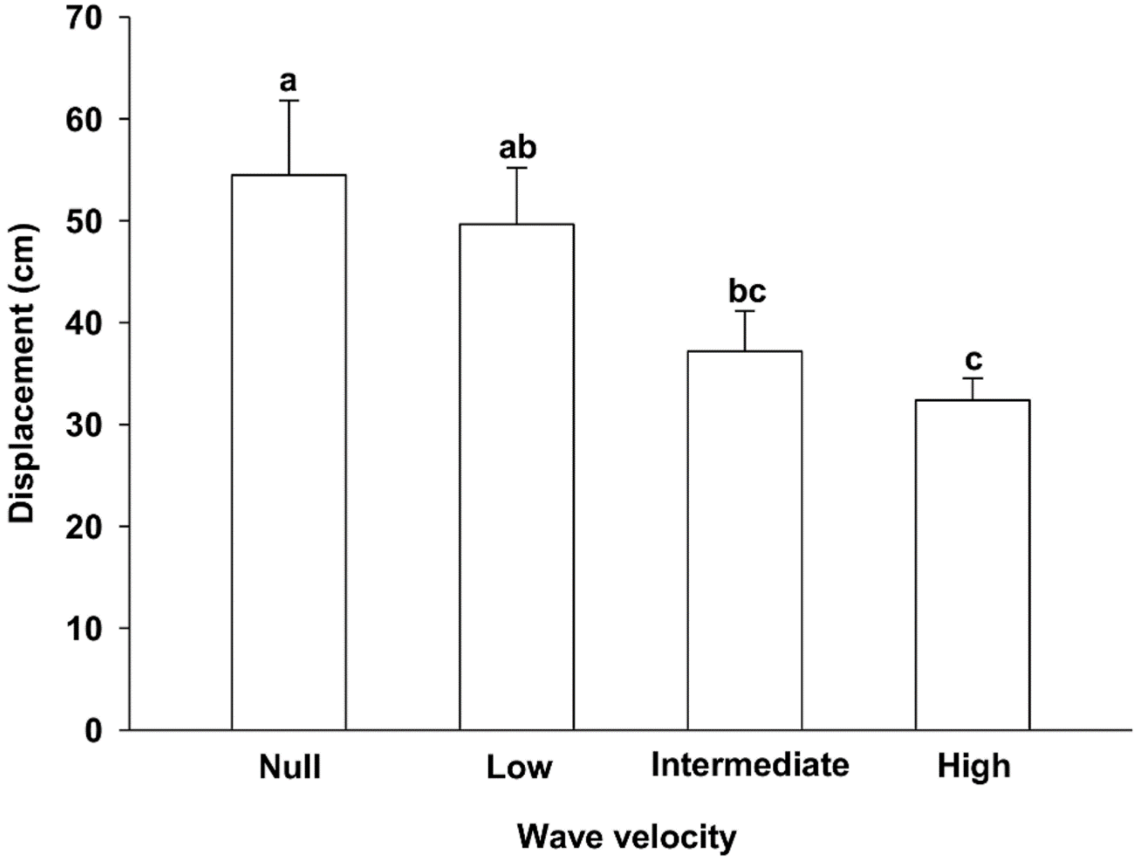


Fig. 3.2. Mean (+SE) displacement of green sea urchins (*Strongylocentrotus droebachiensis*) at null, low, intermediate, and high wave velocity (0.0, 0.1, 0.2, and 0.3 m s^{-1}, respectively) (Experiment 1). Bars not sharing the same letter are different (LS means tests, $p<0.05$; n=10 for each velocity).

univariate ANOVAs showed that wave velocity affected the (standardized) proportion of urchins in three of the six microhabitats: flat, crevice, and wall (one-way MANOVA, $F_{18,99}=3.294$; $p<0.001$, Table 3.3). The proportion of urchins on flat surfaces was significantly higher at null and low (~10%) than at intermediate and high (~7%) velocities (LS means, $p<0.001$; Fig. 3.3). Wave velocity markedly affected the proportion of urchins in crevices, with a twofold increase from null (20%) to high (43%) velocity (Fig. 3.3). At high velocity, there were at least two times more urchins in crevices than in any other microhabitat (Fig. 3.3). The proportion of urchins on the tank walls was consistently low (<4%) at all velocities. Nevertheless, it was significantly higher at null and low than at intermediate and high velocities (LS means, $p<0.001$; Fig. 3.3). Wave velocity had no perceptible effect on the proportion of urchins in the protrusion, depression, and ledge microhabitats (Table 3.3), where it ranged from 14% (ledge at high velocity) to 27% (protrusion at null velocity; Fig. 3.3).

3.3.2 Experiment 2

Analysis of data from Experiment 2 indicated that the degree of aggregation (nearest neighbour R-ratio, R) of urchins with a clumped distribution (R significantly lower than 1) varied with urchin density among the four wave velocity treatments (a significant interaction between the factors Waves and Density, Table 3.4). R ranged from 0.19 (highly aggregated) at high density and high velocity to 0.45 (moderately aggregated) at intermediate density and null velocity (LS means, $p<0.001$; Fig. 3.4). Velocity had no effect on aggregation at low density, as shown by non-significant changes in R from 0.31 (low) to 0.35 (high) (Fig. 3.4). However, aggregation at

Table 3.3. Summary of one-way ANOVAs (applied to logit-transformed data) examining the effect of Waves (null, low, intermediate, and high wave velocity) on proportions of green sea urchins (*Strongylocentrotus droebachiensis*) in the six microhabitats in Experiment 1 (see Section 3.2.3 for a description of the experiment).

Microhabitat	**Source of variation**	***df***	**MS**	***F*-value**	***p***
Flat	Waves	3	0.23	17.57	<0.001
	Error	36	0.01		
	Corrected total	39			
Protrusion	Waves	3	0.06	1.74	0.177
	Error	36	0.04		
	Corrected total	39			
Depression	Waves	3	0.03	0.90	0.450
	Error	36	0.03		
	Corrected total	39			
Ledge	Waves	3	0.05	1.32	0.283
	Error	36	0.04		
	Corrected total	39			
Crevice	Waves	3	0.53	49.63	<0.001
	Error	36	0.01		
	Corrected total	39			
Wall	Waves	3	0.86	15.80	<0.001
	Error	36	0.05		
	Corrected total	39			

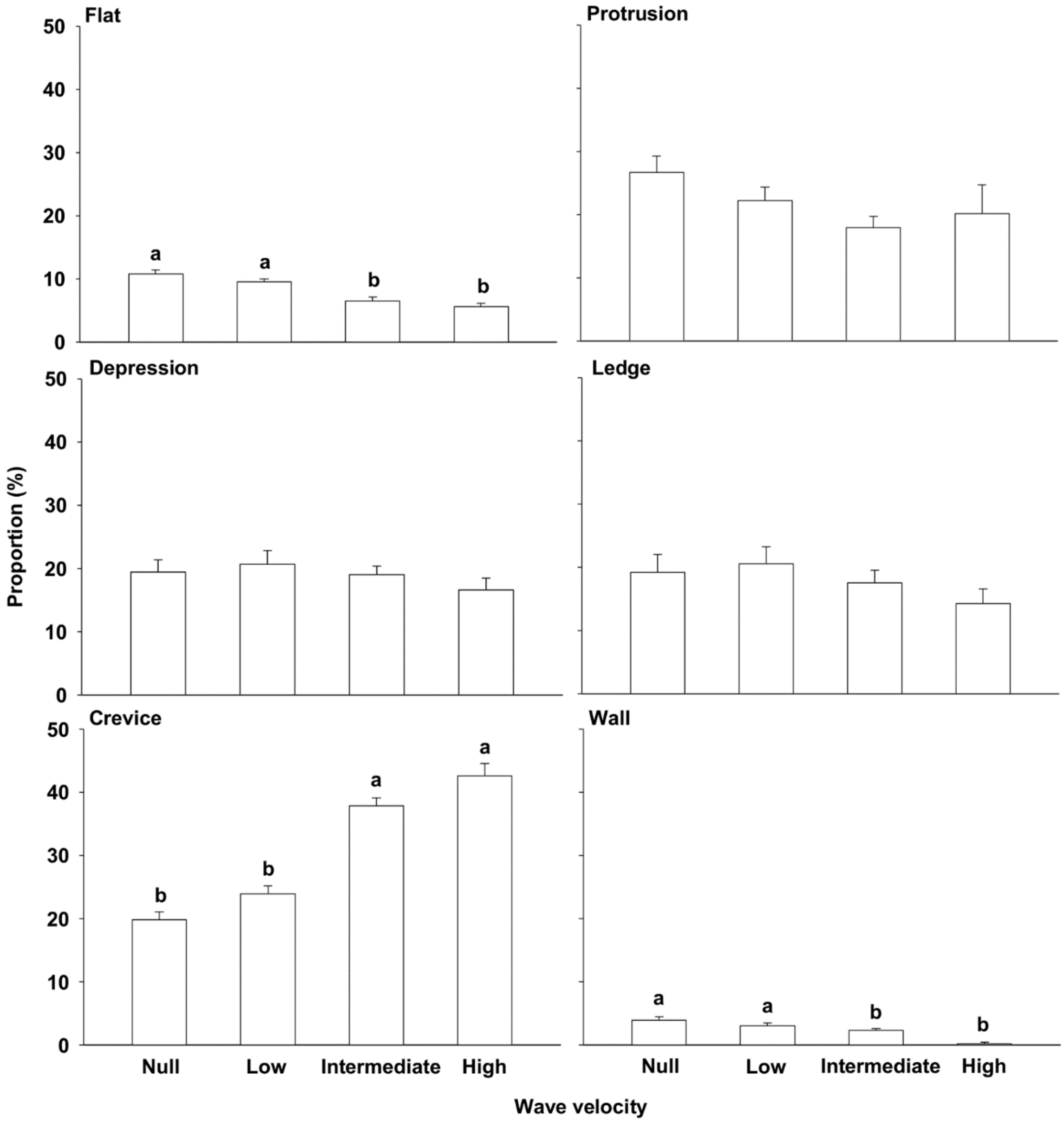


Fig. 3.3. Proportion (+SE) of green sea urchins (*Strongylocentrotus droebachiensis*) in each of the six microhabitats at null, low, intermediate, and high wave velocity (0.0, 0.1, 0.2, and 0.3 m s^{-1}, respectively) (Experiment 1). Bars not sharing the same letter are different (LS means tests, p<0.05; n=10 for each wave velocity in each microhabitat).

