

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

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ABSTRACT: The paucity of robust empirical demonstrations of wave-induced shifts in the spatial dynamics of functionally important consumers limits the ability to formulate accurate predictions about the frequency and magnitude of changes in marine communities resulting from ongoing shifts in sea state. We used 2 experiments in an oscillatory wave tank and observations over 6 mo at 2 barrens sites in Newfoundland to examine effects of the wave environment and population density on the spatial dynamics of the green sea urchin *Strongylocentrotus droebachiensis* in food-depleted habitats. The 2 experiments mimicked barrens conditions to identify wave velocities and urchin densities triggering shifts in displacement, microhabitat use, distribution, and aggregation. Field observations tested the generality of results from the laboratory experiments by examining variation in wave height and associated changes in microhabitat use and distribution. Results demonstrated that as wave velocity increases, *S. droebachiensis*: (1) proportionately reduces displacement; (2) progressively abandons flat, horizontal surfaces and avoids vertical ones in favor of microhabitats that facilitate anchorage; and (3) increasingly forms 2-dimensional aggregations, whose physiognomy varies with velocity and urchin density. We established that shifts in wave velocity and population density in the order of 0.1 m s^{-1} and a few tens of individuals m^{-2} , respectively, can elicit important changes in the way urchins disperse, cluster, and use seabed topography. The strong inclination of *S. droebachiensis* to reduce displacement, favor microhabitats that facilitate anchorage, and increasingly form 2-dimensional aggregations as wave velocity increases in the absence of food, is most likely a behavioral adaptation to mitigate hydrodynamic forces while reinforcing attachment to minimize dislodgement risk.

KEY WORDS: Spatial dynamics · Urchin barrens · Wave action · Displacement · Aggregation · Habitat use · Population density · Microcosm experiments

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INTRODUCTION

As climate-driven alterations to sea state accelerate on a global scale, there is a growing concern about the 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 the consequences of extreme low or high hydrodynamic forces on distribution, abundance, mortal-

ity, and population recovery of numerically dominant organisms (e.g. Harris et al. 1984, Ebeling et al. 1985, Seymour et al. 1989, Underwood 1999, Siddon & Witman 2003). Rigorous experimental testing of the effects of waves and currents on the ability of mobile consumers to displace and exert top-down community control has lagged behind observational studies of pattern (but see Kawamata 1998, Gagnon et al. 2006, St-Pierre & Gagnon 2015). The paucity of robust empirical demonstrations of wave-induced shifts in the spatial dynamics of functionally impor-

tant 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 & 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 & Bertness 2001) kelps (Scheibling et al. 1999, Gagnon et al. 2004, Lauzon-Guay & Scheibling 2007b, Frey & Gagnon 2015). A few correlational field studies indicate that individual displacement, the formation of grazing fronts, and rate of kelp bed destruction by fronts are negatively related to wave height or current speed (Dumont et al. 2006, Lauzon-Guay & 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 behavioral aspects that ultimately determine destructive potential. Recent experiments examining the sole effect of hydrodynamic forces on *S. droebachiensis* highlighted the species' adaptability to water flow by establishing the magnitude of changes in individual displacement (Morse & Hunt 2013) and aggregative feeding (Frey & Gagnon 2015) across water current velocity ranges. A number of 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 & Scheibling 2014, Ling et al. 2015). However, fewer studies have examined the influence of the hydrodynamic environment (Siddon & Witman 2003, Dumont et al. 2006) and seabed topography (Garnick 1978, Hagen & Mann 1994) on displacement, distribution, and aggregation in the barrens, where urchin food is scarce and less likely to drive spatial dynamics.

Marine consumers can take advantage of seabed topography and its influence on water flow in ways that ultimately increase fitness (Denny 1988, Barry & Dayton 1991, Guichard & Bourget 1998, St-Pierre & Gagnon 2015). One poorly studied aspect of green sea urchin ecology is the ability to associate with different seabed topographies in barrens in response to shifts in hydrodynamic conditions. Casual field observations suggest that green sea urchins largely cluster in crevices and along the base of rocky out-

crops during periods of strong wave action (Garnick 1978, Vadas et al. 1986, Scheibling et al. 1999, Frey & Gagnon 2015). The ability to switch to such topographically complex microhabitats may confer an ecological advantage by facilitating attachment of body parts to both horizontal and upright surfaces, thereby reducing the risk of dislodgement under hydrodynamically challenging conditions (Denny 1987, 1988, Lau & Martinez 2003, Siddon & Witman 2003, St-Pierre & Gagnon 2015). But barrens can also be topographically simple, and not all urchins may find suitable topographies for stable attachment. For these urchins, forming aggregations by interlocking spines with well-attached conspecifics may be another strategy to avoid dislodgement (Siddon & Witman 2003, Lauzon-Guay & Scheibling 2007b, Feehan et al. 2012).

Because green sea urchin displacement in barrens is largely random (Dumont et al. 2006, 2007, Lauzon-Guay et al. 2006, Lauzon-Guay & Scheibling 2007b), the rate of encounters between individuals likely increases with urchin density, and hence aggregation size may increase with both population density and water flow (Bernstein et al. 1983, Hagen & Mann 1994). The interaction between urchin density and water flow would be particularly worth testing during summer, when urchin activity peaks (Scheibling et al. 1999, Gagnon et al. 2004, Lauzon-Guay & Scheibling 2007b, Frey & Gagnon 2015). 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 & Scheibling 2005). 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 & Nolan 2008, DFO 2012).

In the present study, we report on the results of 2 experiments in an oscillatory wave tank and observations over 6 mo at 2 barrens sites in southeastern Newfoundland to examine effects of the wave environment and population density on the spatial dynamics of *S. droebachiensis* in food-depleted habitats. The 2 experiments, carried out at different times of year (winter and summer), mimic barren conditions, including the back-and-forth flow of waves, to identify wave velocities and urchin densities triggering shifts in displacement, microhabitat use, distribution, and aggregation. Field observations test the

generality of results from the laboratory experiments by examining variation in wave height and sea temperature, and associated changes in microhabitat use and distribution.

