

RESEARCH ARTICLE

Intertidal sea stars (*Pisaster ochraceus*) alter body shape in response to wave action

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SUMMARY

Sea stars are some of the largest mobile animals able to live in the harsh flow environment of wave-exposed, rocky intertidal shores. In addition, some species, such as the northeastern Pacific *Pisaster ochraceus*, are ecologically significant predators in a broad range of environments, from sheltered lagoons to the most wave-exposed shorelines. How they function and survive under such an extreme range of wave exposures remains a puzzle. Here we examine the ability of *P. ochraceus* to alter body form in response to variation in flow conditions. We found that sea stars in wave-exposed sites had narrower arms and were lighter per unit arm length than those from sheltered sites. Body form was tightly correlated with maximum velocity of breaking waves across four sites and also varied over time. In addition, field transplant experiments showed that these differences in shape were due primarily to phenotypic plasticity. Sea stars transplanted from a sheltered site to a more wave-exposed site became lighter per unit arm length, and developed narrower arms, after 3 months. The tight correlation between water flow and morphology suggests that wave force must be a significant selective factor acting on body shape. On exposed shores, narrower arms probably reduce both lift and drag in breaking waves. On protected shores, fatter arms may provide more thermal inertia to resist overheating, or more body volume for gametes. Such plastic changes in body shape represent a unique method by which sea stars adapt to spatial, seasonal and possibly short-term variation in flow conditions.

Supplementary material available online at <http://jeb.biologists.org/cgi/content/full/216/9/1717/DC1>

Key words: Echinodermata, Asteroidea, phenotypic plasticity, wave exposure, hydrodynamics, marine invertebrate, aspect ratio, rocky shores, lift, drag.

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INTRODUCTION

Wave-swept intertidal shores are among the most extreme flow environments on earth (Denny, 1988). Crashing waves can generate extreme accelerations and velocities that exceed 15 m s^{-1} on wave-exposed shores (Helmuth and Denny, 2003). As a consequence, organisms inhabiting these shores commonly suffer wave-induced damage and mortality (Denny, 1995). Such extreme forces significantly affect the size, form, behaviour and distribution of intertidal organisms (Dayton, 1971; Paine and Levin, 1981). Despite these extreme forces, some large-bodied mobile animals, such as the sea star *Pisaster ochraceus*, not only survive on wave-exposed shores, they also have a major impact on the ecological structure of rocky intertidal communities over a wide range of wave exposures (Dayton, 1971; Levin and Paine, 1974). How does a large-bodied mobile animal cope with such a broad range of flow conditions?

Intertidal organisms may be dislodged by either lift or drag forces, and these in turn are directly influenced by body size and shape (Denny, 1995). Many organisms exhibit changes in form with increasing flow: mussels develop shells with a lower height to width ratio (Akester and Martel, 2000), kelp produce narrower blades (Fowler-Walker et al., 2006) and barnacles develop shorter feeding legs (Arsenault et al., 2001; Neufeld and Palmer, 2008) and stouter penises (Arsenault et al., 2001; Neufeld and Palmer, 2008). Within species, individuals from wave-swept environments also tend to be smaller and have a more compact form than individuals from calm sites, as seen in many organisms, including encrusting sponges,

hydrozoans and scleractinian corals (Denny et al., 1985; Kaandorp, 1999).

Phenotypic variation among sites in such heterogeneous environments can be due to genetic differentiation, a plastic phenotypic response, or a combination of the two (Via and Lande, 1985). However, plastic responses seem to be widespread in intertidal environments, probably because they permit (1) accommodation to ever-changing environmental conditions and (2) adaptation to new local conditions following dispersal (which is usually high). In fact, all of the examples of size and form variation cited above are plastic responses to changes in the hydrodynamic environment.

To fully understand the ecological impacts of wave exposure on intertidal organisms one must consider how plastic responses to variation in wave action improve survival in high flow. Although disturbance dynamics have been adequately described in mussels using mechanistic approaches involving only wave exposure (Gaylord et al., 1994; Denny, 1995), the description of these dynamics was greatly improved by accounting for seasonal plastic change in morphology and attachment (Carrington, 2002). Dislodgement of mussels by waves, in turn, has a large impact on the structure of rocky intertidal communities (Dayton, 1971; Levin and Paine, 1974). Given the intimacy of the population dynamics of a keystone predator, the ochre sea star, *Pisaster ochraceus* (Brandt), and its preferred prey, the competitively superior mussel, *Mytilus californianus*, an understanding of the mechanical

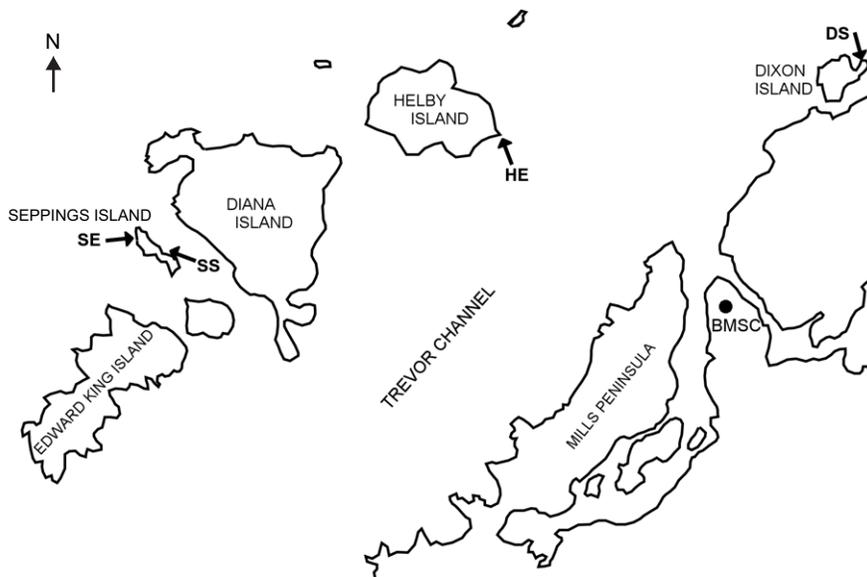


Fig. 1. Study sites in Barkley Sound, near the Bamfield Marine Sciences Centre, Vancouver Island, British Columbia, Canada. SE, Seppings exposed; SS, Seppings sheltered; HE, Helby exposed; DS, Dixon sheltered.

constraints on *P. ochraceus* distribution is equally important for understanding the ecology of northeastern Pacific rocky intertidal communities (Paine, 1969; Paine, 1976).

The ochre sea star is an abundant, widespread sea star in the northeastern Pacific and is one of the largest organisms able to withstand the rigours of life on these rocky intertidal shores (Ricketts et al., 1992; Denny, 1999). To better understand the morphological adaptations that facilitate this impressive feat, we studied the ability of *P. ochraceus* to change body shape in response to variation in wave exposure.