Table 3.4. Summary of three-way ANOVA (applied to square root-transformed data) examining the effect of Waves (null, low, intermediate, and high wave velocity), Density (low, intermediate, and high urchin density), and Block (each block of four days during which one replicate of each treatment was done) on the nearest neighbour R-ratio (R) of green sea urchins (*Strongylocentrotus droebachiensis*) with a clumped distribution (R significantly lower than 1) at the end of trials in Experiment 2 (see Section 3.2.4 for a description of the experiment and R-ratio).

Source of variation	***df***	**MS**	***F*-value**	***p***
Waves	3	0.061	4.17	0.011
Density	2	0.068	5.44	0.007
Block	9	0.024	2.80	0.010
Waves × Density	6	0.022	2.56	0.031
Waves × Block	27	0.015	1.72	0.050
Density × Block	18	0.013	1.47	0.143
Error	48	0.010		
Corrected Total	113			

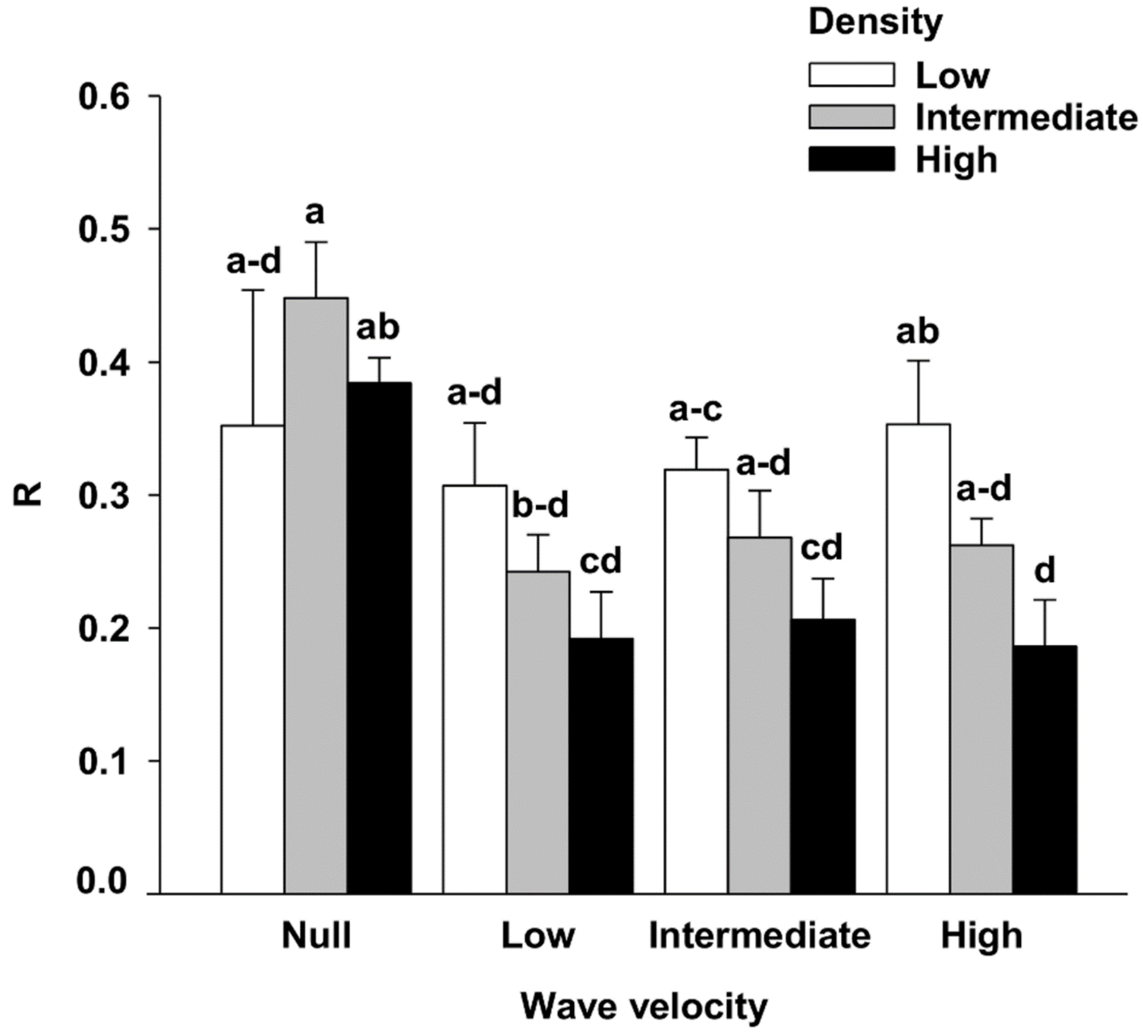


Fig. 3.4. Mean (+SE) nearest neighbour R-ratio (R) of green sea urchins (*Strongylocentrotus droebachiensis*) at the end of trials at null, low, intermediate, and high wave velocity (0.0, 0.1, 0.2, and 0.3 m s^{-1}, respectively), and low, intermediate, and high density (51, 110, and 173 individuals m^{-2}, respectively) (Experiment 2). Bars not sharing the same letter (only ranges are provided for simplicity, e.g. “a-d” means “abcd”) are different (LS means tests, *p*<0.05; n=6-10 for each combination of Waves x Density).

intermediate and high densities increased markedly with the introduction of waves, as shown by 54 and 50% drops in R from null to low velocity, respectively (Fig. 3.4). Changes in R among densities were largest at high velocity, with a 53% drop from low to high density (LS means, *p*=0.007; Fig. 3.4).

Wave velocity and urchin density interactively determined the proportion of urchin aggregations that had formed at the end of trials (Table 3.5). The majority (>73%) of aggregations were bounded (originating from individuals at the base of the tank walls and transverse nettings and expanding towards the centre of the tank) as opposed to unbounded (originating from, and growing around, individuals on the tank bottom away from the walls) (Fig. 3.5). The proportion of bounded aggregations at low density was relatively high (95-100%) at intermediate and lower velocities, but dropped to 73% at high velocity (a significant difference between intermediate and high velocities; LS means, *p*=0.005) (Fig. 3.5). Conversely, velocity had no perceptible effect on the proportion of bounded aggregations at intermediate and high density, as shown by non-significant changes from 79% (high density at null velocity) to 95% (high density at low velocity) (LS means, *p*>0.05; Fig. 3.5). In the absence of waves, the proportion of bounded aggregations decreased steadily with increasing density, with a drop of 21% from low to high density (LS means, *p*=0.007; Fig. 3.5).

The number of urchins per bounded aggregation varied with wave velocity at the three urchin densities tested (Table 3.6). At low density, there were two times more urchins (at least 2.8 [±0.4] individuals) per bounded aggregation at intermediate and high velocities than at null and low velocities (LS means, *p*<0.001; Fig. 3.6). Effects of velocity exacerbated with increasing urchin density, with respectively four and seven

Table 3.5. Summary of two-way ANOVA (applied to logit-transformed data) examining the effect of Waves (null, low, intermediate, and high wave velocity), and Density (low, intermediate, and high urchin density) on the proportion of bounded aggregations of green sea urchins (*Strongylocentrotus droebachiensis*) at the end of trials in Experiment 2 (see Section 3.2.4 for a description of the experiment).

Source of Variation	***df***	**MS**	***F*-value**	***p***
Waves	3	0.773	7.32	<0.001
Density	2	0.163	1.54	0.218
Waves × Density	6	0.375	3.54	0.003
Error	106	0.106		
Corrected Total	117			