MATERIALS AND METHODS

Study and collection site

The present study was carried out with *S. 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 & Gagnon 2014) and intersperse with a few stands of the grazing-resistant kelp *Agarum clathratum* (Gagnon et al. 2005).

Displacement and microhabitat use (Experiment 1)

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 with large (40–60 mm in test diameter) unfed urchins from BCC (see Methods 1 in Supplement 1 at www.int-res.com/articles/suppl/m552p223_supp.pdf). The tank mimicked the back-and-forth flow caused by waves in shallow subtidal habitats (see tank details in Frey & Gagnon 2015, St-Pierre & 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 velocity. 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. The association of urchins with uneven surfaces should also intensify with increasing wave action because displacement in benthic mobile organisms generally decreases as hydrodynamic forces increase (Denny

1988, Siddon & Witman 2003, Gagnon et al. 2006, Frey & Gagnon 2015, St-Pierre & Gagnon 2015).

A total of 48 urchins were allowed to displace and make contact with 6 microhabitats (see next paragraph) at 4 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 center of the experimental area). The corresponding urchin density on the bottom of the tank (surface area of 1.08 m²) at the onset of trials was 44 ind. m⁻² and paralleled that in urchin barrens in the northern Gulf of St. Lawrence and southeastern Newfoundland (Himmelman 1986, Gagnon et al. 2004, Frey & Gagnon 2015). 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 (Gagnon et al. 2006, Frey & Gagnon 2015). 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 (Frey & Gagnon 2015, St-Pierre & Gagnon 2015).

Trials were conducted on a 3 × 4 grid arrangement of concrete tiles (12 tiles, 0.27 × 0.27 × 0.05 m [L, W, H] each) (Fig. 1). The grid was located in the center 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 6 microhabitats: (1) flat; (2) protrusion; (3) depression; (4) ledge; (5) crevice; and (6) wall (Fig. 1, see Methods 2 in Supplement 1). 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). Peak longitudinal water velocity differed

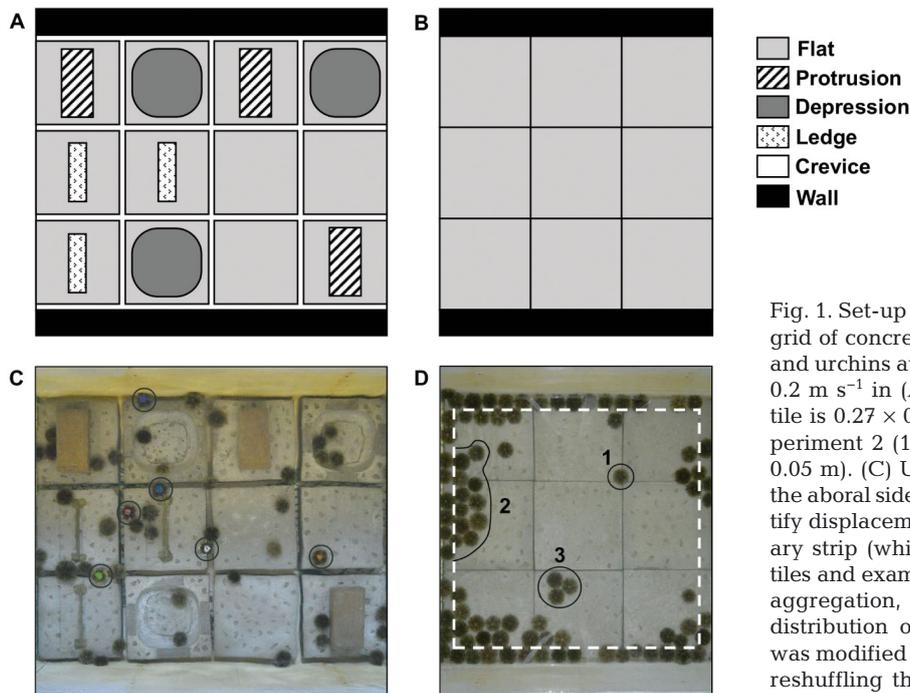


Fig. 1. Set-up of the experimental area (3×4 or 3×3 grid of concrete tiles and 2 longitudinal tank walls) and urchins at the end of a trial at a wave velocity of 0.2 m s^{-1} in (A,C) Experiment 1 (44 ind. m^{-2} ; each tile is $0.27 \times 0.27 \times 0.05$ [L, W, H] m) and (B,D) Experiment 2 (110 ind. m^{-2} ; each tile is $0.30 \times 0.30 \times 0.05$ m). (C) Urchins (6 ind.) with a colored spot on the aboral side (circled for clarity) were used to quantify displacement in Experiment 1. (D) 5-cm boundary strip (white dashed line) bordering the grid of tiles and examples of (1) solitary urchin, (2) bounded aggregation, and (3) unbounded aggregation. The distribution of the microhabitats in Experiment 1 was modified from one trial to the next by randomly reshuffling the position of all tiles within the grid

among microhabitats, as determined from measurement of flow over 2 min at (1) ~ 5 cm above the center of one tile of each of the flat, protrusion, depression, ledge, and crevice microhabitats in the center of the grid of tiles, and (2) ~ 5 cm above the edge of a flat tile flanking the center of one of the tank walls to characterize the wall microhabitat. It ranged 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 S1 in Supplement 2 at www.int-res.com/articles/suppl/m552_p223_supp.pdf). While effects of microhabitats are confounded by those of water velocity with this approach, 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 4 urchins per tile. They were allowed to explore the experimental area in the absence of waves for 1 min following the placement of the last individual. Urchins in treatments with waves were gradually acclimated to the wave environment (see Methods 3 in Supplement 1). The end of the acclimation marked the onset of trials.

The experimental area was photographed at the beginning of each trial and every 5 min 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) and SigmaScan Pro v5.0.0 (Systat Software). They were used to calculate, for each trial, the mean displacement of 6 urchins marked with a few drops of colored lacquer (Fig. 1), as well as the proportion of urchins in each of the 6 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 conspecific, that is 12.5 to 49.3% per trial or on average $29.5 \pm 1.5\%$ (in all cases, \pm refers to SE), were considered as being part of an aggregation. These urchins were discarded from the analysis 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. Quantifying microhabitat use in solitary urchins at a natural urchin density therefore ensured that results incorporated effects of physical interactions among urchins on the decision to aggregate or remain solitary as occurs in urchin barrens, while eliminating any confounding effect between

aggregation and microhabitat use. The number of urchins in each microhabitat was corrected for differences in surface area among microhabitats (see Methods 2 in Supplement 1).