MATERIALS AND METHODS

Collection and field survey

Pisaster ochraceus were collected from four sites in Barkley Sound (British Columbia, Canada) that differed in maximum water velocity. In decreasing order of wave exposure they were: Seppings Island exposed (SE; 48°50'26.54N, 125°12'34.27W) and Helby Island (HE; 48°51'14.34N, 125°9'46.06W), which were considered relatively exposed, and Dixon Island (DS; 48°50'03.16N, 125°05'50.25W) and Seppings Island sheltered (SS; 48°50'22.17N, 125°12'20.25W), which were considered sheltered (Fig. 1). Maximum velocities at two of the sites (SE and HE) were determined by Arsenault et al. (Arsenault et al., 2001). Maximum water velocities at Seppings sheltered were found using 5 days of wave drogue data during this study (8, 11–14 August 2010) that were calibrated to the velocities of Arsenault et al. (Arsenault et al., 2001) by concurrently measuring velocities at Seppings exposed (Carrington Bell and Denny, 1994). Water velocity of the last site (DS) was estimated using dissolution of dissimilar metals (McGehee, 1998). Three replicate dissolution rigs were concurrently placed in all four sites for a period of 10 days and a calibration curve of dissolution rates and maximum water velocities of known sites (SE, HE, SS) was used to estimate maximum water velocity in the unknown site (DS) ($F_{1,11}=45.991$, $P<0.001$, $R^2=0.87$) (see supplementary material Fig. S1).

Pisaster ochraceus ($N=100$) were haphazardly collected at low tide from the windward (exposed) and leeward sides of Seppings Island from 10 to 14 August (mean arm length= 105.5 ± 1.9 and 121.8 ± 2.2 mm, respectively), and from Dixon Island (mean arm length= 106.5 ± 2.8 mm) and Helby Island (mean arm length= 113.3 ± 2.8 mm) sites on 8–11 September 2010 near Bamfield,

British Columbia, Canada (Fig. 1). Only sea stars without obvious injury or evidence of past arm autotomy were collected. The sea stars were transported to the Bamfield Marine Science Centre, where they were housed in water tables connected to a flow-through seawater system. They were then partly dried by allowing them to sit on perforated plexiglass for 3 min and individually weighed and photographed in planar (aboral) and side view along with a calibration scale. These photographs were used to measure the length and width of each arm in ImageJ Version 1.44 (US National Institutes of Health, Bethesda, MD, USA). Arm lengths were measured as the distance from the centre ossicle of the aboral disc to the tip of the arm, and arm width was measured at the base of each arm (Fig. 2). These were used to compute an aspect ratio (length/width) for each arm; a mean aspect ratio was computed for each individual as the average of all five arms. Differences among sites in the grand mean aspect ratio for all individuals were compared using an ANOVA in SYSTAT Version 13 (Systat Software, Chicago, IL, USA). To test the repeatability of arm width

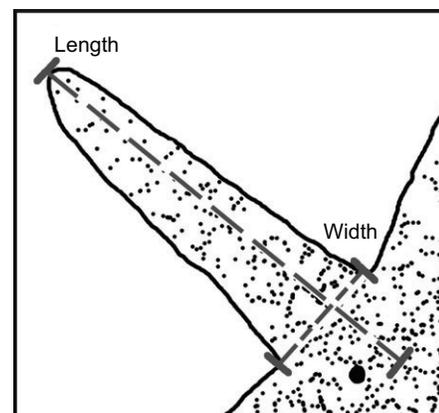


Fig. 2. Aspect ratio calculation for *Pisaster ochraceus* (planar view). The length of an individual arm was measured as the distance from the centre ossicle to the tip of the arm. Width was measured as the distance across the arm at its base. Aspect ratios were calculated as length/width for each arm and averaged over all five arms for each individual, so a higher aspect ratio indicates a relatively more slender arm.

and length measurements, a subset of sea stars was remeasured; replicate measurements were taken from the original photographs ($N=12$) and compared with prior measurements of the mean arm length and width for each individual. Percent error in measurement was 0.11% for arm length and 0.48% for width.

Field transplant experiment

After sea stars were weighed and photographed, each was given a unique external identification by applying Neutral Red to create colored bands at different positions on each arm (K.J.R.H., unpublished). Neutral Red was mixed with seawater to create a 0.2 g ml^{-1} slurry, and a liberal amount was applied to the aboral surface of the arms. The tagged *P. ochraceus* were left out of water for 15 min to allow the stain to set and each individual's arm code (a combination of mark position on each arm and arm number) was recorded. Stars were returned to each site by placing them on rocks nearby other non-transplanted *P. ochraceus* at low tide. Sea stars from the exposed side of Seppings (SE) were transplanted to the sheltered side (SS) and *vice versa* on 11–15 August 2010. Sea stars were also reciprocally transplanted between Helby and Dixon Islands on 9–12 September 2010.

After 3 months, sea stars from each transplant were collected. Because recovery rates varied, sample sizes differed: 15 were recovered from Helby (HE), 21 from Dixon (DS) and 15 from the leeward side of Seppings (SS). No transplanted individuals were recovered from the windward side of Seppings (SE), likely because of their higher vulnerability to dislodgement. To determine natural seasonal change in aspect ratio, 15 non-transplanted stars (seasonal controls) were collected from each of the four release sites at the same time marked sea stars were recovered. All collected *P. ochraceus* (transplanted and seasonal controls) were taken to the laboratory and immediately photographed and weighed. To ensure that their arms were fully extended, sea stars were placed on plastic window screen suspended in flow-through seawater tables beforehand. Using the Neutral Red markings, transplanted individuals were identified and the change in aspect ratio was calculated. Final aspect ratios were computed and compared with initial values using pair-wise *t*-tests and between sites using an ANOVA in Systat Ver 13.

Drag and lift determination

Digital photographs of *P. ochraceus* from the aboral perspective were used to measure the planar area of a subset of sea stars from both the exposed ($N=30$) and sheltered ($N=25$) sides of Seppings Island. Measurements were made using ImageJ Version 1.44. Using lateral profile photographs, the height of each sea star was measured in ImageJ. Lateral projected area was not directly measured because projected area varies with arm orientation. This height and previously measured values of average arm length were used to calculate an estimate of maximum lateral projected area (A_{MLP}), the side area of a sea star with one arm perpendicular to view and all remaining arms spread equally. This was estimated by:

$$A_{MLP} = [1 + \cos(36)]A_h, \quad (1)$$

where the long axis of the other arm making up the profile of the sea star was 36 deg from the long axis of the arm that was perpendicular to view, and A_h is the projected area of one half of the sea star when viewed from the side, given by:

$$A_h = [1/2(h_C - h_T)A_L] + [h_T A_L], \quad (2)$$

where h_C is the height of the sea star in the centre of the body, h_T is the height of the tip of the sea stars' arm and A_L is the average

arm length of that individual. This was repeated for 38 individuals from the exposed side of Seppings and 32 from the protected side. Analysis of covariance (ANCOVA) was performed for both planar area and A_{MLP} with site as a factor and arm length as a covariate (using SYSTAT 13).