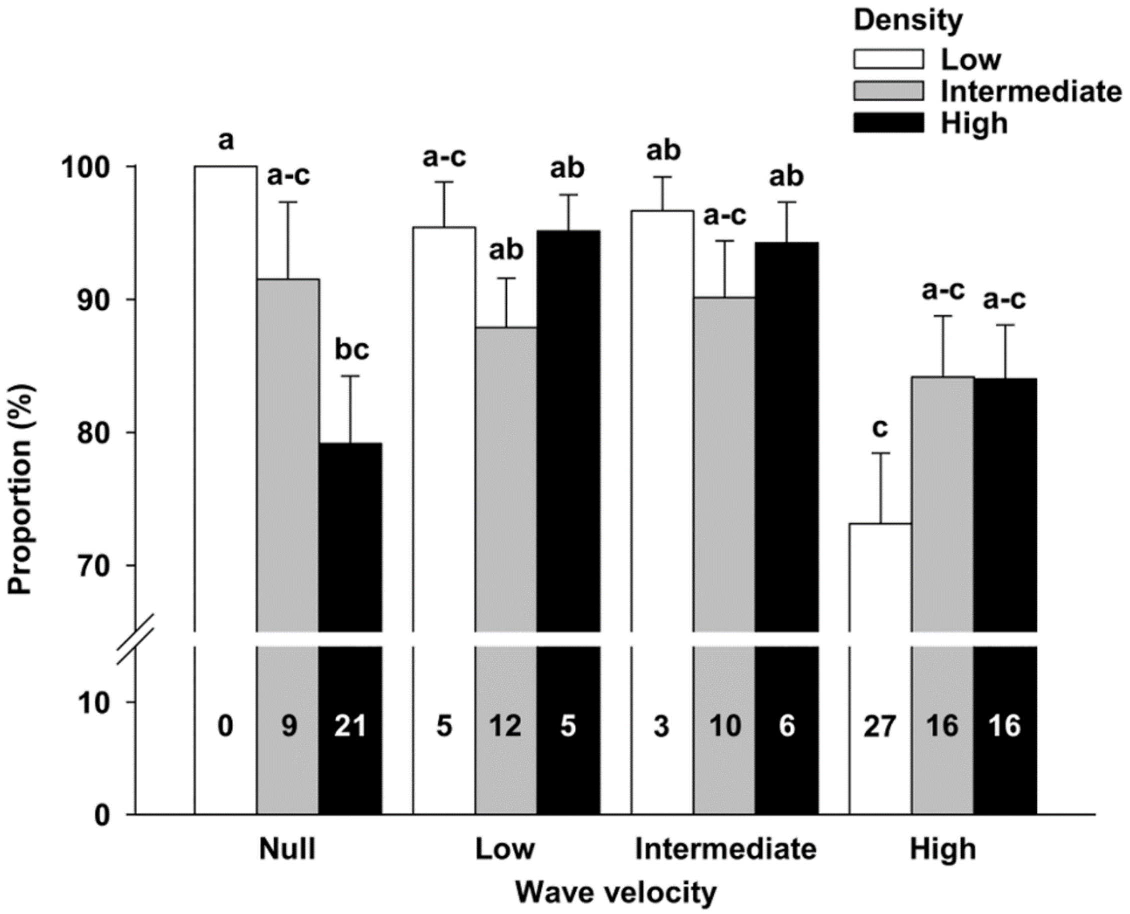


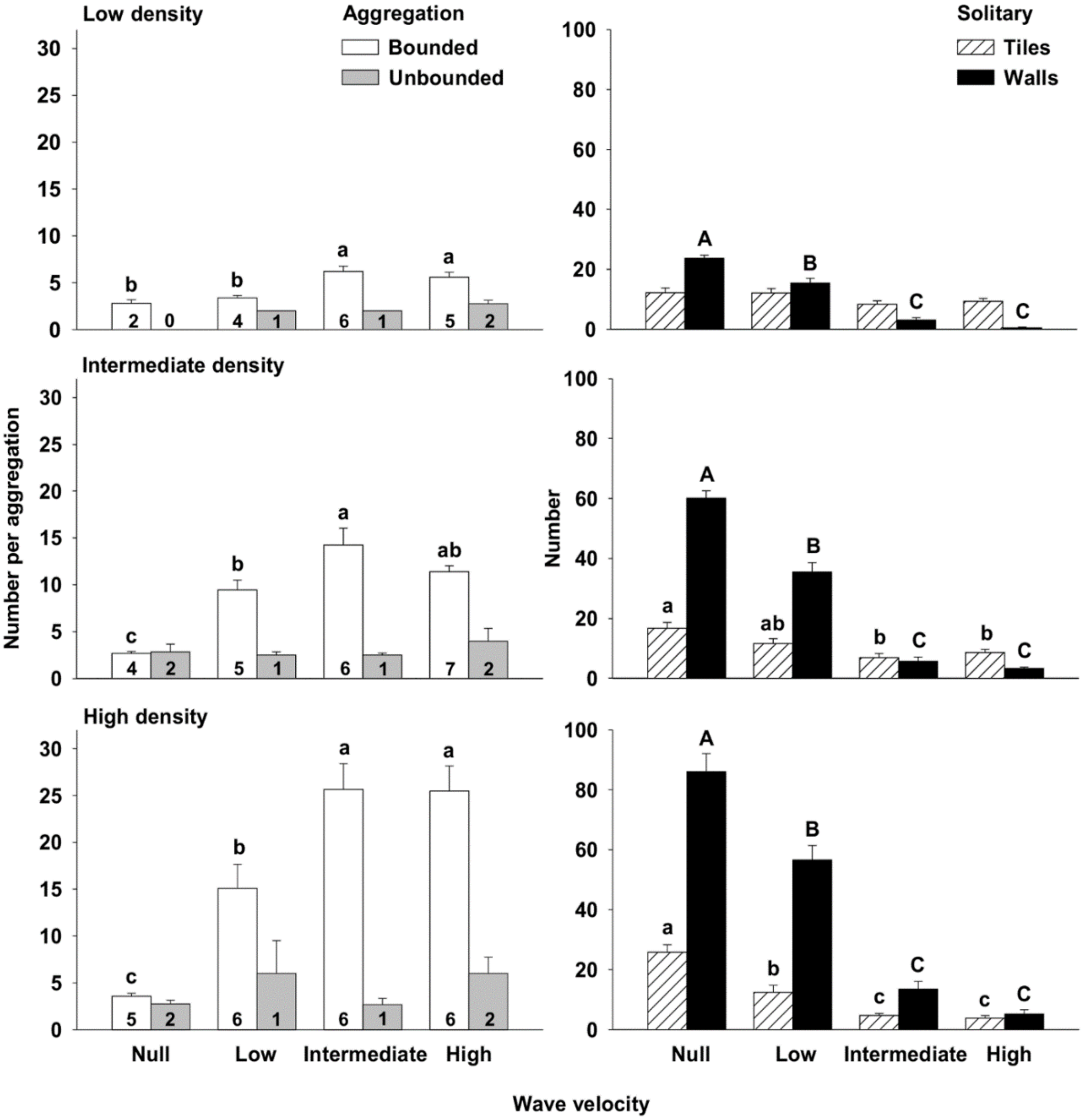
Fig. 3.5. Mean (+SE) proportion of bounded aggregations of green sea urchins (*Strongylocentrotus droebachiensis*) at the end of trials at null, low, intermediate, and high wave velocity (0.0, 0.1, 0.2, and 0.3 m s^{-1}, respectively), and low, intermediate, and high density (51, 110, and 173 individuals m^{-2}, respectively) (Experiment 2). Values within bars are proportions of unbounded aggregations. Bars not sharing the same letter (only ranges are provided for simplicity, e.g. "a-c" means "abc") are different (LS means tests, $p<0.05$; n=8-10 for each combination of Waves x Density).

Table 3.6. Summary of two-way ANOVAs (applied to log[x+1]-transformed[1] and raw[2] data) examining the effect of Waves (null, low, intermediate, and high wave velocity) and Block (each block of four days during which one replicate of each treatment was done) on the number of green sea urchins (*Strongylocentrotus droebachiensis*) per bounded and unbounded aggregation and number of solitary urchins on the tiles and tank walls under three densities at the end of trials in Experiment 2 (see Section 3.2.4 for a description of the experiment).

Configuration	**Density**	**Source of variation**	***df***	**MS**	***F*-value**	***p***
Bounded aggregation	Low[1]	Waves	3	0.177	17.15	<0.001
		Block	9	0.017	1.64	0.153
		Error	27	0.010		
		Corrected Total	39			
	Intermediate[1]	Waves	3	0.581	45.32	<0.001
		Block	9	0.020	1.56	0.182
		Error	25	0.013		
		Corrected Total	37			
	High[1]	Waves	3	1.261	67.66	<0.001
		Block	9	0.038	2.02	0.077
		Error	27	0.019		
		Corrected Total	39			
Unbounded aggregation	Low[2]	Waves	2	0.198	2.23	0.310
		Block	6	0.849	9.55	0.098
		Error	2	0.089		
		Corrected Total	10			
	Intermediate[1]	Waves	3	0.019	0.64	0.614
		Block	9	0.022	0.73	0.679
		Error	7	0.030		
		Corrected Total	19			
	High[1]	Waves	3	0.070	2.99	0.096
		Block	9	0.069	2.95	0.071
		Error	8	0.023		
		Corrected Total	20			

Table 3.6. (continued)

Configuration	**Density**	**Source of variation**	***df***	**MS**	***F*-value**	***p***
Solitary on tiles	Low[2]	Waves	3	39.09	2.53	0.078
		Block	9	25.30	1.64	0.154
		Error	27	15.44		
		Corrected Total	39			
	Intermediate[2]	Waves	3	184.70	8.07	0.001
		Block	9	26.88	1.17	0.350
		Error	27	22.89		
		Corrected Total	39			
	High[2]	Waves	3	1035.69	35.96	0.001
		Block	9	41.11	1.43	0.226
		Error	27	28.80		
		Corrected Total	39			
Solitary on walls	Low[2]	Waves	3	1176.29	104.52	<0.001
		Block	9	10.45	0.93	0.517
		Error	27	11.25		
		Corrected Total	39			
	Intermediate[2]	Waves	3	7267.83	254.19	<0.001
		Block	9	91.51	3.20	0.009
		Error	27	28.59		
		Corrected Total	39			
	High[2]	Waves	3	14378.62	102.80	<0.001
		Block	9	251.70	1.80	0.115
		Error	27	139.90		
		Corrected Total	39			


Low density
Aggregation
Bounded
Unbounded
Solitary
Tiles
Walls
Intermediate density
High density
Number per aggregation
Number
Null
Low
Intermediate
High
Wave velocity
b
b
a
a
2
0
4
1
6
1
5
2
A
B
C
C
c
b
a
ab
4
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C

Fig. 3.6. Mean (+SE) number of green sea urchins (*Strongylocentrotus droebachiensis*) per bounded and unbounded aggregation (left hand panels) and mean (+SE) number of solitary (non-aggregated) urchins on the tiles and tank walls (right hand panels) at the end of trials at null, low, intermediate, and high wave velocity (0.0, 0.1, 0.2, and 0.3 m s^{-1}, respectively) and low, intermediate, and high density (51, 110, and 173 individuals m^{-2}, respectively) (Experiment 2). Values within bars in left hand panels are mean numbers (rounded for clarity) of bounded and unbounded aggregations at each wave velocity. Bars not sharing the same letter (lower-case for bounded aggregations and tiles, upper-case for walls) are different (LS means tests, $p<0.05$; n=2-10 for each bar).

times more urchins (up to 25.7 [±2.7] individuals) per bounded aggregation at high than null velocity at intermediate and high densities, respectively (Fig. 3.6). Wave velocity had no perceptible effect on the number of urchins per unbounded aggregation at any urchin density (Table 3.6), with <6.0 (±1.8) individuals aggregation^{-1} (Fig. 3.6). There were two to six times more bounded than unbounded aggregations regardless of wave velocity and urchin density (Fig. 3.6).