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 (4 trials per day). The order of the treatments was randomized within each day. The distribution of the microhabitats was modified from one trial to the next by reshuffling randomly the position of all tiles within the grid. This procedure ensured that any influence of microhabitats on water velocity within each tile and among adjacent tiles was not consistently applied to the same areas within the tank, therefore preventing systemic bias in microhabitat use associated with the inevitable confounding effect between water flow and microhabitat distribution. 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 $4.5 \pm 0.2^\circ\text{C}$.

Distribution and aggregation (Experiment 2)

In the present study, 'urchin aggregation' refers to any group of 2 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 with large (40–60 mm test diameter) fed urchins from BCC (see Methods 1 in Supplement 1). The experiment was conducted in June, July, and August (summer) 2012, when sea surface temperature in Newfoundland, including BCC, typically rises and peaks (Caines & Gagnon 2012, Blain & Gagnon 2013, Frey & Gagnon 2015) and urchins readily displace and aggregate (Frey & Gagnon 2015). The experiment tested the prediction that the degree of aggregation and size of aggregations increase with increasing wave action and urchin density.

Urchins at varying densities (41, 89, or 140 urchins in the tank) 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 rea-

sons given in Experiment 1. The corresponding urchin densities on the bottom of the tank (surface area of 0.81 m^2) at the onset of trials (51 ind. m^{-2} = low, 110 ind. m^{-2} = intermediate, and 173 ind. m^{-2} = high), paralleled 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 (Himmelman 1986, Gagnon et al. 2004, Frey & Gagnon 2015).

Trials were conducted on a 3×3 grid arrangement of concrete tiles in the center of the tank (9 tiles, $0.3 \times 0.3 \times 0.05 \text{ m}$ [L, W, H] each) (Fig. 1). Like in Experiment 1, the grid was delimited longitudinally by the tank walls and transversally by nylon netting, and the upper surface of the tiles was sculpted with small holes and cracks. In contrast to Experiment 1, no topographical features were added to the tiles and there was no space (grooves) between them (Fig. 1). Urchins therefore had access to 2 microhabitats, flat (the 9 tiles) and wall (the 2 longitudinal tank walls), which had different water velocities (Table S1) 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 evenly across the 9 tiles, oral surface down, and allowed to explore the experimental area in the absence of waves for 1 min following the placement of the last individual. Urchins in treatments with waves were gradually acclimated to the wave environment (see Methods 3 in Supplement 1). The end of the acclimation marked the onset of trials. The experimental area was photographed at the beginning, midway through, and at the end of each trial with a digital camera (Nikon D5000) located 1.3 m above the water surface. The nearest neighbor R-ratio, termed R (Clark & Evans 1954), was calculated from each image with PhotoImpact v6.0 (Ulead Systems) and ImageJ v1.44p (National Institutes of Health, USA). This ratio is 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). Calculations included only urchins on the tiles that had >50% of the test outside of a 5-cm boundary strip bordering the 4 sides of the grid of tiles (Fig. 1, see Methods 4 in Supplement 1 for a detailed description of calculations).

Inspection of images and complementary observations during trials indicated that urchin aggregations initially 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. 1). Aggregations of the former type, termed 'bounded aggregations', were bound on one side (walls or nettings). They 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. They could expand in any direction until contacting another aggregation or vertical surface, like aggregations in barrens that form on bare bedrock platforms. Only a few (<4%) unbounded aggregations contacted the tank walls or transverse nettings as more urchins joined in. Aggregations resulting from the merger of bounded and unbounded aggregations (~12%) were designated as bounded. Both types of aggregations consisted of urchins attached to the bottom with podia and interlocking spines. However, they fundamentally differed in that bounded aggregations originated from urchins located at a topographic discontinuity (bottom-wall interface), providing both horizontal and vertical surfaces for attachment, whereas unbounded aggregations originated from urchins that could attach only to horizontal surfaces. In the presence of waves, considerably more effort was required to manually detach urchins at a bottom-wall interface than those on tiles away from walls (D. Frey pers. obs.). The distinction between both types of aggregations was therefore primarily based on the likely ecological advantage of a reduced risk of dislodgement provided by joining a tighter, more firmly attached core of urchins in bounded aggregations. 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 at the end of the trial. 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 at the end of the trial. Solitary (non-aggregated) urchins on the tiles and tank walls, designated as such by applying the same criteria as in Experiment 1, 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 (3 trials per day) over 4 consecutive days (12 trials per block of 4 d). 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 $11.9 \pm 1.1^\circ\text{C}$.

Microhabitat use and distribution in barrens (field surveys)

Microhabitat use and distribution of urchins and their relationship with thermal and wave environments were assessed by tracking changes over 6 mo in sea temperature, wave conditions, and the number and location of urchins on 2 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 'Results') and preliminary surveys in the barrens suggested that urchins readily associated with the flat, crevice, and protrusion microhabitats. Accordingly, the present surveys focused on urchins on flat bedrock, in crevices, and on artificial protrusions identical in shape and size (see next paragraph).

Microhabitat use was quantified in 10 plots of 0.5×0.5 m on the inner bedrock platform. The position and orientation of all plots, which were at least 5 m away from one another, was 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 ($0.2 \times 0.1 \times 0.05$ 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 boul-

ders because the former had an 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 5 to 16 d until 25 October 2012 (22 times). The contour of each plot was made visible by inserting, before the photograph, one corner of a 0.5×0.5 m frame into the embossed portion of the marking marine epoxy.

The images of the plots and bricks were analyzed with PhotoImpact v6.0. 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 2 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 Table S2 in Supplement 2 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 2 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 (0.4×0.3 m) centered 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 4 corners of the zone were perma-

nently 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 5 to 15 d until 25 October 2012 (22 times). On each sampling event, 2 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 1×6 -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 0.5×0.5 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. 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 neighbor R-ratio and mean urchin density on each sampling event (see Experiment 2 above for meaning and calculations of R-ratio).