The lift force (F_L ; N) experienced by an individual sea star should be directly proportional to its planar area (projected area when viewed perpendicular to flow) as:

$$F_L = C_L 1/2 \rho V^2 A_{\text{planar}}, \quad (3)$$

where C_L is the coefficient of lift, ρ is the density of seawater (kg m^{-3}), V is the water velocity (m s^{-1}) and A_{planar} is the planar area (m^2). Drag force (F_D) should be proportional to A_{MLP} as:

$$F_D = C_D 1/2 \rho V^2 (A_{MLP}), \quad (4)$$

where C_D is the coefficient of drag.

Coefficients of lift and drag were calculated using computational fluid dynamics analysis (ANSYS CFX Ver. 13, ANSYS, Canonsberg, PA, USA) on simulated 3-D models of typical, average-sized sea stars from both the sheltered and exposed site, $C_L=0.53$ and $C_D=0.4$ for a sheltered sea star and $C_L=0.42$ and $C_D=0.34$ for an exposed sea star (coefficients used were calculated at 5 m s^{-1}) (K.J.R.H., M. S. Warhing and C. F. Lange, unpublished). The 3-D model was created in DS SolidWorks (Dassault Systèmes SolidWorks Corporation, Vélizy, France) before being imported into the ANSYS Workbench. Fluid flow was always oriented with one arm pointing directly into the flow and all other arms spread equally. Using these force equations and the known relationships of both A_{MLP} and planar areas with arm length for each site (see Results, 'Variation in shape'), the wave-induced dislodgement force of sheltered and exposed sea stars was calculated as the vector sum of drag and lift.

RESULTS

Field survey

We observed differences in aspect ratio among the four sites of different wave exposure. On average, sea stars from the most exposed site had arms that were 12% narrower at the base compared with those from the most sheltered site for a given arm length ($P<0.001$). The aspect ratio was closely correlated with variation in water velocity of breaking waves when all individuals were included in the analysis ($R^2=0.36$, $P<0.001$; Fig. 3). Variation in mean aspect ratio among sites was even more highly correlated with water velocity: water velocity accounted for 99% of the variation in mean aspect ratio ($R^2>0.99$, $P=0.003$; Fig. 3).

Arm length also varied significantly with water velocity among sites ($R^2=0.042$, $P<0.001$; Fig. 4A). Although the relationship was significant, water velocity was a poor predictor of size within each site, explaining only 4% of the variation among all sampled individuals. Despite this, on average, sea stars from the most wave-exposed site had 15% shorter arms than those from the most sheltered site.

Mass was not used as a measure of body size because it depended heavily on aspect ratio: as aspect ratio increased, wet mass per unit arm length decreased. Mass also increases as sea stars grow (increase in arm length). The slope of this relationship was consistent between sites and intercepts differed significantly: wet masses were consistently higher at more sheltered sites (ANCOVA, $P<0.001$; Table 1). Using this common relationship between mass and arm length, one can determine the expected mass of a sea star with a typical arm length (Fig. 4B, Table 1). At the overall mean arm length (111.2 mm) a sea star from the most sheltered site was 35% heavier than one from the most exposed site. These expected masses declined

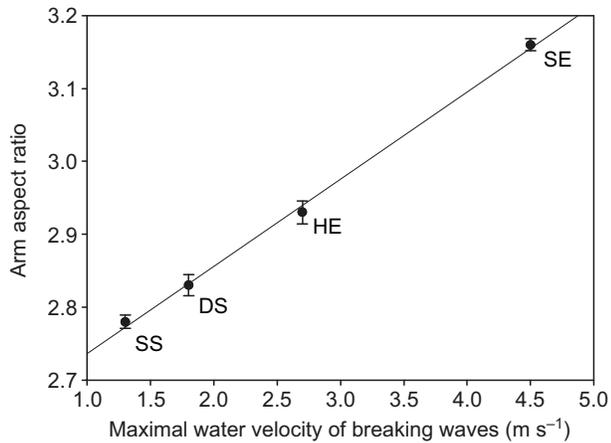


Fig. 3. Arm aspect-ratio variation (length/width) in *Pisaster ochraceus* as a function of wave exposure among four intertidal sites in Barkley Sound (see Fig. 1). Maximum water velocity is a relative measure of the average observed daily maximum velocities experienced at each site over several days during late summer. The sites are (left to right) Seppings Island sheltered (SS), Dixon Island (DS), Helby Island (HE) and Seppings Island exposed (SE). All points are observed means \pm s.e.m. for that site. Ordinary least-squares linear regressions: raw data, $F_{1,417}=232.8$, $P<0.001$, $R^2=0.36$; population means, $P=0.003$, $R^2>0.99$.

significantly with increasing water velocity among sites ($R^2=0.90$, $P=0.035$; Fig. 4B).

Transplant experiment

During the experimental period (September–December 2010), native (non-transplanted) sea stars at each site showed a temporal increase in aspect ratio. Aspect ratios of sea stars increased by 5% ($P<0.001$) on the leeward side of Seppings (SS), by 5% ($P=0.022$) on Dixon Island (DS) and by 6% ($P<0.001$) at the exposed site on Helby (HE; Fig. 5A). This change in aspect ratio coincided with increased storm activity in winter compared with early autumn. The monthly mean offshore wave height was 1.7 m in September compared with 3.1 m in December (Fisheries and Oceans Canada, La Perouse Bank buoy historical data; <http://www.meds-sdmm.dfo-mpo.gc.ca/isdm-gdsi/waves-vagues/index-eng.htm>).