Wave velocity affected the number of solitary urchins on the tiles at intermediate and high densities only (Table 3.6 and Fig. 3.6). At low density, urchins on the tiles were relatively abundant, ~8-12 individuals, regardless of velocity (Fig. 3.6). At intermediate and high densities, there were respectively two and seven times more urchins on the tiles at null than high velocity (Fig. 3.6). At all densities, the number of solitary urchins on the tank walls decreased steadily as wave velocity increased from null to intermediate, with no further change from intermediate to high (Table 3.6 and Fig. 3.6). There were 8, 10, and 6 times more urchins on the walls in the absence of waves than at intermediate velocity at low, intermediate, and high densities, respectively (Fig. 3.6).

3.3.3 Field observations

Sea temperature and significant wave height (SWH) at Bread and Cheese Cove (BCC) were generally lowest and highest during the first month of the survey (May), with minima and maxima of respectively -0.6°C and 0.59 m (Fig. 3.7). Temperature generally increased until mid-August, when it peaked to 16.7°C, and remained relatively high, between 7.1 and 16.6°C, until the end of the survey (October). SWH was relatively low

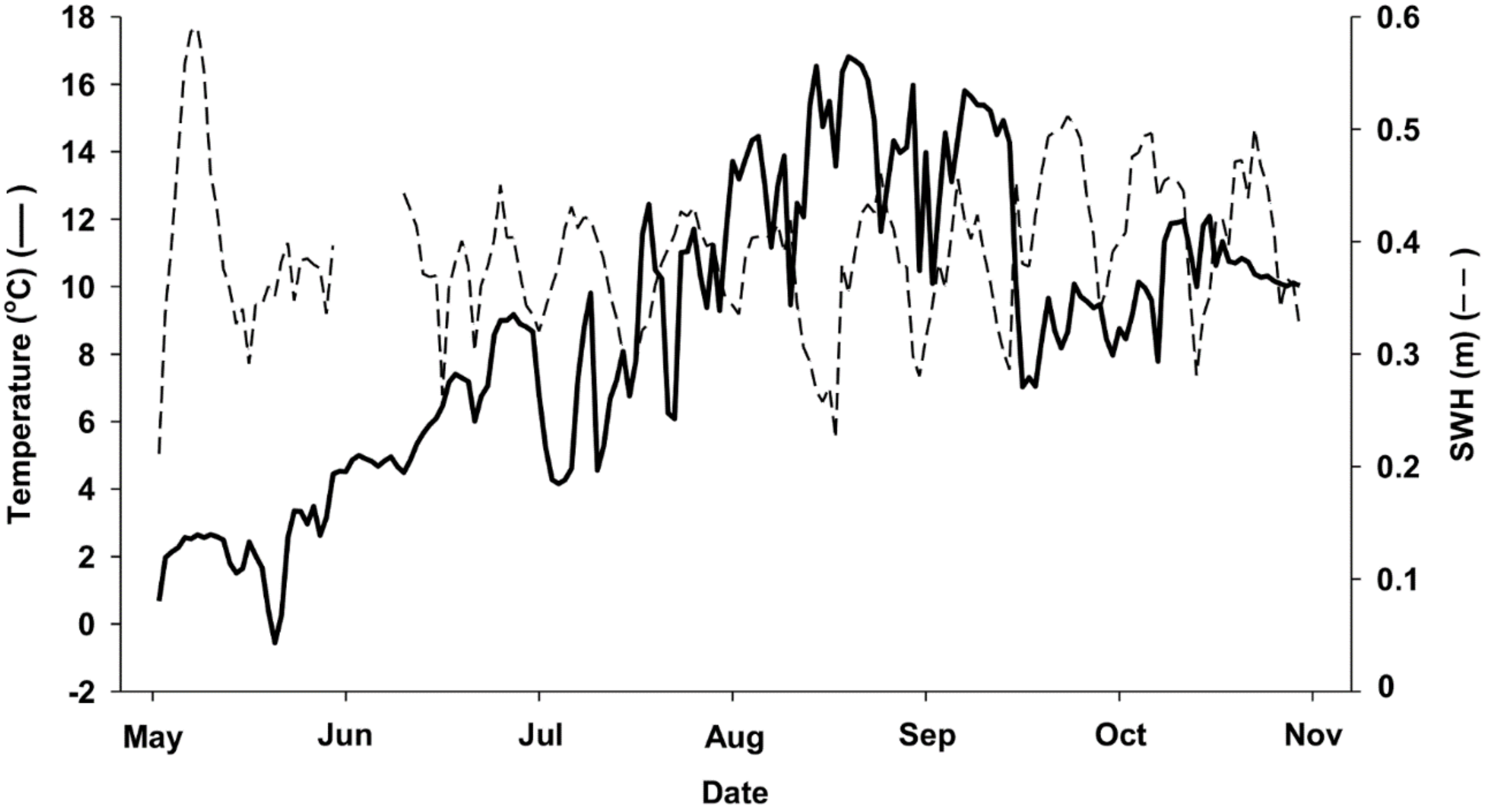

Fig. 3.7. Change in mean daily sea temperature and significant wave height (SWH) at Bread and Cheese Cove from 30 April to 25 October, 2012. Sea temperature and wave height data were acquired every 30 and 1 minute(s), respectively, with one temperature logger and one water level logger secured to the seabed at a depth of 5 m.

(0.37±0.01 m) from early June to mid-August and gradually increased afterwards, with frequent peaks of up to 0.59 m (Fig. 3.7). That SWH did not exceed ~0.6 m speaks to the relatively mild wave environment at BCC throughout the survey.

Overall, the proportion of urchins in crevices (80%) on the inner bedrock platform at BCC from 30 April to 25 October, 2012, was four times higher than that of urchins on flat surfaces (20%) (two-tailed t-test [two-sample assuming equal variance], $t_{0.05(2),42}=25.25$, $p<0.001$). Multiple linear regression analysis showed that sea temperature had no perceptible effect on the proportion of urchins in crevice, flat, and protrusion microhabitats (Table 3.7). The proportion of urchins on protrusions was, however, positively correlated with significant wave height (SWH) (Table 3.7). It increased by a factor of 9.7 for every 0.1 m increase in SWH (Table 3.7), peaking to 77% on 2 October, 2012, when SWH was 0.49 m, near the maximum wave height (0.59 m) during the survey (Fig. 3.7). There was no significant relationship between SWH and the proportion of urchins in crevices or on flat surfaces (Table 3.7).

Urchins on the outer bedrock platform at BCC exhibited a clumped distribution ($R<1$) in crevices and on flat surfaces on every sampling event from 8 May to 25 October, 2012. In general, urchins in crevices were more tightly aggregated ($R=0.35\pm0.02$) than urchins on flat surfaces ($R=0.42\pm0.01$) (two-tailed t-test [two sample assuming equal variance], $t_{0.05(2),42}=-3.76$, $p=0.001$). Multiple linear regression analysis showed that the degree of aggregation of urchins was unrelated to SWH in both microhabitats and negatively correlated with sea temperature in crevices only (Table 3.8). Urchin density in both microhabitats did not vary with temperature or SWH throughout the survey

Table 3.7. Results of multiple linear regression analyses (applied to raw data) examining relationships between the proportion of green sea urchins (*Strongylocentrotus droebachiensis*) in crevice, flat, and protrusion microhabitats, and sea temperature (Temp, in °C) and significant wave height (SWH, in m) at Bread and Cheese Cove from 30 April to 25 October, 2012.

					Full model		
Microhabitat	**Parameter**	**Coefficient (±SE)**	***t*-value**	***p***	**r^2**	**$F_{(df)}$**	***p***
Crevice	Intercept	59.71 (12.33)	4.86	<0.001	0.133	$1.46_{2,19}$	0.257
	Temp	-0.03 (0.36)	-0.08	0.934			
	SWH	52.61 (30.80)	1.71	0.104			
Flat	Intercept	40.28 (12.31)	3.28	0.004	0.133	$1.46_{2,19}$	0.257
	Temp	0.03 (0.36)	0.08	0.934			
	SWH	-52.61 (30.80)	-1.71	0.104			
Protrusion	Intercept	19.00 (12.24)	1.56	0.134	0.329	$9.78_{1,20}$	0.005
	SWH	97.35 (31.12)	3.13	0.005			

Table 3.8. Results of multiple linear regression analyses (applied to raw data) examining relationships between the nearest neighbour R-ratio (R) and density (individuals m^{-2}) of green sea urchins (*Strongylocentrotus droebachiensis*) in flat and crevice microhabitats, and sea temperature (Temp, in °C) and significant wave height (SWH, in m) at Bread and Cheese Cove from 8 May to 25 October, 2012.

						Full model		
Microhabitat	**Variable**	**Parameter**	**Coefficient (±SE)**	***t*-value**	***p***	**r^2**	**F$_{(df)}$**	***p***
Crevice	R-ratio	Intercept	0.412 (0.032)	12.96	<0.001	0.213	5.42$_{(1,20)}$	0.030
		Temp	-0.008 (0.003)	-2.33	0.030			
	Density	Intercept	92.4 (20.2)	4.57	<0.001	0.110	1.17$_{(2,19)}$	0.331
		Temp	0.9 (0.7)	1.29	0.212			
		SWH	-25.3 (44.7)	-0.57	0.578			
Flat	R-ratio	Intercept	0.451 (0.071)	6.37	<0.001	0.098	1.03$_{(2,19)}$	0.377
		Temp	0.002 (0.003)	0.96	0.350			
		SWH	-0.136 (0.157)	-0.87	0.396			
	Density	Intercept	115.2 (23.1)	4.98	<0.001	0.143	1.59$_{(2,19)}$	0.231
		Temp	-0.7 (0.8)	-0.81	0.428			
		SWH	-87.4 (51.1)	-1.71	0.103			

(Table 3.8). Density was relatively low and stable in both microhabitats throughout the survey, with ~21% more urchins in crevices (90.5±3.0 individuals m^{-2}) than on flat surfaces (74.5±3.5 individuals m^{-2}) (two-tailed t-test [two sample assuming equal variance], $t_{0.05(2),42}$=3.49, *p*=0.001).