Sea temperature at BCC was recorded every 30 min throughout the study with a temperature logger ($\pm 0.5^\circ\text{C}$, 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 2 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 (www.climate.weather.gc.ca/, Station St. John's Intl A). Each cor-

rected 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 (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 Frey & Gagnon 2015 for data quality assessment using this method).

Statistical analysis

Note: See Supplement 1 for additional details about Analyses 2, 4, 5, 6, and 7.

Experiment 1:

Analysis 1. A 2-way ANOVA with the factors Waves (null, low, intermediate, and high wave velocity) and Block (each daily block of 1 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 ($n = 40$).

Analysis 2. A 1-way MANOVA (Scheiner & 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 6 microhabitats (flat, protrusion, depression, ledge, crevice, and wall) during trials. Proportions of urchins in each of the 6 microhabitats differed among velocity treatments (see 'Results'), and hence univariate 1-way ANOVAs (with the factor Waves) were carried out to identify which response variables contributed to the multivariate effect. The MANOVA ($n = 240$) and ANOVAs ($n = 40$ for each analysis) were applied to the logit-transformed data (Warton & Hui 2011) to correct for heterogeneity of the residuals in the analysis of the raw data.

Experiment 2:

Analysis 3. 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 $s_r = 0.26136(Np)^{-0.5}$, 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 p is the urchin density (see Methods 4 in Supplement 1 and

Clark & Evans 1954). Urchins were randomly distributed ($R = 1$) if $|z| \leq 1.96$ (2-tailed test of significance at $\alpha = 0.05$), clumped if $|z| > 1.96$ and $R < 1$, or uniformly distributed if $|z| > 1.96$ and $R > 1$ (Krebs 1999).

Analysis 4. A 3-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 4 d during which 1 replicate of each treatment was done) was used to examine the effects of wave action and urchin density on the nearest neighbor 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 ($n = 114$).

Analysis 5. A 2-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. The analysis was applied to the logit-transformed data to correct for heterogeneity of the residuals in the analysis on the raw data ($n = 118$).

Analysis 6. Three 2-way ANOVAs (one for each urchin density) with the factor Waves (null, low, intermediate, and high wave velocity) and Block (each block of 4 d during which 1 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 that would have resulted from using 3-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 Analysis 4 above) because calculations of R controlled for density effects (see Methods 4 in Supplement 1). 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 ($n = 38$ –40) and unbounded ($n = 11$ –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 surveys:

Analysis 7. Multiple regression analysis was used to relate (1) proportions of urchins in crevice, flat, and protrusion microhabitats on the inner bedrock platform at BCC; and (2) the distribution (R) and density of urchins in flat and crevice microhabitats on the outer bedrock platform, to sea temperature and significant wave height (SWH, the average height of the highest one-third of the wave data) calculated over the 48 h preceding each sampling event. All regressions were applied to the raw data ($n = 22$ for each regression). 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, sample plots on the 2 bedrock platforms were spatially fixed. Inspection of all regression analyses indicated that residuals were not autocorrelated.

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 & Cochran 1989). All MANOVAs met all the customary assumptions, including multivariate normality, homogeneity of variance-covariance matrices, and absence of multicollinearity (Scheiner & Gurevitch 2001). Tukey HSD multiple comparison tests (comparisons based on least-square means, Sokal & Rohlf 2012) were used to detect differences among levels within a factor (ANOVAs and MANOVAs). The Pillai's trace multivariate statistic was used in the MANOVAs to determine which factors were statistically significant (Scheiner & 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.

RESULTS

Note: ANOVA tables are provided in Tables S3–S7 in Supplement 2 at www.int-res.com/articles/suppl/m552p223_supp.pdf.

Experiment 1

The distance moved by urchins over 45 min varied among the 4 wave velocities tested (Table S3). Displacement peaked at 54.5 ± 7.3 cm in the absence of waves and dropped steadily (by $\sim 40\%$ in total, to 32.4 ± 2.1 cm) as velocity increased from null to high (Fig. 2). The MANOVA and associated univariate ANOVAs showed that wave velocity affected the proportion of urchins in 3 of the 6 microhabitats: flat, crevice, and wall (1-way MANOVA, $F_{18,99} = 3.294$; $p < 0.001$, Table S4). The proportion of urchins on flat surfaces was higher at null and low ($\sim 10\%$) than at intermediate and high ($\sim 7\%$) velocities (LS means, $p < 0.001$; Fig. 3). Wave velocity affected the proportion of urchins in crevices, with a 2-fold increase from null (20%) to high (43%) velocity (Fig. 3). At high velocity, there were at least 2 times more urchins in crevices than in any other microhabitat (Fig. 3). The proportion of urchins on the tank walls was low ($< 4\%$) at all velocities. It was nevertheless higher at null and low than at intermediate and high velocities (LS means, $p < 0.001$; Fig. 3). Wave velocity had no perceptible effect on the proportion of urchins in the protrusion, depression, and ledge microhabitats (Table S4), ranging from 14% (ledge at high velocity) to 27% (protrusion at null velocity; Fig. 3).

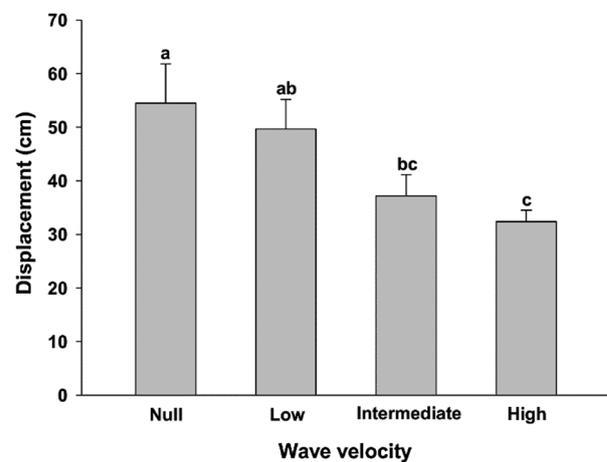


Fig. 2. Mean (+SE) displacement of green sea urchins *Strongylocentrotus droebachiensis* at null, low, intermediate, and high wave velocity (0.0, 0.1, 0.2, and 0.3 m s^{-1} , respectively) (Experiment 1). Bars not sharing the same letter are significantly different (LS means tests, $p < 0.05$; $n = 10$ for each velocity)