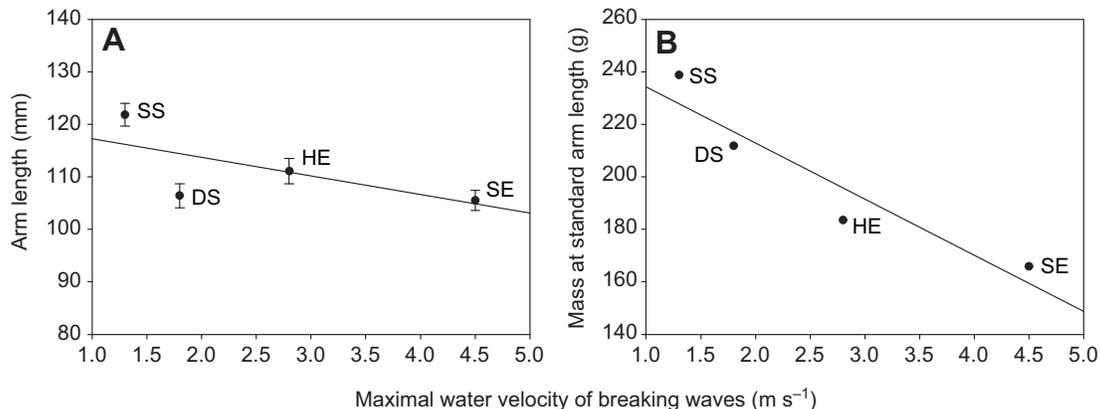


Fig. 4. Body form of *Pisaster ochraceus* as a function of wave exposure at four sites in Barkley Sound (sites as in Fig. 3). (A) Mean arm lengths. All points are means \pm s.e.m. Ordinary least-squares linear regression: raw data, $F_{1,417}=18.4$, $P<0.001$, $R^2=0.042$. (B) Wet mass standardized to a common arm length of 111.2 mm by analysis of covariance (ANCOVA performed with both axes on a log scale). Ordinary least-squares linear regression: population means, $F_{1,3}=27.5$, $P=0.034$, $R^2=0.90$.

Table 1. Results of ANCOVA for the relationship between arm length and wet mass of *Pisaster ochraceus* across four sites of varying wave exposure in Barkley Sound, British Columbia, Canada

Source of variation	Wet body mass		
	d.f.	MS	<i>P</i>
Site	3	0.529	<0.001
Arm length (covariate)	1	23.571	<0.001
Error	414	0.009	
Equality of slopes	1	0.001	0.94

Analysis was performed on the relationship between log(wet mass) and log(arm length).

Sea stars transplanted from a sheltered site, Dixon Island (DS), to the more exposed site Helby Island (HE) showed a significant increase in aspect ratio ($P=0.004$) and they were not significantly different from native (non-transplanted) individuals at the end of the experiment ($P=0.30$; Fig. 5B). During this time, wet mass of the transplanted sea stars decreased by 18% ($P<0.001$) while arm length did not change significantly ($P=0.46$). In the reciprocal transplant (HE to DS; Fig. 5C) aspect ratio was not expected to change because of the effects of the seasonal increase in wave action (Fig. 5A). The final form of transplanted sea stars did not differ from expected ($P=0.40$), and as a result aspect ratio did not differ from the initial value ($P=0.59$). Both wet mass and arm length decreased slightly ($P<0.001$ and $P=0.042$, respectively). However, mass per unit arm length did not change significantly ($P=0.19$). *Pisaster ochraceus* transplanted from the exposed side of Seppings Island (SE) to the more protected side (SS) produced stouter arms ($P<0.001$) and the mean final aspect ratio did not differ significantly from the nearby native stars ($P=0.40$; Fig. 5D). During the experiment, wet mass significantly increased by approximately 6% ($P=0.015$) despite arm length decreasing by approximately 5% ($P=0.041$). No individuals transplanted to the exposed side of Seppings Island (SE) could be recovered, presumably because they were more vulnerable to dislodgement and were lost before they had time to adapt to the new conditions.

Variation in shape with increasing arm length

Planar area and A_{MLP} increased with increasing size (arm length) in sea stars from both the sheltered (SS) and exposed (SE) sides of

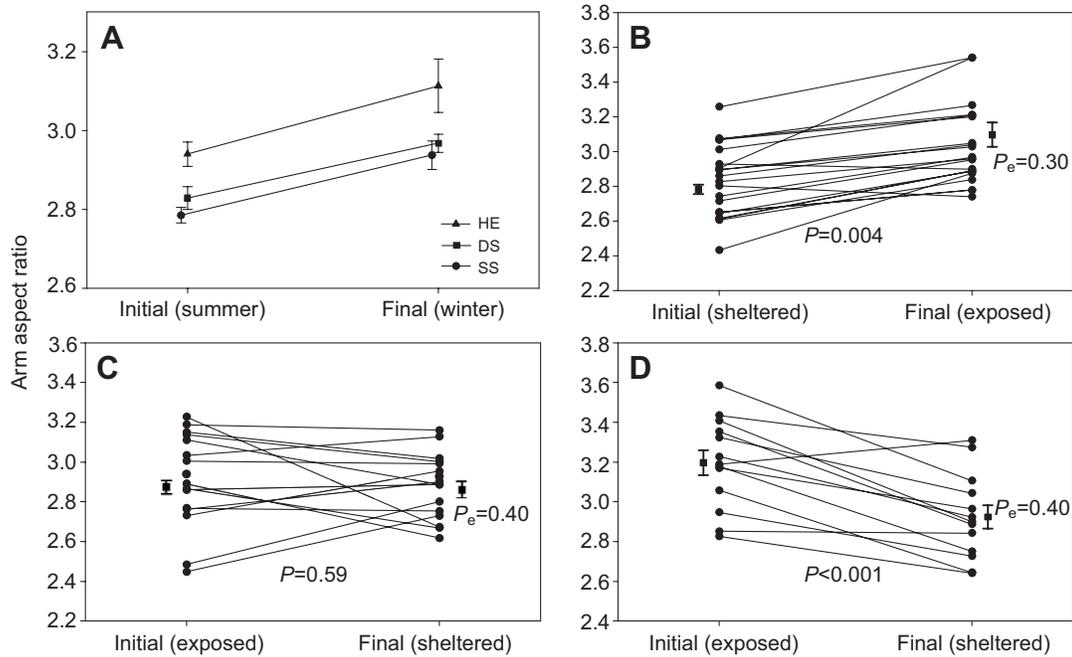


Fig. 5. Arm aspect ratio (length/width) of *Pisaster ochraceus* from three different source populations before and after a 3 month period from late summer to early winter 2010. (A) Mean \pm s.e.m. aspect ratio of individuals haphazardly sampled from the transplant sites at the beginning and end of the transplant experiment to characterize natural, temporal change in aspect ratio. (B) Individuals transplanted from a sheltered (DS) to an exposed site (HE). (C) Individuals transplanted from an exposed (HE) to a sheltered site (DS). (D) Individuals transplanted from an exposed (SE) to a sheltered site (SS). Closed squares in B–D represent the mean (\pm s.e.m.) initial aspect ratio (on the left) and the expected mean final aspect ratio (on the right), assuming that the final aspect ratio was the same as that of native (non-transplanted) sea stars sampled in winter (from A). Closed circles in B–D represent individually marked sea stars before and after transplant. P -values are shown for the difference between initial and final aspect ratio of transplanted stars (P) and for the difference between the observed mean and expected final aspect ratio (closed squares) of transplanted stars (P_e).