3.4 DISCUSSION

Our two experiments in a wave tank mimicking barrens conditions provide evidence that wave action governs the spatial dynamics of *Strongylocentrotus droebachiensis* in food-depleted habitats. We show that as wave velocity increases, *S. droebachiensis* (1) proportionately reduces displacement; (2) progressively abandons flat, horizontal surfaces and avoids vertical ones in favour of microhabitats that facilitate anchorage; and (3) increasingly forms two-dimensional aggregations, whose physiognomy varies with velocity and urchin density.

Displacement and microhabitat use

Experiment 1, carried out in winter when water temperature was ~4.5°C, established that urchin displacement dropped by ~13% with every increase of 0.1 m s^{-1} from null (0.0 m s^{-1}) to high (0.3 m s^{-1}) wave velocity. Studies of *S. droebachiensis* from the northern Gulf of St. Lawrence and southeastern Newfoundland carried out with wave tanks similar or identical to that in the present study, used the number of urchins on the walls of the tanks as an index of the tendency of urchins to move (Chapter II, Gagnon et al. 2006). These studies, conducted in summer in relatively warm (7 and 14°C) water, reported, like the present study, a general decrease in the tendency of urchins to move, with proportionately fewer urchins on the walls as wave velocity increased. Kawamata (1998) documented a similar effect in the urchin *Mesocentrotus nudus* (formerly *Strongylocentrotus nudus*): displacement in oscillatory flows decreased with increasing flow velocity, and ceased at ~0.7 m s^{-1}. The decrease in displacement of *S. droebachiensis* in the present study was gradual, with no clear threshold, or stopping velocity, over the range of wave velocities (0 to 0.3 m s^{-1}) tested. One main conclusion, therefore, is that *S. droebachiensis* is sensitive to shifts in hydrodynamic conditions, immediately adjusting displacement at velocities well below those likely to dislodge them (Siddon and Witman 2003, Dumont et al. 2006, Lauzon-Guay and Scheibling 2007b, Morse and Hunt 2013). Although much reduced, displacement still occurred at the highest velocity, indicating that urchins remain physically operational even during the cold winter months in eastern Canada.

Experiment 1 also provided vital and novel information about how *S. droebachiensis* uses topographical complexity in relation to wave velocity. There was no clear pattern in urchin-microhabitat associations among protrusions, depressions, ledges, and crevices in the absence of waves, with ~20-25% of individuals in each microhabitat. However, increasing wave velocity from 0.1 to 0.3 m s^{-1} elicited a strong directional response: urchins increasingly left or avoided flat horizontal and vertical surfaces, instead converging on crevices. This pattern is consistent with abundant, yet casually reported, clusters of green sea urchins along bedrock cracks and crevices in barrens in winter, and during periods of high wave action throughout the rest of the year, in the northwestern Atlantic (Garnick 1978, Vadas et al. 1986, Scheibling et al. 1999, P. Gagnon, unpublished data). Of the six microhabitats tested, crevices exhibited some of the weakest water flows within each wave velocity treatment. They also provided a combination of suitably-sized, sharp-angled, hard surfaces and empty spaces, in which to insert protruding body parts without losing balance. This particular arrangement most likely facilitates anchoring and bracing of a greater number of podia and spines, the primary attachment organs in urchins (Santos and Flammang 2007), ultimately enhancing purchase and reducing the likelihood of dislodgement by waves. The proportion of urchins on protrusions, depressions, and ledges remained relatively high despite increasing wave velocity. Protrusions contained sharp-angled surfaces like crevices, whereas flows were weakest in depressions and ledges. Yet, none of these microhabitats had sufficiently narrow spaces to insert podia and brace spines. These three moderately complex bottom configurations may provide resident urchins with sufficient purchase or protection against waves, limiting emigration.

Several other studies qualitatively support the notion that sea state affects microhabitat use in sea urchins. The fidelity of the crowned sea urchin, *Centrostephanus coronatus*, to its burrow, is generally higher in turbulent than calm hydrodynamic environments (Lissner 1980). Red (*Strongylocentrotus franciscanus*), purple (*Strongylocentrotus purpuratus*), and rock (*Paracentrotus lividus*) sea urchins are generally more abundant in bedrock crevices and holes than on flat surfaces (Harrold and Reed 1985, Hernandez and Russell 2009, Jacinto et al. 2013, Nichols et al. 2015). Although informative, the observational and largely dichotomous nature of such patterns does not provide the resolution necessary to establish causal relationships between microhabitat use and the wave environment. The present study goes one step further by specifically quantifying changes in the response of *S. droebachiensis* to measured changes in wave velocities. St-Pierre and Gagnon (2015) used a similar approach combining laboratory microcosm experiments with field surveys and demonstrated a similar inclination to associate with uneven topographies with increasing wave velocity in the common sea star, *Asterias rubens*.

Distribution and aggregation

Experiment 2, carried out in summer when water temperature averaged ~12°C, determined that the degree of aggregation of urchins (proximity of neighbouring individuals) with a clumped distribution ($R<1$) increases with wave velocity, albeit only at or above a density of 110 individuals m^{-2}. The lack of a relationship with wave velocity at the lowest density (51 individuals m^{-2}) tested, establishes a threshold density, between 51 and 110 individuals m^{-2}, above which *S. droebachiensis* actively seeks tighter contact with conspecifics as wave velocity increases. The existence of threshold urchin densities in feeding aggregations (fronts) triggering kelp bed destruction is well documented for *S. droebachiensis* and other urchin species (reviewed by Filbee-Dexter and Scheibling 2014, Ling et al. 2015). But the present study is, to our knowledge, the first to formally establish a threshold density eliciting the formation of tighter urchin aggregations in barrens-like habitats, and its relationship with the wave environment. These findings solidify and expand the notion that population density is an important determinant of green sea urchin aggregation in grazing fronts and barrens (Breen and Mann 1976, Bernstein et al. 1983, Hagen and Mann 1994, Scheibling et al. 1999, Gagnon et al. 2004, Lauzon-Guay and Scheibling 2007a).

Another important contribution of Experiment 2 is it provides novel information about modes of formation and frequency of occurrence of urchin aggregations in the absence of food. The majority (73%) of urchin aggregations that formed were "bounded", i.e. originating from individuals at the base of the tank walls and expanding towards the centre of the tank. The rest of the aggregations were "unbounded", i.e. originating from, and growing around, individuals on the tank bottom away from the walls. All aggregations were two-dimensional, with only one layer of urchins. Yet, wave velocity and urchin density interactively influenced the proportion of bounded aggregations, with (1) a marked decrease between 0.2 and 0.3 m s^{-1} at low density; (2) no effect of velocity at intermediate and high densities; and (3) a proportional decrease with increasing density in the absence of waves. These findings, together with those from Experiment 1, indicate that topographies enabling stable attachment of urchins facilitate the formation of urchin aggregations in barrens. Accordingly, we propose that an individual establishing contact with crevices, or other sharp-angled topographies such as the base of rocks, immobilizes if wave velocity is too high. Other individuals gradually contact and interlock spines with urchins at the periphery of the forming aggregation, which grows at a speed that depends on wave velocity and urchin density: slower at high velocities and low densities, faster at low velocities and high densities. Aggregations become tighter (more compact) as velocity increases because urchins further reduce distances among each other to increase purchase. This pattern of aggregation is also well supported by the findings in Experiment 2 that the number of urchins per bounded aggregation increased with velocity at all densities, whereas the number of urchins per unbounded aggregation was consistently low, regardless of velocity or density. Displacement of *S. droebachiensis* in barrens is largely random (Dumont et al. 2006, Lauzon-Guay et al. 2006, Dumont et al. 2007, Lauzon-Guay and Scheibling 2007b). The likelihood of establishing contact with conspecifics is, therefore, positively related to urchin density, further explaining the accelerating increase in size and speed of formation of aggregations with increasing density.

Field surveys

Patterns established by the two laboratory experiments generally occurred throughout the 6-month surveys in the barrens at Bread and Cheese Cove (BCC). Urchins exhibited the same strong preference for crevices, with 80% of the individuals occurring in this microhabitat on the inner bedrock platform. Urchins in crevices on the outer bedrock platform were also more abundant and more tightly aggregated than urchins on flat surfaces, a pattern most likely caused by the natural clumping effect of crevices on urchin displacement. BCC is a small, semi-protected cove, in a coastal area characterized by relatively mild wave regimes (Blain and Gagnon 2013, Chapter II, the present study). SWH was consistently low (<0.6 m) throughout the survey, which may explain why the urchin-crevice associations and patterns of aggregation were unrelated to variation in SWH, whereas the proportion of urchins on protrusions was positively correlated with SWH. Hydrodynamic forces may have been too low to influence frequency of association with crevices, distribution, and aggregation, and not high enough to discourage urchins from seeking topographically higher points.

Wave action and sea temperature markedly affect feeding and the physiognomy and destructive potential of feeding aggregations (fronts) of *S. droebachiensis* (Chapter II, Scheibling et al. 1999, Lauzon-Guay and Scheibling 2007a, b). Interestingly, urchin aggregations in crevices became increasingly tighter as sea water gradually warmed up between May (beginning of survey) and October (end), regardless of SWH. This pattern could reflect a natural inclination to aggregate in anticipation of a feeding opportunity as sea temperature approaches annual peaks that typically coincide with mass fragmentation and export of kelp tissues to barrens (Chapter II, Scheibling and Gagnon 2009, Krumhansl and Scheibling 2011, 2012).Urchin density in crevices and on flat surfaces was consistently low and stable throughout the survey. It exceeded, on only one out of 22 sampling events, the threshold range of 51 to 110 individuals m^{-2} above which urchins in Experiment 2 formed increasingly tighter aggregations with increasing wave velocity. Urchin density was therefore likely too low and hydrodynamic forces too weak, for the latter to affect the degree of aggregation of urchins in the barrens.