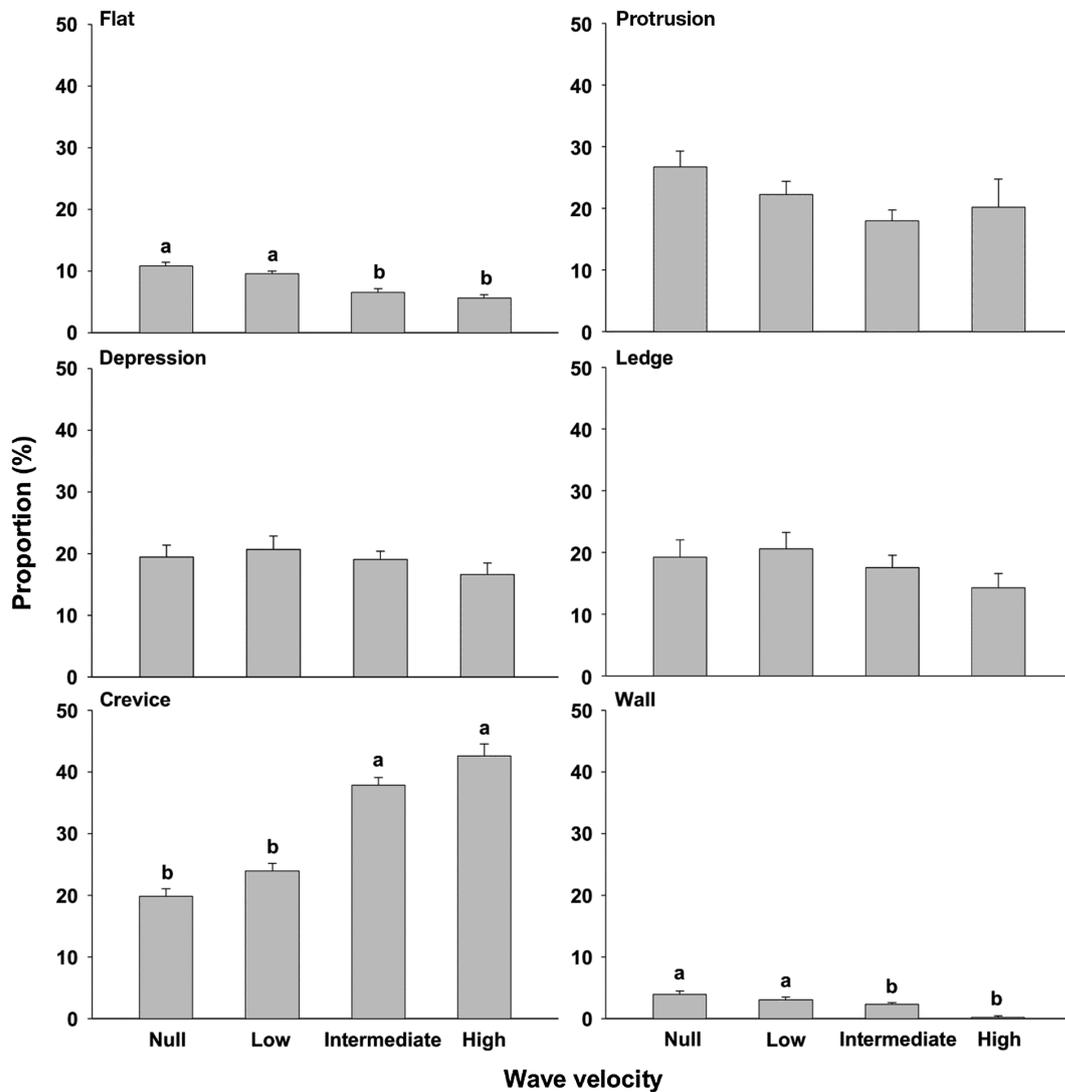


Fig. 3. Proportion (+SE) of green sea urchins *Strongylocentrotus droebachiensis* in each of the 6 microhabitats at null, low, intermediate, and high wave velocity (0.0, 0.1, 0.2, and 0.3 m s⁻¹, respectively) (Experiment 1). Bars not sharing the same letter are significantly different (LS means tests, $p < 0.05$; $n = 10$ for each wave velocity in each microhabitat)

Experiment 2

The degree of aggregation (nearest neighbor R-ratio, R) of urchins with a clumped distribution ($R < 1$) varied with urchin density among the 4 wave velocity treatments (a significant interaction between the factors Waves and Density, Table S5). 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. 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. 4). However, aggregation at 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. 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. 4).

Wave velocity and urchin density interactively determined the proportion of urchin aggregations that had formed at the end of trials (Table S6). The majority (>73%) of aggregations were bounded (originating from individuals at the base of the tank walls and transverse nettings and expanding towards the center of the tank) as opposed to unbounded (originating from, and growing around, individuals on the tank bottom away from the walls) (Fig. 5). The proportion of bounded aggregations at low density