Seppings Island (Fig. 6). Slopes of these relationships did not differ between exposure conditions for planar area ($P=0.65$) or A_{MLP} ($P=0.77$), but planar area was negatively allometric ($P<0.001$) while A_{MLP} was positively allometric ($P<0.001$; Table 2). Sea star planar area (A_{planar} , mm^2) increased with arm length (mm) as $A_{planar}=3.05A_L^{1.762}$ for sheltered and $A_{planar}=2.05A_L^{1.814}$ for exposed *P. ochraceus*, where A_L is average arm length of all five arms of an individual. A_{MLP} (mm^2) increased with increasing arm length as $A_{MLP}=0.067A_L^{2.32}$ for sheltered and $A_{MLP}=0.094A_L^{2.21}$ for exposed *P. ochraceus*.

If the relationship between these areas and arm length were isometric, the scaling exponent a in the equation $A_{MLP}=kA_L^a$ would equal two. In the case of planar area it is less; therefore, larger sea stars have a proportionally smaller planar area than smaller ones for a given arm length. In contrast, A_{MLP} exhibited positive allometry, so larger sea stars have proportionally larger projected areas. For both planar area and A_{MLP} the sheltered population had consistently and significantly higher areas for a given arm length. For planar area it was greater by 16% ($P<0.001$) and for A_{MLP} by 22% ($P<0.001$; Fig. 7, Table 2).

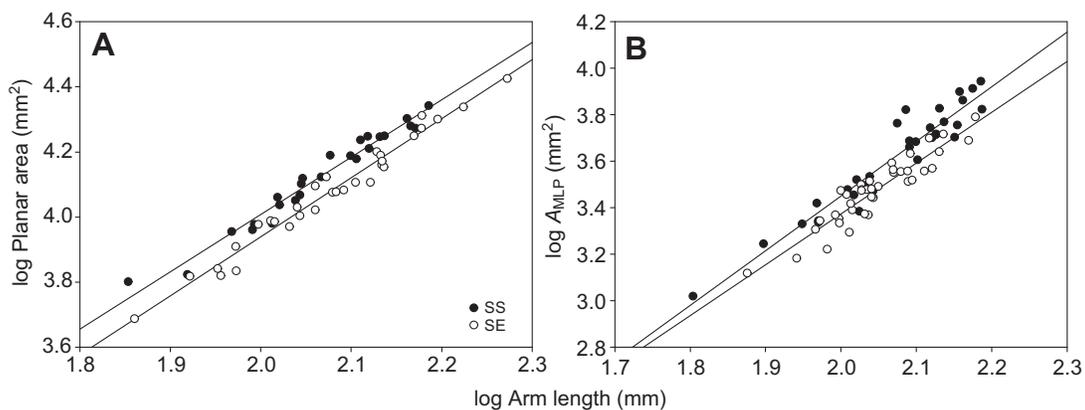


Fig. 6. Morphological differences between *Pisaster ochraceus* from the exposed (SE) and sheltered (SS) sides of Seppings Island. Each point represents a single individual. (A) Planar area as a function of arm length. The difference between slopes was not significant ($P=0.65$); the difference between intercepts was highly significant ($P<0.001$). (B) Maximum lateral projected area (A_{MLP}) as a function of arm length. The difference between slopes was not significant ($P=0.77$); the difference between intercepts was highly significant ($P<0.001$). See Table 2 for complete statistics.

Table 2. Results of ANCOVA for the relationships of arm length to planar area (Fig. 6A) and maximum lateral projected area (A_{MLP} ; Fig. 6B) for *Pisaster ochraceus* from an exposed site (SE) and a sheltered site (SS)

Source of variation	Planar area			A_{MLP}		
	d.f.	MS	<i>P</i>	d.f.	MS	<i>P</i>
Site	1	0.058	<0.001	1	0.127	<0.001
Arm length (covariate)	1	1.368	<0.001	1	2.075	<0.001
Error	68	0.001		68	0.001	
Equality of slopes	1	<0.001	0.65	1	0.002	0.70

Analysis was performed on the log–log relationship between arm length and each area measurement.

Because of their relatively larger planar and projected areas per unit arm length, sheltered stars would experience a 19% higher dislodgement force at a given water velocity (Fig. 8).

DISCUSSION

Is body form in *P. ochraceus* plastic?

The close correlation between body form and local environmental conditions could result from either phenotypic plasticity, where form is directly induced by environment, or genetically distinct populations formed by low rates of migration, differential mortality of new recruits due to a mismatch between environment and phenotype, or selective recruitment of genetically distinct juveniles into suitable sites (Schlichting and Pigliucci, 1998). Only transplant experiments, or studies of seasonal variation of marked individuals, can distinguish among these alternative hypotheses.

Our field surveys strongly suggested a plastic response of sea star shape because *P. ochraceus* arm aspect ratios varied in both space and time. Aspect ratios were significantly higher in exposed-shore *P. ochraceus*: for a given arm length, exposed-shore individuals weighed significantly less than sheltered-shore individuals. *Pisaster ochraceus* also appeared to undergo seasonal changes in aspect ratio (Fig. 5A), presumably to better match seasonal changes in wave-exposure conditions.

We confirmed this implied phenotypic plasticity experimentally (Fig. 5B–D). When sheltered-shore *P. ochraceus* were transplanted to a wave-exposed site, they developed a higher aspect ratio (relatively more slender arms), while the opposite occurred in

transplants from exposed to sheltered sites. Such plastic responses to local flow conditions occur in many other organisms that live on wave-swept rocky shores (Akester and Martel, 2000; Arsenault et al., 2001; Carrington, 2002; Marchinko, 2003; Neufeld and Palmer, 2008).

Two confounding variables that might impact seasonal shape change in *P. ochraceus* (Fig. 5A) are changes in gonad and pyloric cecum sizes throughout the year. Gonad mass tends to decrease during the period when seasonal change in shape was measured, so this could have had some impact on changes in arm volume (increase in aspect ratio) in winter. However, decreases in gonads are generally accompanied by increases in pyloric cecum mass, which actually makes up a larger proportion of the coelom in the arm (Pearse and Eernisse, 1982). Also, changes in either gonad or pyloric cecum status appear to have little effect on overall mass in *P. ochraceus* (Pearse and Eernisse, 1982). Given the tight correlation of shape with exposure (Fig. 3) we feel that seasonal changes in organ indices would have had little impact on overall aspect ratio compared with changes in wave exposure.