Conclusions and future research directions

The present study provides the first quantitative demonstration and breakdown of the effects of wave velocity and population density on displacement, microhabitat use, distribution, and aggregation of *S. droebachiensis* in food-depleted habitats. It establishes that shifts in velocity and population density in the order of 0.1 m s^{-1}, and a few tens of individuals m^{-2}, can elicit important changes in the way urchins disperse, cluster, and use seabed topography. A few observational studies in natural habitats provided partial understanding of the effects of waves on patterns of formation of grazing fronts at the lower edge of kelp beds (Chapter II, Cowen et al. 1982, Sivertsen 1997, Scheibling et al. 1999, Gagnon et al. 2004, Lauzon-Guay and Scheibling 2007a, b). Considerably less effort has been devoted to examining the causes and consequences of spatial dynamics of urchins in barrens (but see Dumont et al. 2006, Lauzon-Guay et al. 2006, Dumont et al. 2007). Current evidence suggests that shoreward migration of green sea urchins across barrens is the primary mechanism of repopulation of grazing fronts following disturbance (Scheibling et al. 1999, Brady and Scheibling 2005). Additional quantitative studies are required to assess the importance of urchin spatial dynamics in barrens to the stability of urchin grazing fronts, while generally increasing knowledge about factors that regulate mixing and exchange of urchins within and between barrens and kelp bed communities. Results from the present study highlight the critical importance of incorporating the hydrodynamic environment in such studies.

Different approaches were used to quantify the wave environment: horizontal wave velocity in the oscillatory wave tank and amplitude of the vertical displacement of the sea surface in the barrens. As a result, it was not possible to compare directly the effects of waves on the spatial dynamics of urchins between experimental and natural environments. Nevertheless, similarities among laboratory and field patterns, including the strong inclination of urchins to frequent crevices, underscore the value of conducting laboratory microcosm experiments to unequivocally establish causal links between environmental variability and spatial dynamics. Only such studies in laboratory setups can provide the reproducibility and resolution necessary to gather crucial information about threshold flow speeds that can potentially trigger ecological cascades in marine systems. The present study identifies threshold wave velocities and population densities that trigger shifts in urchin displacement, microhabitat use, distribution, and aggregation. In doing so, it provides novel and critical information that can be used to feed predictive models of marine benthic community dynamics (e.g. Lauzon-Guay and Scheibling 2010, Marzloff et al. 2011, Sala and Dayton 2011). This kind of information is urgently needed in an era where accelerating changes in sea state and temperature caused by climate change represent a real challenge to accurately predicting and managing associated shifts in coastal resources, including green sea urchin populations (Scheffer et al. 2001, Andrew et al. 2002, deYoung et al. 2008, Halpern et al. 2008, Burrows et al. 2011).

CHAPTER IV

Summary

4.1 Overall objective of the study

Interactions between the green sea urchin, *Strongylocentrotus droebachiensis*, and foundational kelps markedly affect the structure and function of shallow reef communities in the northwestern Atlantic (NWA). Grazing by dense fronts of *S. droebachiensis* typically removes kelp biomass over large tracts of seabed, limiting ecological and socio-economic services. A number of largely observational studies focusing on displacement, distribution, and aggregation of urchins near and at the kelp-barrens interface have provided a reasonably good understanding of the cycles of alternation between kelp bed and urchin barrens community states in the NWA. However, far fewer studies have integrated experimental work to examine the strict effects of hydrodynamic and thermal regimes on feeding and foraging of *S. droebachiensis* at the kelp-barrens interface and in the barrens. This knowledge gap limits the ability to formulate accurate predictions about the frequency and magnitude of changes in marine communities in the NWA resulting from accelerating shifts in sea state and temperature.

The overall objective of this research was to test the effects of abiotic (wave action, water temperature) and biotic (body size, population density) factors on (1) individual and aggregative feeding on the winged kelp, *Alaria esculenta* [Chapter II]; and (2) displacement, microhabitat use, distribution, and aggregation in food-depleted habitats [Chapter III] to increase understanding of the causes of feeding and foraging variability in *S. droebachiensis*. Work involved laboratory experiments in water baths and an oscillatory wave tank at the Ocean Sciences Centre of Memorial University of Newfoundland with *S. droebachiensis* collected from Bread and Cheese Cove (BCC) in

Bay Bulls (southeastern Newfoundland, SEN), as well as surveys of urchin populations and kelp-bed boundary dynamics at BCC and an adjacent site, Cape Boone Cove (CBC).

4.2 Urchin feeding and kelp-bed boundary dynamics

Chapter II tested the hypothesis that water temperature can predict short-term (over a few months) kelp bed destruction by *S. droebachiensis* in calm hydrodynamic environments. Specifically, it used two laboratory experiments to investigate effects of water temperature (3, 6, 9, 12, 15, and 18°C) and urchin body size (small [25-35 mm test diameter, t.d.] and large [40-60 mm t.d.]) on individual feeding (Experiment 1), as well as of wave velocity (0.0 m s^{-1} [Null], 0.1 m s^{-1} [Low], 0.2 m s^{-1} [intermediate], 0.3 m s^{-1}[high]) on aggregative feeding at two times of year differing in sea temperature (spring [5°C] and summer [14°C]) (Experiment 2). It also quantified variation in kelp-bed boundary dynamics, sea temperature, and wave height over three months at CBC to study relationships between environmental variability and urchin density at the kelp-barrens interface. Results from the latter survey were used to generate data against which to test the validity of thermal tipping ranges and regression equations derived from laboratory results.

Experiment 1 showed that individual feeding obeyed a non-linear, size- and temperature-dependent relationship. Kelp consumption generally increased with temperature across the 3-12°C range, and dropped markedly within and above the 12-15°C range. This relationship was more apparent in large than small urchins, with large individuals consuming at least 2.5 times more kelp than small individuals at any given temperature. Experiment 2 showed that aggregative feeding was (1) >2.5 times higher in the absence of waves than at intermediate and high wave velocities; and (2) >1.5 times higher in summer when temperature was within the 12-15°C tipping range of Experiment 1, than spring when temperature was lower, ~5°C. The number of urchins feeding or on the tank walls also decreased significantly with increasing wave velocity. Daily rates of kelp loss over ~3 months at CBC were highly (88%) correlated with those calculated from sea temperature at the site and regression equations derived from results of Experiment 1. Measurements of wave height, sea temperature, and urchin density in the barrens at various distances from the kelp-barrens interface at CBC indicated that density did not vary with significant wave height (SWH) in the barrens. However, urchin density at the front and in the kelp bed was positively and negatively related to temperature, respectively. Effects of wave action did not override those of temperature, speaking to the generally mild (SWH <0.50 m) wave environment at CBC.

4.3 Spatial dynamics of urchins in food-depleted habitats

Chapter III tested the effects of varying hydrodynamic conditions on the spatial dynamics of *S. droebachiensis* in food-depleted habitats. It used two laboratory experiments designed to mimic barrens conditions, including the back-and-forth flow of waves, to identify wave velocities (0.0 m s^{-1} [Null], 0.1 m s^{-1} [Low], 0.2 m s^{-1} [intermediate], 0.3 m s^{-1} [high]) and urchin densities (51 individuals m^{-2} [low], 110 individuals m^{-2} [intermediate], and 173 individuals m^{-2} [high]) triggering shifts in displacement and microhabitat use (Experiment 1) and distribution and aggregation

(Experiment 2). It also examined variation in wave height and sea temperature, and associated changes in microhabitat use and distribution, over six months in the barrens at BCC to test the generality of the laboratory results.

Experiment 1 showed that urchin displacement dropped steadily by ~40% as wave velocity increased. There was no clear pattern in urchin-microhabitat associations among protrusions, depressions, ledges, and crevices in the absence of waves, with ~20-25% of individuals in each microhabitat. As velocity increased from null to high, urchins increasingly left or avoided flat horizontal and vertical surfaces and converged on crevices. The proportion of urchins in crevices more than doubled across the aforementioned velocity range. Experiment 2 showed that the degree of aggregation of urchins (proximity to neighbouring individuals) with a clumped distribution ($R<1$) increased with wave velocity, but only at or above intermediate density (110 individuals m^{-2}). The majority (73%) of urchin aggregations that formed were “bounded”, i.e. originating from individuals at the base of the tank walls and expanding towards the centre of the tank. The rest of the aggregations were “unbounded”, i.e. originating from, and growing around, individuals on the tank bottom away from the walls. All aggregations were two-dimensional, with only one layer of urchins. Yet, wave velocity and urchin density interactively influenced the proportion of bounded aggregations, with (1) a marked decrease between 0.2 and 0.3 m s^{-1} at low density; (2) no effect of velocity at intermediate and high densities; and (3) a proportional decrease with increasing density in the absence of waves.

Patterns in the two laboratory experiments were generally similar to those in the barrens at BCC. The proportion of urchins in crevices (80%) on the inner bedrock platform was four times higher than that of urchins on flat surfaces (20%) throughout the survey, but proportions in the latter two microhabitats did not vary with SWH. However, the proportion of urchins on protrusions was positively related to SWH. Urchins in crevices on the outer bedrock platform were also more abundant and more tightly aggregated than urchins on flat surfaces, but the distribution of urchins did not vary with SWH. Urchin aggregations in crevices became increasingly tighter as sea temperature gradually increased, regardless of SWH. Urchin density rarely exceeded the threshold density (110 individuals m^{-2}) at or above which urchins in Experiment 2 formed increasingly tighter aggregations with increasing wave velocity. SWH also remained consistently low (<0.6 m) throughout the survey. Hydrodynamic forces may therefore have been too low to discourage urchins from associating with topographically high points like protrusions or affect the frequency of association with crevices on the inner platform. The combination of low SWH and insufficient urchin density is also likely responsible for the absence of a relationship between the wave environment and variation in distribution and aggregation on the outer platform.

4.4 Importance of the study

The present study is the first comprehensive analysis of the effects of wave action, water temperature, body size, and population density on feeding and spatial dynamics in *S. droebachiensis*. Chapter II provides compelling evidence that water temperature and urchin body size are important determinants of kelp bed destruction by urchin fronts, particularly in calm hydrodynamic environments. Results speak to the importance of considering both hydrodynamic and thermal regimes in studies of individual and aggregative feeding and kelp-bed boundary dynamics. Chapter III provides the first quantitative demonstration of the effects of wave velocity and population density on the spatial dynamics of urchins in food-depleted habitats. It establishes that changes in velocity and population density, in the order of 0.1 m s^{-1} and a few tens of individuals m^{-2}, can affect patterns of urchin displacement, microhabitat use, distribution, and aggregation. The latter finding is particularly meaningful as it provides a foundational understanding of the drivers of spatial dynamics of *S. droebachiensis* in barrens and potential consequences for the formation of grazing fronts. The present study also identifies thresholds and gradients of wave velocity and water temperature triggering shifts in urchin feeding and spatial dynamics, providing vital information for improvement of mathematical models aimed at predicting the timing and magnitude of community phase shifts in the NWA.