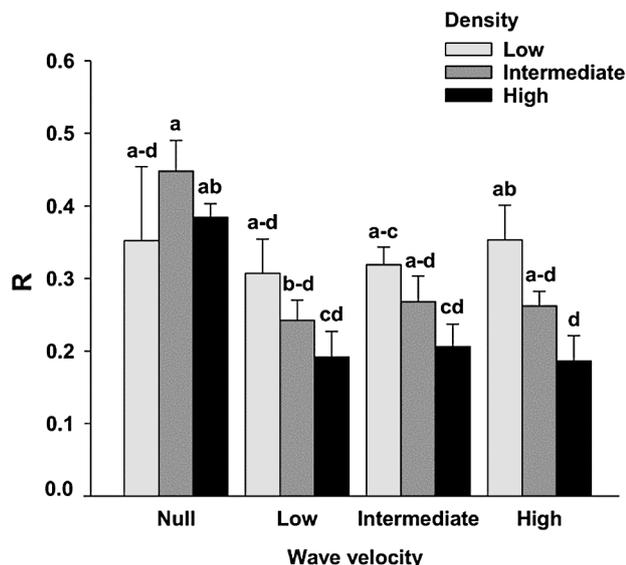


Fig. 4. Mean (+SE) nearest neighbor R-ratio (R) of green sea urchins *Strongylocentrotus droebachiensis* at the end of trials at null, low, intermediate, and high wave velocity (0.0, 0.1, 0.2, and 0.3 m s⁻¹, respectively), and low, intermediate, and high density (51, 110, and 173 ind. m⁻², respectively) (Experiment 2). Bars not sharing the same letter (only ranges are provided for simplicity, e.g. 'a-d' means 'abcd') are significantly different (LS means tests, $p < 0.05$; $n = 6-10$ for each combination of Waves \times Density)

was relatively high (95–100%) at intermediate and low velocities, but dropped to 73% at high velocity (a significant difference between intermediate and high velocities; LS means, $p = 0.005$) (Fig. 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. 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. 5).

The number of urchins per bounded aggregation varied with wave velocity at the 3 urchin densities tested (Table S7). At low density, there were 2 times more urchins (at least 2.8 ± 0.4 ind.) per bounded aggregation at intermediate and high velocities than at null and low velocities (LS means, $p < 0.001$; Fig. 6). Effects of velocity exacerbated with increasing urchin density, with respectively 4 and 7 times more urchins (up to 25.7 ± 2.7 ind.) per bounded aggregation at high than null velocity at intermediate and high densities, respectively (Fig. 6). Wave velocity had no perceptible effect on the number of urchins per unbounded aggregation at any urchin density (Table S7), with $< 6.0 \pm 1.8$ ind. aggregation⁻¹

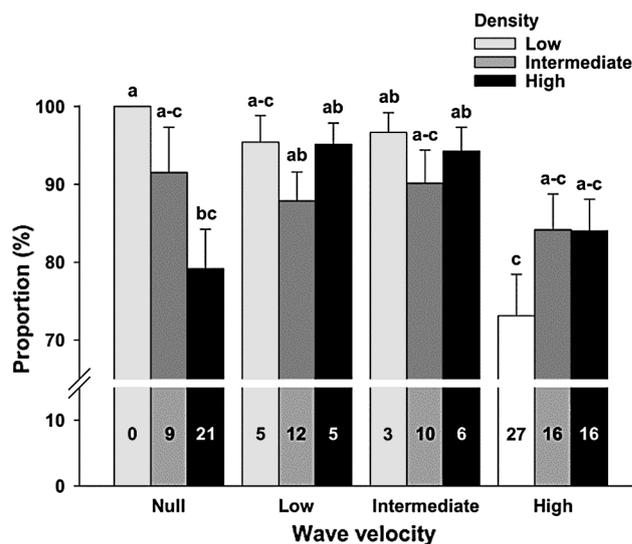


Fig. 5. Mean (+SE) proportion of bounded aggregations of green sea urchins *Strongylocentrotus droebachiensis* at the end of trials at null, low, intermediate, and high wave velocity (0.0, 0.1, 0.2, and 0.3 m s⁻¹, respectively), and low, intermediate, and high density (51, 110, and 173 ind. m⁻², respectively) (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 significantly different (LS means tests, $p < 0.05$; $n = 8-10$ for each combination of Waves \times Density)

(Fig. 6). There were 2 to 6 times more bounded than unbounded aggregations regardless of wave velocity and urchin density (Fig. 6).

Wave velocity affected the number of solitary urchins on the tiles at intermediate and high densities only (Table S7, Fig. 6). At low density, urchins on the tiles were relatively abundant (~8–12 ind.), regardless of velocity (Fig. 6). At intermediate and high densities, there were respectively 2 and 7 times more urchins on the tiles at null than high velocity (Fig. 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 S7, Fig. 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. 6).

Field surveys

Sea temperature was lowest (-0.6°C) and significant wave height (SWH) highest (0.59 m) at Bread and Cheese Cove (BCC) during the first month of the survey (May; Fig. 7). Temperature generally increased until mid-August when it peaked to 16.7°C , and