Our demonstration that *P. ochraceus* shape varies plastically in response to variation in wave exposure easily explains some remarkable and puzzling observations (Feder, 1970). Feder reported that *P. ochraceus* raised in the laboratory, or found on sheltered shores, appeared ‘inflated’ compared with those on wave-exposed shores. He thought these differences arose because exposed-shore individuals had less access to food than sheltered-shore individuals or those fed in the laboratory. In addition, he observed that under

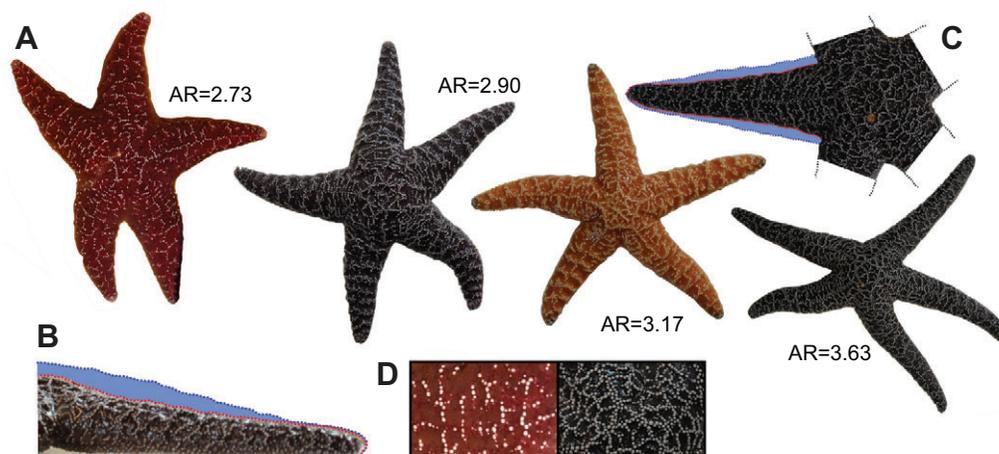


Fig. 7. (A) Typical aspect ratios of *Pisaster ochraceus* from different wave-exposure regimes in Barkley Sound, British Columbia. Sites and arm lengths from left to right (most sheltered to most wave exposed): Grappler Narrows (129 mm), DS (131 mm), HE (129 mm), SE (121 mm). Lateral (B) and planar (C) projected areas of a single arm of a typical *Pisaster ochraceus* from the exposed (SE; narrower arm) and the sheltered (SS, fatter arm) sides of Seppings Island. Arm length=120 mm. Note the apparently higher ossicle density in the most wave-exposed sea stars in A. This is illustrated in D, a magnified view of ossicles of the most sheltered individual (left) and the most exposed individual (right).

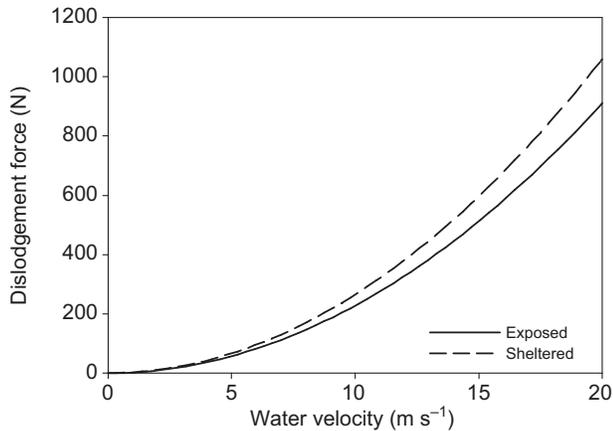


Fig. 8. Expected wave-induced dislodgement force as a function of water velocity for an average *Pisaster ochraceus* with an arm length of 111.2 mm. Dislodgement force was calculated as the vector sum of both lift and drag expected from the planar and maximum lateral projected areas shown in Fig. 6. Drag and lift coefficients used in these computations were obtained from computational fluid-dynamic model simulations on a 3-D model of *P. ochraceus*.

laboratory conditions a change in arm length was always accompanied by a change in body mass in the same direction, regardless of whether these changes were positive or negative. In contrast, he noted that all four combinations of changes in arm length or body mass (i.e. increase or decrease in either or both) could occur over time in the field. All three of Feder's (Feder, 1970) curious observations are consistent with plastic responses of *P. ochraceus* shape to flow: (1) low aspect ratios would be expected in low flow environments, which would cause the 'inflated' appearance he observed in quiet-water sea stars or those grown in the laboratory; (2) in the laboratory, aspect ratio should remain relatively constant so any growth would yield proportional increases in both body mass and arm length; and (3) in the field, changes in wave exposure and therefore shape could yield all combinations of changes in arm length and body mass (e.g. if growth was also accompanied by an increase in wave exposure, arm length could increase due to growth but mass could decrease due to plastic 'deflation').

The ability of *P. ochraceus* to adapt actively to wave-exposure conditions may be important for several reasons. First, wave-swept intertidal shores are among the most heterogeneous flow environments on earth, and can experience huge day-to-day variation in wave activity (Denny, 1988). Second, seasonal variation in storm activity can be extreme: average wave heights in winter are commonly double those in summer, and maximum and daily wave heights can be 10 times higher in winter than summer (Fisheries and Oceans Canada, La Perouse Bank buoy historical data; <http://www.meds-sdmm.dfo-mpo.gc.ca/isdm-gdsi/waves-vagues/index-eng.htm>). Third, *P. ochraceus* has a long planktonic period (up to 8 months) and as a result, genetically similar larvae from one parent may be spread over a wide range of environments (Strathmann, 1978). Fourth, *P. ochraceus* is a highly mobile predator, so plasticity in body form may facilitate foraging if individuals migrate among different microhabitats in search of prey (Robles et al., 1995).

Differences in maximum water velocities accounted for almost all (99.7%) of the among-site variation in overall mean aspect ratio, but accounted for only 36% of the total among-individual variation (Fig. 3). Such high intra-population variation is not unexpected because most rocky shores are quite heterogeneous topographically,

which would create considerable variation in flow conditions within a site. For example, an individual in a crevice or on a surface facing away from incoming waves probably experiences lower water velocities than one occupying a flat surface or a surface oriented towards the waves, as seen in intertidal snails that use habitat microcomplexity as refugia during periods of high flow (Emson and Faller-Fritsch, 1976; Trussell, 1997).

Potential benefits of higher aspect ratios

Mobile organisms that live on wave-swept shores are vulnerable to dislodgement and death if waves become too large (Denny, 1988). On wave-exposed shores, the probable benefit of the observed changes in *P. ochraceus* body form is reduced vulnerability to drag and lift. We found that an increased aspect ratio induced by a rapid flow was associated with reduced planar area and A_{MLP} for a given arm length that, in turn, would yield lower lift and drag forces. Considering the close link between wave exposure and body form, wave activity is probably a major constraint not only on morphology but also on behaviour and distribution.