4.5 Future directions

The present thesis provides a framework for further research on the effects of environmental variability on the feeding ecology and spatial dynamics of *S. droebachiensis* in Newfoundland. Longer-term experimental and mensurative studies of urchin-kelp interactions at multiple sites spanning broader geographical, thermal, and hydrodynamic ranges are required to test the generality of the findings. Further studies should also attempt to resolve effects of other biotic (e.g. reproductive stage, kelp bed detrital production) and abiotic (e.g. light, salinity, pH, nutrient concentration) factors on feeding, displacement, microhabitat selection, distribution, and aggregation in *S. droebachiensis*. The present study suggests that urchins in barrens, and to a lesser extent those in kelp beds, join grazing fronts, contributing to their stability. Additional quantitative studies are required to test the latter hypothesis, while investigating factors that regulate mixing and exchange of urchins within and between barrens and kelp bed communities. The green sea urchin fishery targets grazing fronts because they contain the largest urchins with the largest gonads. Establishment and management of a sustainable green sea urchin fishery in Newfoundland depend on a sound understanding of the ability of the species to cope with environmental variability. The present study is one important step in this direction. For example, the finding that temperature regimes can drive kelp bed destruction by urchins in calm hydrodynamic environments suggests that harvesting sites could be selected based on local temperature and wave regimes to maximize gonad yield. How the species and fishery would adapt to accelerating, climate-driven shifts in sea state and temperature is yet another area that would deserve ongoing research by multidisciplinary teams.

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Appendix A

Specifications of the wave tank system used in Chapter II and Chapter III and general patterns of water flow

The oscillatory wave tank system used in Experiment 2 of Chapter II (see Section 2.2.4) and in Experiment 1 and Experiment 2 of Chapter III (see Sections 3.2.3 and 3.2.4) consisted of a 1500 W electric motor with adjustable rotation speed (2000 rpm maximum; TB Woods Incorporated, X4C1S010C) connected with a perforated metal bar to the top of a ply-wood panel hinged to the bottom of a fiberglass-coated wooden tank (488[L]×90[W]×62[H] cm) (Fig. A1). Null (0.0 m s^{-1}), low (0.1 m s^{-1}), intermediate (0.2 m s^{-1}), and high (0.3 m s^{-1}) wave velocity treatments were achieved by adjusting the height of the water column in the tank to 36, 36, 40, and 45 cm, respectively. The current meter data on water flow measured at 5 cm above the centre of the experimental area indicated that urchins were exposed to oscillatory flow, with the greatest velocities along the longitudinal axis (*x*-direction, Table A1, Fig. A2).

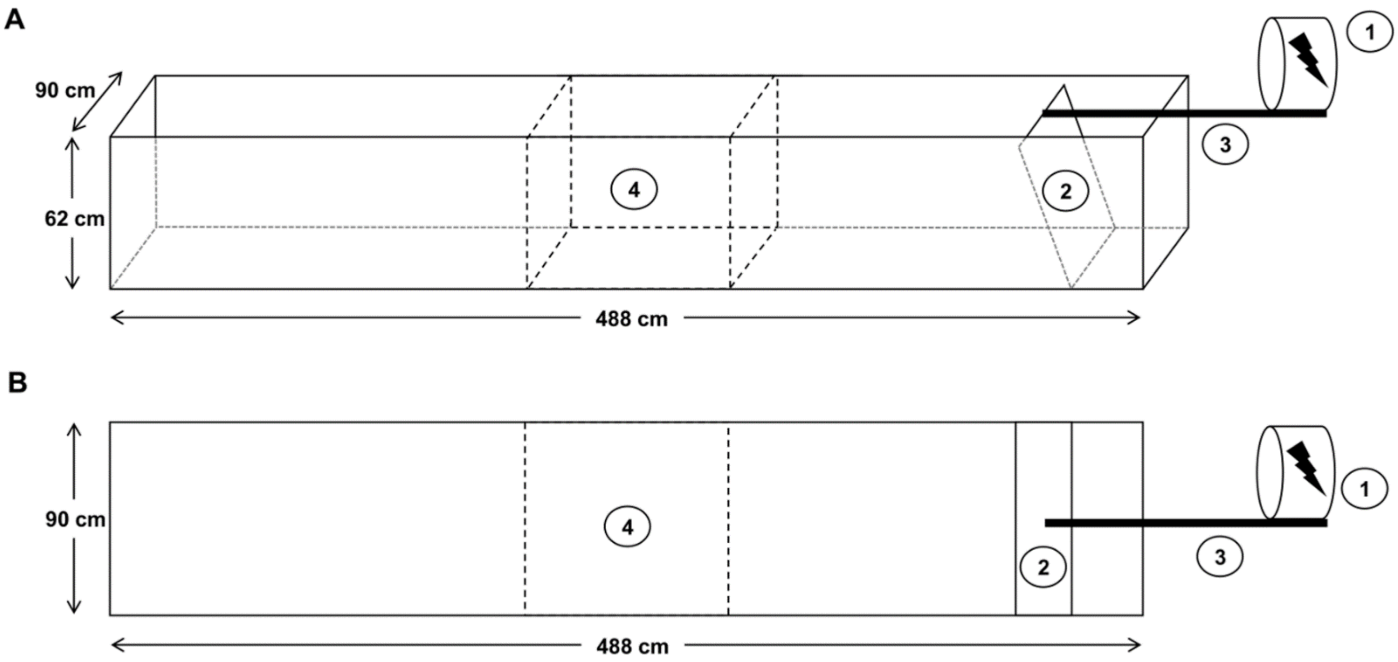

Fig. A1. Side (A) and top (B) views of the oscillatory wave tank system. The rotational force of the motor (1) was converted into a bi-directional force that moved the top of a plywood panel (2) hinged to the bottom of the tank to produce waves**.** A 1-cm gap between the panel and the sides and bottom of the tank allowed the water to circulate from one side of the panel to the other. The amplitude of the waves could be varied with the depth of water in the tank, the speed of rotation of the motor, and the position on the perforated metal bar (3) to which the bar connecting the panel was attached. The experimental area (4) was located in the centre of the tank.

Table A1. Peak current velocities in the null (0.0 m s^{-1}), low (0.1 m s^{-1}), intermediate (0.2 m s^{-1}), and high (0.3 m s^{-1}) velocity treatments. Velocities are the mean absolute values (±SE) for the top third of waves measured over two minutes.

Velocity treatment	Velocity (m s^{-1})		
	Longitudinal	Lateral	Vertical
Null	0.0151 (0.0003)	0.0116 (0.0002)	0.0103 (0.0001)
Low	0.0996 (0.0006)	0.0635 (0.0005)	0.0082 (0.0001)
Intermediate	0.2239 (0.0010)	0.1406 (0.0009)	0.0170 (0.0002)
High	0.3074 (0.0018)	0.1898 (0.0012)	0.0234 (0.0003)

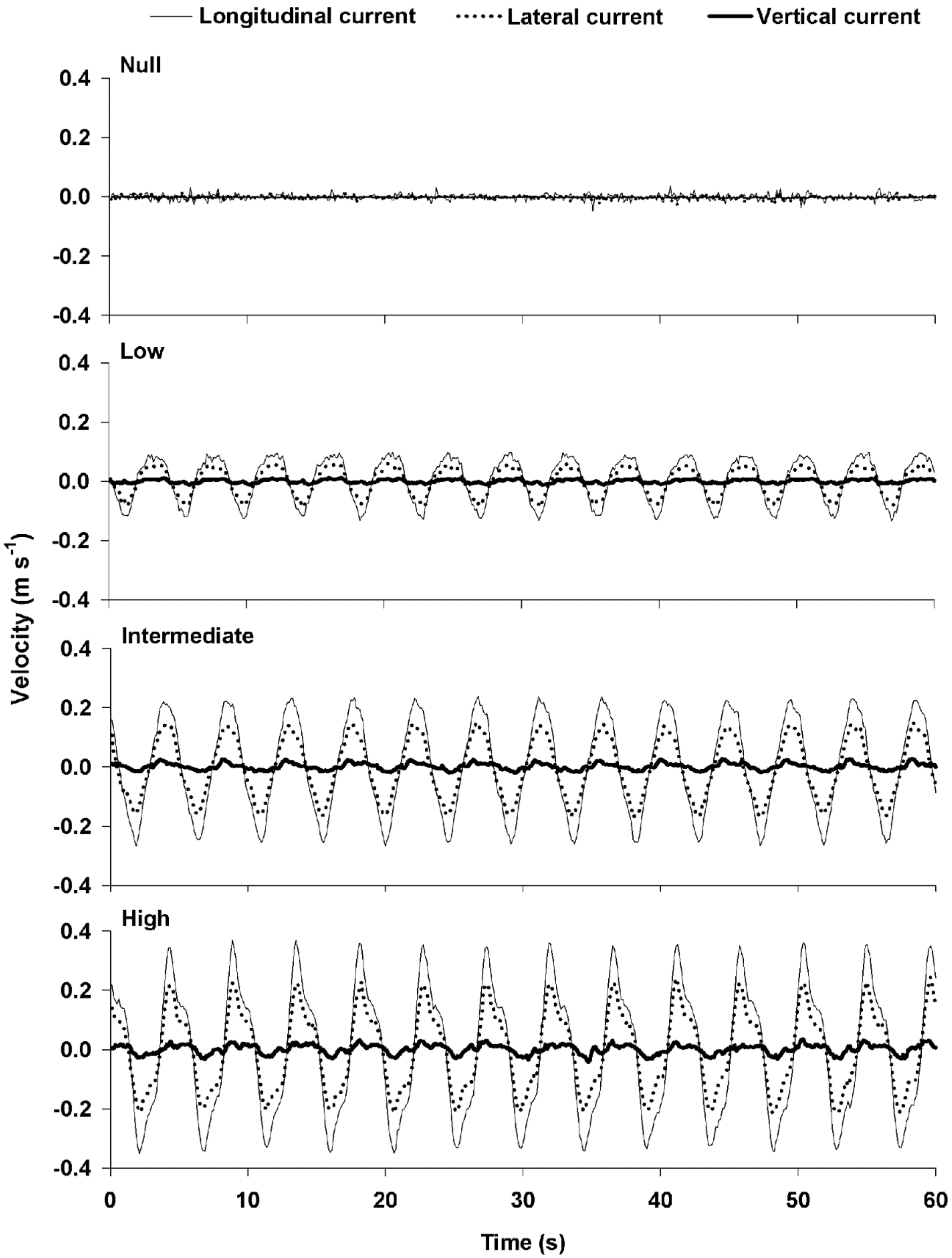
Longitudinal current
Lateral current
Vertical current
Null
Low
Intermediate
High
0.4
0.2
0.0
-0.2
-0.4
Velocity (m s-1)
0
10
20
30
40
50
60
Time (s)