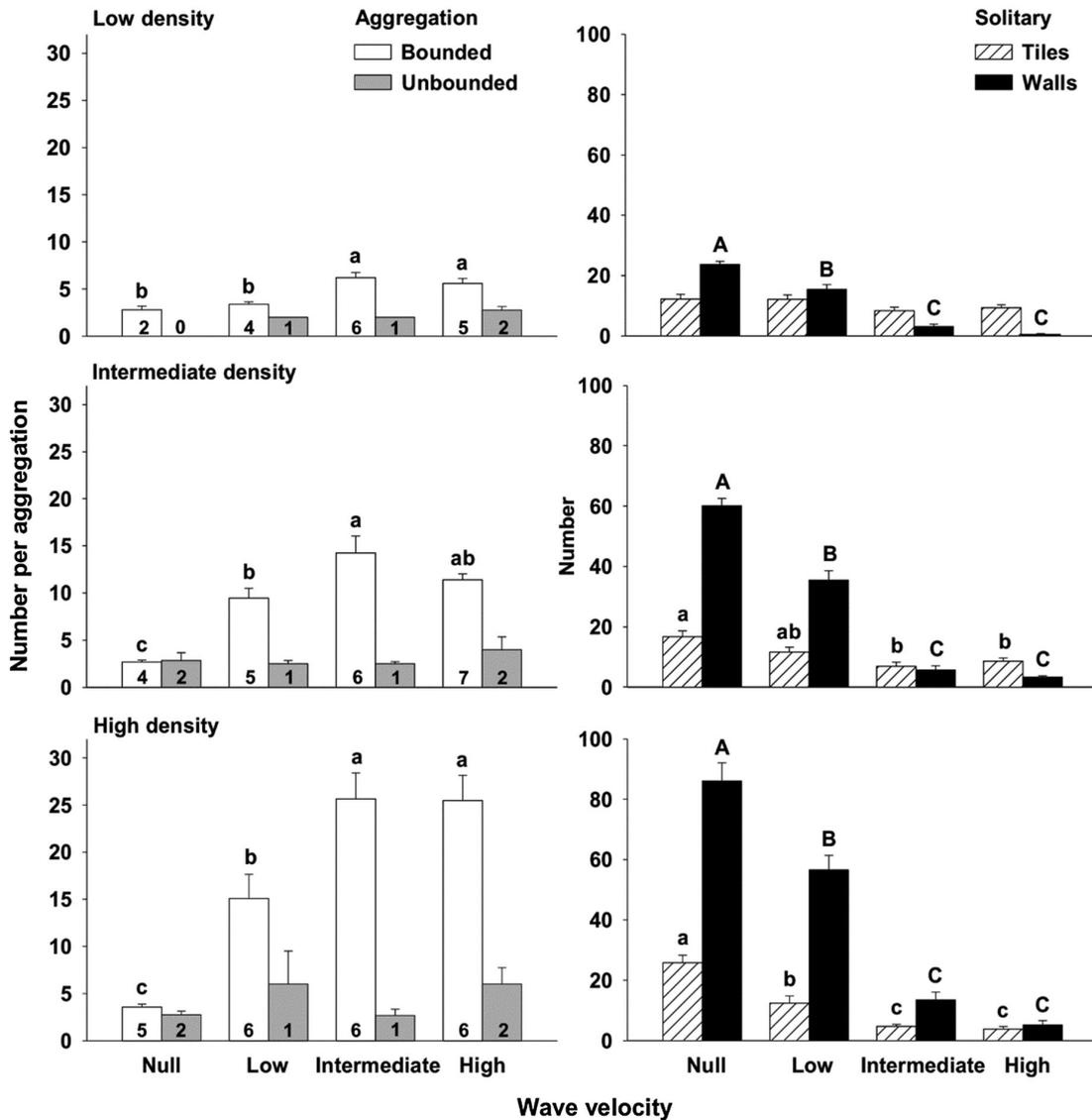


Fig. 6. Mean (+SE) number of green sea urchins *Strongylocentrotus droebachiensis* per bounded and unbounded aggregation and mean (+SE) number of solitary (non-aggregated) urchins on the tiles and tank walls at the end of trials at null, low, intermediate, and high wave velocity (0.0, 0.1, 0.2, and 0.3 m s⁻¹, respectively) and low, intermediate, and high density (51, 110, and 173 ind. 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 significantly different (LS means tests, $p < 0.05$; $n = 2-10$ for each bar)

remained relatively high, between 7.1 and 16.6°C, until the end of the survey (October). SWH was relatively low (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. 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 4 times higher than that of urchins on flat surfaces (20%) (2-tailed t -test assum-

ing equal variance, $t_{42} = 25.25$, $p < 0.001$). Multiple linear regression analysis showed that sea temperature had no perceptible effect on the proportion of urchins in crevice, flat, and protrusion microhabitats (Table 1). The proportion of urchins on protrusions was, however, positively correlated ($r^2 = 0.329$) with significant wave height (SWH) (Table 1). It increased by a factor of 9.7 for every 0.1 m increase in SWH (Table 1), peaking at 77% on 2 October, when SWH was 0.49 m, near the maximum wave height (0.59 m) during the survey (Fig. 7). There was no significant rela-

tionship between SWH and the proportion of urchins in crevices or on flat surfaces (Table 1).

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 ($R = 0.35 \pm 0.02$) than urchins on flat surfaces ($R = 0.42 \pm 0.01$) (2-tailed t -test assuming equal variance, $t_{42} = -3.76$, $p = 0.001$). Multiple linear regression analysis showed that the degree of aggregation of urchins was unrelated to SWH in both microhabitats and negatively correlated ($r^2 = 0.213$) with sea temperature in crevices only (Table 2). Urchin density in both microhabitats did not vary with temperature or SWH throughout the survey (Table 2). Density was rela-

tively low and stable in both microhabitats, with $\sim 21\%$ more urchins in crevices (90.5 ± 3.0 ind. m^{-2}) than on flat surfaces (74.5 ± 3.5 ind. m^{-2}) (2-tailed t -test assuming equal variance, $t_{42} = 3.49$, $p = 0.001$).

DISCUSSION

Our experiments in a wave tank mimicking barrens conditions demonstrate that wave action strongly influences 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 favor of microhabitats that

Table 1. 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

Microhabitat	Parameter	Coefficient (SE)	t	p	Full model			
					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 2. Results of multiple linear regression analyses (applied to raw data) examining relationships between the nearest neighbor R-ratio and density (ind. m^{-2}) of green sea urchins *Strongylocentrotus droebachiensis* in crevice and flat 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

Microhabitat	Variable	Parameter	Coefficient (SE)	t	p	Full model			
						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				
		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				
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				
		Temp	-0.7 (0.8)	-0.81	0.428				
		SWH	-87.4 (51.1)	-1.71	0.103				

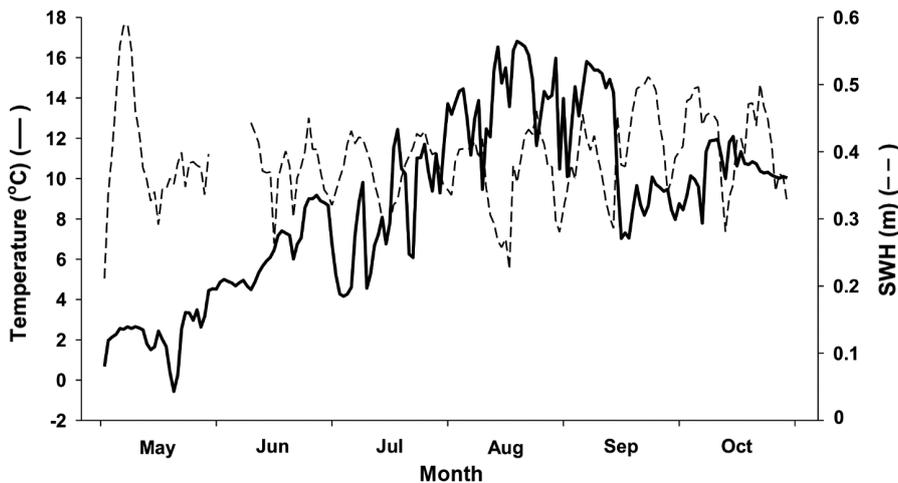


Fig. 7. Change in mean daily sea temperature and significant wave height (SWH) at Bread and Cheese Cove from 30 April to 25 October 2012. Sea temperature and wave height data were acquired every 30 and 1 min, respectively, with one temperature logger and one water level logger secured to the seabed at a depth of 5 m

facilitate anchorage; and (3) increasingly forms 2-dimensional aggregations, whose physiognomy varies with velocity and urchin density.