In addition, larger body sizes appeared to be selected against in wave-exposed sites (Fig. 4), as predicted by Denny et al. (Denny et al., 1985; Kaandorp, 1999). Attachment area for a sea star is restricted to the ambulacral groove area in contact with the substratum (which should be proportional to planar area). The negative allometry observed in this planar area (Fig. 6A), combined with a positive allometry in A_{MLP} (Fig. 6B), could yield a mismatch between dislodgement force and tenacity as *P. ochraceus* grow. Although lift and attachment would remain in balance because both are based on planar area, positive allometry in A_{MLP} would mean that larger stars would be subjected to a proportionally larger drag force relative to attachment force. However, the trend towards smaller body sizes at the more exposed site was not universal at all sites and was probably also affected by the age of cohorts in each site, as settlement events tend to be episodic (Sewell and Watson, 1993).

Small-scale differences in shape between ecotypes affected coefficients of lift and drag for each: exposed sea stars had lower coefficients of drag and lift than sheltered forms. These differences in shape were readily apparent in the upper margin of the arms from tip to base: exposed-shore sea stars had a more concave shape while sheltered ecotypes tended to have a straighter margin (Fig. 7B).

Potential costs of higher aspect ratios

The large difference in *P. ochraceus* form between wave-exposed and sheltered sites (Fig. 7) implies a cost to higher aspect ratios in quiet waters. Two potential costs seem likely: (1) decreased thermal inertia, and (2) decreased gonad volume. Sea stars with an exposed-shore morphology (higher aspect ratio) will be more prone to overheating than those from sheltered sites, which have much more wet mass per unit body length and therefore a larger surface-to-volume ratio (Helmuth, 1998). Upper zonal limits for intertidal organisms are typically set by temperature and desiccation stresses, as temperature fluctuations during aerial exposure can be extreme and occasionally lethal (Foster, 1971; Tsuchiya, 1983). In *P. ochraceus*, changes in body temperature greatly affect physiological processes and feeding rates up to the approximate lethal limit of 35°C (Sanford, 1999; Pincebourde et al., 2008). Because average sheltered sea stars (e.g. SS) were 44% heavier than exposed stars (e.g. SE) for any given arm length, they would be better able to resist desiccation and thermal stress. Therefore, wave-induced changes in body shape must be considered when making predictions about the vertical zonation limits for *P. ochraceus* (Harley and Helmuth, 2003; Szathmary et al., 2009).

and, as a consequence, its impact as a keystone predator on rocky intertidal shores (Paine, 1969; Paine, 1976).

Lowered fecundity may be another cost associated with higher aspect ratios in exposed-shore *P. ochraceus*. In many marine invertebrates, fecundity is proportional to body mass (Giese, 1959), and this is well known in echinoderms including sea stars (Farmanfarmaian et al., 1958), sea cucumbers (Conand, 1993) and sea urchins (Conor, 1972). *Pisaster ochraceus* with higher aspect ratios (thinner arms) have lower body mass per unit arm length (see Results, Field survey). So, other things being equal, they should have lower gonad volumes and hence lower fecundity.

The higher thermal inertia likely associated with lower arm aspect ratios introduces a possible confounding variable when trying to explain the advantages of higher aspect ratios on more wave-exposed shores (previous section): different wave-exposure regimes may have different thermal-stress regimes. Wave action creates wash and spray, which can be important cooling mechanisms (Harley and Helmuth, 2003). Therefore, these may reduce the disadvantage to higher aspect ratios on wave-exposed shores (Szathmary et al., 2009). In *P. ochraceus*, for example, increased temperatures elicit an increase in water retention and thus thermal inertia (Pincebourde et al., 2009): high-temperature treatments caused an increase of wet mass by approximately 8% of total body mass over times as short as 5 days, compared with low-temperature controls. However, the increase in mass (per unit arm length) we observed with decreasing wave exposure was much greater than that induced by Pincebourde et al. (Pincebourde et al., 2009) via thermal stress. Therefore, wave forces seem likely to be a more important factor influencing *P. ochraceus* form on rocky intertidal shores. Nonetheless, it would still be interesting to investigate the tradeoffs associated with *P. ochraceus* shape variation in summer, when thermal stress is high and wave forces are low, and in winter, when the opposite is true.

Causes and ecological consequences of phenotypic plasticity

The mechanism by which *P. ochraceus* decrease arm aspect ratio under lower flow conditions is likely similar to that for increasing mass in response to heat (Pincebourde et al., 2009): uptake of seawater during high tide. We observed little change in arm length during the transplant experiments and the small decreases observed were probably due to decreased feeding during the storm season. Given the large changes in aspect ratio (and therefore mass per unit arm length) over a three-month period (Fig. 5), and the slow growth rate of *P. ochraceus* (Paine, 1976), the change in form we observed was likely due to inflation with seawater rather than to tissue growth or restructuring.

Pisaster ochraceus undergo large daily changes in volume (20% of total mass), and intake or expulsion of water through the madreporite appears to be the primary means of fluid flux (Ferguson, 1992). We suspect that *P. ochraceus* modifies form in response to changes in wave-exposure using a similar method. Sea stars from sheltered shores also tended to be much less stiff than those with high aspect ratio arms (K.J.R.H., personal observation), suggesting a role for body wall muscles or mutable collagen.

The positive relationship between ossicle density and aspect ratio observed in *P. ochraceus* (Fig. 7) provides further evidence for this mechanism; surface rugosity and ossicle density tend to increase with increasing aspect ratio, as would be expected if the shape of *P. ochraceus* is achieved through deflation. Sheltered and exposed forms of *P. ochraceus* have previously been described as separate subspecies due to differences in ossicle density and pattern (Fisher, 1930). However, these differences may alternatively be due to phenotypically plastic changes in body shape through uptake or expulsion of seawater.

Aspect-ratio changes may therefore occur much more rapidly than reported here. On two separate occasions during field sampling, aspect ratios of 50 haphazardly sampled stars were significantly higher than 50 stars sampled from the same location 2 days earlier. In both cases these increases coincided with increased wave action (K.J.R.H., unpublished). If increased water uptake is the mechanism by which *P. ochraceus* decreases aspect ratio under conditions of lower wave action, it would represent an elegant method for adapting to local conditions of thermal and wave stress, even over periods as short as hours or days.