Fig. A2. Cyclic changes over one minute in longitudinal (x-direction, solid line), lateral (y-direction, dashed line), and vertical (z-direction, bold line) current velocities during the null (0.0 m s^{-1}), low (0.1 m s^{-1}), intermediate (0.2 m s^{-1}), and high (0.3 m s^{-1}) wave velocity treatments. Readings (8 readings per second) were made 5 cm above the bottom in the centre of the experimental area with a Doppler current meter (Vector Current Meter; Nortek).

Appendix B

Statistical fit between significant wave height data from Cape Boone Cove and offshore surface buoys in Chapter II

Table B1. Details of buoys and correlation tests (Pearson's product-moment correlation) used to examine the fit between mean daily SWH recorded by the water pressure logger at Cape Boone Cove (CBC) and mean daily SWH recorded by surface buoys located offshore (see Section 2.2.5 for a description of SWH calculations).

Buoy or site	**Location**	**Distance to CBC (km)**	**Data availability**	**Mean (±SE) SWH (m)**	**Sample size (n)**	**Pearson's *r***	***p***
SmartAtlantic Placentia Bay[1]	46°58'48.6" N 54°41'9.5" W	150	3 Jul - 25 Sep 2012	1.568±0.078	85	0.474	<0.001
C44139 Banqureau Bank[2]	44°16'12.0" N 57°4'48.0" W	470	3 Jul - 25 Sep 2012	1.294±0.063	85	0.502	<0.001
C44251 Nickerson Bank[2]	46°26'24.0" N 53°23'24.0" W	100	3 Jul - 14 Jul 2012	1.588±0.143	12	0.596	0.041
CBC	47°18'30.4" N 52°47'11.1" W	-	3 Jul - 25 Sep 2012	0.316±0.008	85	-	-

[1] data source: http://www.smartatlantic.ca/PlacentiaBay/buoy.php

[2] data source: http://www.meds-sdmm.dfo-mpo.gc.ca/isdm-gdsi/waves-vagues/search-recherche/index-eng.asp

Appendix C

Model parameters from statistical analyses in Chapter II

Table C1. Details of the model parameters from the various statistical analyses presented in Chapter II. Refer to core tables listed in the first column for general results of the statistical analyses.

Table 2.1	**Range**	**Parameter**	**Coefficient**	**SE**	***t*-ratio**	***p***
	[3-12]°C	Intercept	-814.9	206.7	-3.94	<0.001
		Temp	36.8	14.8	2.49	0.016
		Size	31.6	4.2	7.47	<0.001
	]12-18]°C	Intercept	-2363.9	656.3	-3.60	0.001
		Temp	140.9	43.3	3.25	0.002
		Size	122.0	15.5	7.87	<0.001
		Temp*Size	-7.0	1.0	-6.80	<0.001
Table 2.2		**Parameter**	**Coefficient**	**SE**	***t*-ratio**	***p***
		Intercept	288.3	28.2	10.21	<0.001
		Waves:				
		Null	199.5	48.9	4.08	<0.001
		Low	73.6	48.9	1.50	0.138
		Intermediate	-99.9	48.9	-2.04	0.046
		Season:				
		Spring	-73.6	28.2	-2.60	0.012
		Waves*Season:				
		Null*Spring	-15.5	48.9	-0.32	0.752
		Low*Spring	-18.9	48.9	-0.39	0.701
		Intermediate*Spring	43.0	48.9	0.88	0.384
Table 2.4	**Activity or location**	**Parameter**	**Coefficient**	**SE**	***t*-ratio**	***p***
	Feeding	Intercept	-0.65	0.05	-13.38	<0.001
		Waves:				
		Null	0.5	0.08	6.34	<0.001
		Low	0.2	0.08	2.13	0.038
		Intermediate	-0.2	0.08	-2.20	0.033
		Season:				
		Spring	-0.1	0.05	-1.56	0.126
		Waves*Season:				

Table C1. (continued)

Table 2.4	**Activity or location**	**Parameter**	**Coefficient**	**SE**	***t*-ratio**	***p***
		Null*Spring	0.01	0.08	0.12	0.906
		Low*Spring	0.2	0.08	1.81	0.077
		Intermediate*Spring	-0.1	0.08	-0.93	0.355
	Underneath the kelp canopy	Intercept	-0.6	0.03	-19.72	<0.001
		Waves:				
		Null	-0.1	0.05	-1.64	0.108
		Low	-0.04	0.05	-0.75	0.457
		Intermediate	0.1	0.05	0.98	0.334
		Season:				
		Spring	-0.1	0.03	-2.02	0.048
		Waves*Season:				
		Null*Spring	0.01	0.05	0.28	0.780
		Low*Spring	-0.1	0.05	-1.72	0.092
		Intermediate*Spring	0.1	0.05	2.10	0.041
	On the tiles outside of the area swept by kelp	Intercept	-0.3	0.04	-8.33	<0.001
		Waves:				
		Null	-0.7	0.07	-10.48	<0.001
		Low	-0.2	0.07	-2.40	0.020
		Intermediate	0.3	0.07	4.50	<0.001
		Season:				
		Spring	0.1	0.04	2.79	0.007
		Waves*Season:				
		Null*Spring	0.03	0.07	0.38	0.707
		Low*Spring	-0.02	0.07	-0.31	0.761
		Intermediate*Spring	-0.03	0.07	-0.38	0.707
	On the tank walls	Intercept	-0.7	0.04	-17.77	<0.001
		Waves:				
		Null	0.3	0.07	4.46	<0.001
		Low	0.3	0.07	5.10	<0.001
		Intermediate	-0.1	0.07	-2.16	0.035
		Season:				
		Spring	-0.04	0.04	-0.96	0.343
		Waves*Season:				
		Null*Spring	0.07	0.07	1.08	0.285
		Low*Spring	-0.01	0.07	-0.08	0.936
		Intermediate*Spring	-0.08	0.07	-1.23	0.225

Table C1. (continued)

Table 2.5		**Parameter**	**Coefficient**	**SE**	***t*-ratio**	***p***
		Intercept	115.5	39.3	2.936	0.012
		SWH	-51.2	87.5	-0.585	0.569
		Temp	-4.1	2.0	-1.994	0.069
		Zone:				
		Barrens	-116.5	55.6	-2.095	0.058
		Front	-62.1	55.6	-1.116	0.286
		Kelp Bed	-41.0	55.6	-0.737	0.475
		SWH*Zone:				
		SWH*Barrens	253.1	123.7	2.046	0.063
		SWH*Front	46.9	123.7	0.379	0.711
		SWH*Kelp Bed	46.5	123.7	0.376	0.713
		Temp*Zone:				
		Temp*Barrens	6.3	2.9	2.171	0.051
		Temp*Front	10.6	2.9	3.678	0.003
		Temp*Kelp Bed	1.1	2.9	0.369	0.718

Table 2.6	**Zone**	**Parameter**	**Coefficient**	**SE**	***t*-ratio**	***p***
	Barrens	Intercept	78.6	25.9	3.03	0.039
		Temp	-0.1	2.5	-0.03	0.981
	Pre-front	Intercept	95.3	23.5	4.06	0.015
		Temp	-3.5	2.2	-1.57	0.192
	Front	Intercept	51.7	17.4	2.97	0.041
		Temp	6.6	1.7	3.99	0.016
	Bed	Intercept	72.7	6.7	10.9	<0.001
		Temp	-3.0	0.6	-4.66	0.010

Table 2.7	**Data**	**Parameter**	**Coefficient**	**SE**	***t*-ratio**	***p***
	25 Sep in	Intercept	-374.1	473.0	-0.79	0.473
		Slope (Expected)	9.9	7.9	1.25	0.279
	25 Sep out	Intercept	-361.2	96.3	-3.75	0.033
		Slope (Expected)	8.8	1.6	5.46	0.012

Appendix D

Conversion factors for plots surveyed in Bread and Cheese Cove in Chapter III

Table D1. Surface area of crevice and flat microhabitats and corresponding conversion factors for each of the 10 plots of 0.5 x 0.5 m surveyed at Bread and Cheese Cove between 30 April and 25 October, 2012. Each conversion factor is the ratio of the surface area of the largest microhabitat across plots (flat, plot 9, 0.22 m^2) to the surface area of the corresponding microhabitat in the plot.

Microhabitat	**Plot**	**Surface area (m^2)**	**Conversion factor**
Crevice	1	0.047	4.68
	2	0.085	2.59
	3	0.037	5.95
	4	0.045	4.89
	5	0.070	3.14
	6	0.087	2.53
	7	0.080	2.75
	8	0.065	3.38
	9	0.030	7.33
	10	0.062	3.55
Flat	1	0.203	1.08
	2	0.165	1.33
	3	0.213	1.03
	4	0.205	1.07
	5	0.180	1.22
	6	0.163	1.35
	7	0.170	1.29
	8	0.185	1.19
	9	0.220	1.00
	10	0.188	1.17