Displacement and microhabitat use

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 (Gagnon et al. 2006, Frey & Gagnon 2015). These studies, conducted in summer in relatively warm (7 and 14°C) water, reported—like Experiment 1 in the present study carried out in winter in colder (~4.5°C) water—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 (i.e. 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 relatively small shifts in hydrodynamic conditions, immediately adjusting displacement at velocities well below those likely to dislodge them (Siddon & Witman 2003, Dumont et al. 2006, Lauzon-Guay & Scheibling 2007b, Morse & Hunt 2013). Notably, displacement still occurred at all velocities, indicating that urchins remain active even during the cold, stormy winter months in eastern Canada.

Experiment 1 also provided novel information about ways *S. droebachiensis* uses topography 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 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 unpubl. data). Of the 6 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 structures of attachment in urchins (Santos & 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. But none of these microhabitats had sufficiently narrow spaces to insert podia and brace spines. These 3 moderately complex bottom configurations may provide urchins with sufficient purchase or protection against waves, limiting emigration. Experiment 1 intended to char-

acterize changes in microhabitat use as a result of shifting wave velocity. The reshuffling of microhabitats within the tank from one trial to the next prevented systemic bias in microhabitat use associated with the inevitable confound between water flow and microhabitat distribution. This confounding effect certainly also affects urchins in natural habitats and would have been more serious if our objective had been to compare microhabitats within a water velocity.

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 (*S. purpuratus*), and rock (*Paracentrotus lividus*) sea urchins are generally more abundant in bedrock crevices and holes than on flat surfaces (Harrold & Reed 1985, Hernández & Russell 2010, 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 & 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 $\sim 12^{\circ}\text{C}$, determined that the degree of aggregation of urchins (proximity of neighboring individuals) with a clumped distribution ($R < 1$) increases with wave velocity, albeit only at or above a density of 110 ind. m^{-2} . The lack of a relationship with wave velocity at the lowest density tested (51 ind. m^{-2}) establishes a threshold density (between 51 and 110 ind. m^{-2}) above which *S. droebachiensis* 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 & Scheibling 2014, Ling et al. 2015). But the present study is, to our knowledge, the first to 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 & Mann 1976, Bernstein et al. 1983, Hagen & Mann 1994, Scheibling et al. 1999, Gagnon et al. 2004, Lauzon-Guay & Scheibling 2007a).

Another important contribution of Experiment 2 is 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', originating from individuals at the base of the tank walls and expanding towards the center of the tank. The rest of the aggregations were 'unbounded', originating from, and growing around, individuals on the tank bottom away from the walls. All aggregations were 2-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 incipient 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 Experiment 2, which showed 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, 2007, Lauzon-Guay et al. 2006, Lauzon-Guay & Scheibling 2007b). The likelihood of establishing contact with conspecifics is, therefore, positively related to urchin density, further explaining the increase in size of aggregations with increasing density.

Field surveys

Throughout the 6-mo survey of the inner bedrock platform at Bread and Cheese Cove (BCC), most (80%) urchins exhibited the same strong tendency to frequent crevices as in Experiment 1. 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 & Gagnon 2013, Frey & Gagnon 2015, the present study). SWH was consistently low (<0.6 m) throughout the survey, which may explain why 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 affect feeding and the physiognomy and destructive potential of feeding aggregations (fronts) of *S. droebachiensis* (Scheibling et al. 1999, Lauzon-Guay & Scheibling 2007a,b, Frey & Gagnon 2015). 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 (Scheibling & Gagnon 2009, Krumhansl & Scheibling 2011, 2012, Frey & Gagnon 2015). Urchin density in crevices and on flat surfaces was consistently low and stable throughout the survey. It exceeded, on only 1 out of 22 sampling events, the threshold range of 51 to 110 ind. 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, 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 partitioning 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 wave velocity and population density in the order of 0.1 m s⁻¹ and a few tens of ind. m⁻¹ respectively, can elicit important changes in the way urchins disperse, cluster, and use seabed topography. The strong inclination of *S. droebachiensis* to reduce displacement, favor microhabitats that facilitate anchorage of body parts, and increasingly form 2-dimensional aggregations as wave velocity increases in the absence of food, is most likely a behavioral adaptation to mitigate hydrodynamic forces while reinforcing attachment to minimize dislodgement risk. Additional quantitative studies are required to assess the importance of urchin spatial dynamics in barrens to the stability of urchin grazing fronts (Brady & Scheibling 2005), and to increase 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 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 directly compare the effects of waves on the spatial dynamics of urchins between experimental and natural environments. Nevertheless, similarities among laboratory and field patterns, including the inclination of urchins to frequent crevices, underscore the value of conducting laboratory microcosm experiments to establish causal links between environmental variability and spatial dynamics. Only such studies in laboratory setups can provide the reproducibility and resolution necessary to gather information about threshold flow speeds that can potentially trigger ecological cascades in marine systems. The present study identifies threshold wave velocity and population density ranges that trigger shifts in urchin displacement, microhabitat use, distribution, and aggregation. It provides novel information that can be used to feed predictive models of marine benthic community dynamics (e.g. Lauzon-Guay & Scheibling 2010, Marzloff et al. 2011, Sala & Dayton 2011). This kind of information is critically needed in the Anthropocene where accelerating changes in sea state and temperature pose a major challenge to accurately predicting and managing shifts in coastal resources, including urchin populations (Scheffer et al. 2001, Andrew et al. 2002, deYoung et al. 2008, Halpern et al. 2008, Burrows et al. 2011).

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