Phenotypically plastic responses to flow occur in several other intertidal species from the northeast Pacific, including barnacles (Arsenault et al., 2001; Marchinko, 2003; Neufeld and Palmer, 2008) and mussels (Akester and Martel, 2000; Carrington, 2002). This plasticity has likely facilitated their success as dominant space-holders on rocky intertidal shores. *Pisaster ochraceus*, unlike mussels and barnacles, are highly mobile and remove these sessile, dominant space-holders. As a result, *P. ochraceus*'s actions help maintain high species diversity on intertidal shores (Paine, 1966). The ability of *P. ochraceus* to alter aspect ratio, and hence ameliorate dislodgement risk, may therefore greatly affect their impact on intertidal community structure.

In summary, *P. ochraceus* body shape appears to respond to spatial and seasonal variation in wave exposure in a way that reduces the probability of dislodgement when exposure is higher. These shape changes are likely achieved by short-term changes in the volume of water within the body. Reduced dislodgement risk via increased aspect ratio (more slender arms) may impose a cost in terms of reduced desiccation resistance or fecundity. The ability of *P. ochraceus* to adapt to short-term changes in wave-exposure likely facilitates its role as a keystone predator (Paine, 1969) both in winter, when wave forces are high and thermal stress low, and in summer, when the opposite is true.

LIST OF SYMBOLS AND ABBREVIATIONS

A_h	lateral projected area of one half of the sea star (mm^2)
A_L	average arm length (mm)
A_{MLP}	maximum lateral projected area (mm^2)
ANCOVA	analysis of covariance
A_{planar}	planar area (mm^2)
C_D	coefficient of drag
C_L	coefficient of lift
DS	Dixon Island, sheltered
F_D	force of drag (N)
F_L	force of lift (N)
h_C	height of the sea star in the centre of the body (mm)
HE	Helby Island, exposed
h_T	height at the tip of the sea stars arm (mm)
N	sample size
SE	Seppings Island, exposed
SS	Seppings Island, sheltered
V	water velocity (m s^{-1})
ρ	density of seawater (kg m^{-3})

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AUTHOR CONTRIBUTIONS

K.J.R.H. designed and performed the transplant experiment, collected and measured samples, analysed the data and wrote the original draft of the manuscript. A.R.P. suggested the original study, and provided input on experimental design, statistical analysis, data presentation, and manuscript preparation. T. MacKeracher provided helpful comments on an early version manuscript.

COMPETING INTERESTS

No competing interests declared.

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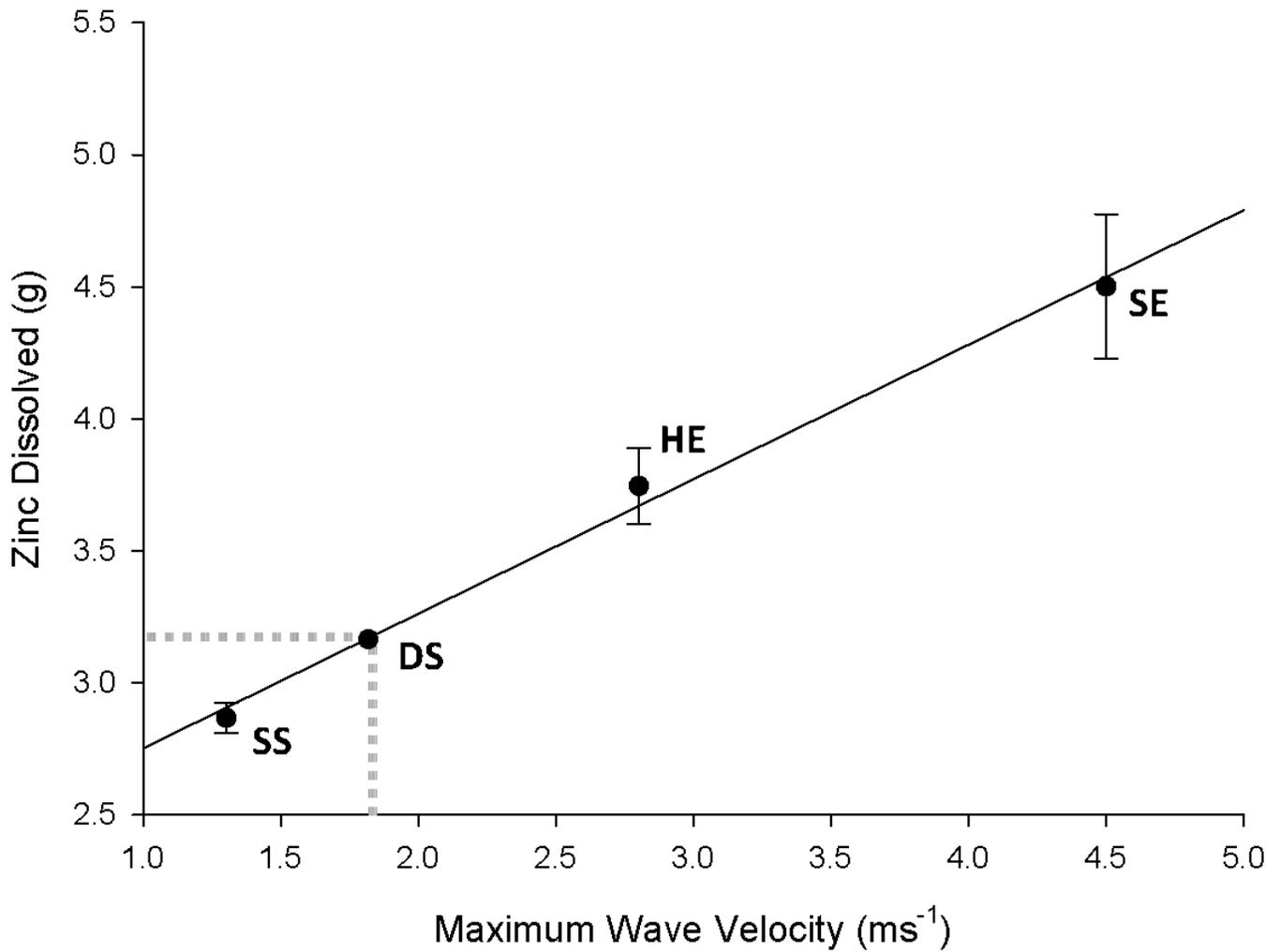


Fig. S1. Calibration curve for determination of maximum water velocity on the sheltered shore of Dixon Island (DS). Three replicate dissolution rigs were concurrently placed in all four sites for a period of 10 days. The amount of zinc dissolved from three sites (SS, HE, SE) were plotted against their known maximum water velocity from wave drogue data and the maximum velocity experienced in Dixon Sheltered (DS) was determined (1.8 m s^{-1}) by the amount of zinc dissolved at the site (3.16 g) and the calibration curve (dotted line). (calibration curve: $F_{1,11}=45.991$, $P<0.001$, $R^2=0.87$)