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Inhibitory effects of wave action on destructive grazing by sea urchins : a review

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Abstract: Wave-induced water motion is one of the key determinant factors protecting kelp assemblages from destructive grazing by sea urchins; however few studies have quantitatively evaluated the hydrodynamic effect on rocky subtidal community ecology due to the complex nature of the water motion. Our quantitative understanding of the effects of waves on urchin foraging behavior has increased substantially over the past 15 years, primarily due to flow tank experiments on the sea urchin *Strongylocentrotus nudus*, which have formed extensive urchin barrens in northern Japan. This review evaluates the mechanism and extent that the oscillatory water flow influences the behaviors of sea urchins. The dislodgement velocity for stationary sea urchins, which has been determined in various studies based on the hydrodynamic theory, is discussed. Previously predicted dislodgement velocities for sea urchins are extremely high (> ca. 5 m/s) while the velocity limit for urchin movement on a smooth and flat substratum is much lower than 1 m/s. The importance of attachment by spines to urchin movement in moving water is discussed. Dense cover of turf algae prevents the effective attachment of the distal suckers of tube feet and thus substantially reduces the critical velocity for urchin movement. Urchin climbing of upright thin objects, such as anchor ropes of buoyed systems for kelp cultivation, to which little attention has been paid, is discussed in relation to oscillatory water motion. Finally, the effect of oscillatory flow on urchin feeding is discussed.

Key words: barrens, grazing, kelp, sea urchin, waves

Introduction

Kelp beds have a fundamental role in maintaining populations of various fish and invertebrates by providing food and habitats (Tegner and Dayton, 2000; Edgar *et al.*, 2004). Many kelp species are both highly productive (Mann, 1982) and have a high nutritive value for various herbivorous animals many of which are of considerable economic importance, in particular abalone and sea urchins (Uki, 1981; Uki *et al.*, 1986; Nabata *et al.*, 1999; Scheibling and Anthony, 2001) However, sea urchins often are extremely abundant and denude the substratum of erect macroalgae, forming extensive 'urchin barrens', and this phenomenon has been recorded worldwide (Harrold and Pearse, 1987; Scheibling *et al.*, 1999).

Urchin barrens generally have low productivity (Mathieson *et al.*, 1991) and are persistent.

In northern Japan, sea urchins, such as *Strongylocentrotus nudus* and *S. intermedius*, also dominate significant areas of subtidal rocky bottom and have formed extensive urchin barrens, limiting the colonization of kelp (Nabata *et al.*, 1992; Abe and Tada, 1994; Muraoka, 2008). These urchins are legally protected as fisheries resources exclusively for the commercial fishing by the local fishermen's cooperative. Nevertheless, few urchins are harvested in barrens due to their poor growth and low quality of the edible gonad, allowing the maintenance of urchin barrens. Many attempts including sea urchin removal and the placement of physical barriers (Kawamata, 2001a), have been made for

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kelp restoration but most of them have failed, partly because of the high mobility of sea urchins.

The wave-induced oscillatory water motion, which increases with decreasing depth, is one of the most important factors controlling urchin grazing. Sea urchins undoubtedly have the ability to move on any type of substrata, including rock overhangs, rugged mussel beds, algal turf areas, plastic netting fences and upright thin ropes, by maneuvering their tube feet and spines. However, sea urchins are rare in wave-exposed shallow areas, allowing macroalgae to survive and grow, with the presence of abundant urchins in the adjacent barrens. Such a distributional pattern of kelp beds and urchin barrens is common in the temperate zone. In rocky subtidal areas on the northeastern Pacific coast of Honshu, the main island of Japan, the sea urchin *Strongylocentrotus nudus*, forms extensive and persistent urchin barrens, but wave-exposed shallow reefs are generally dominated by kelp such as *Eisenia bicyclis*. Although many ecologists have described the importance of wave action in the rocky subtidal community structure, few studies have quantitatively assessed it, partly because wave-induced water motion is highly variable over time and complex. In principle, however, wave-induced water motion can be measured and predicted by engineering techniques, and thus quantitative assessment will provide useful insights into not only the spatial distributions of urchins and algae but also practical methods for kelp restoration.

Our quantitative understanding of the effects

of waves on urchin behavior has increased substantially over the past 15 years, primarily due to flow-tank studies. I have used two different flow tanks for urchin-behavioral studies. The first an oscillating flow tank, which is a U-shaped pipe with a piston, reproducing wave-induced oscillatory flows. In addition, a circuit flume tank which can reproduce standing waves with a reversible impeller. In this review, I discuss the hydrodynamic effects on urchin behaviors in relation to attachment, movement and feeding.

Attachment

The ability of a benthic organism to withstand strong water motion depends on its attachment strength relative to the hydrodynamic forces. Sea urchins apparently achieve greatest attachment strength by the use of both their spines and tube feet for bracing and adhesion in shelter holes or crevices. During foraging outside of shelters, the use of spines in bracing is necessarily reduced, thus making the tube feet the primary mechanism of attachment (Lissner, 1983; Kawamata, 1998). A stationary organism in unsteady, oscillatory water motion experiences the acceleration force in addition to the forces (i.e., drag and lift) caused by instantaneous water velocity (Denny, 1988). At intertidal sites, the acceleration force imposed on a stationary organism is significant because the water acceleration can be extremely high, over 100 m s^{-2} (Denny, 1985; Gaylord, 1999). At subtidal

Table 1. Dislodgement velocity for sea urchins

Species	Dislodgement velocity (m/s)	Reference
<i>Echinometra mathaei</i>	6.3 ¹⁾	Denny and Gaylord (1996)
<i>Strongylocentrotus purpuratus</i>	15.4 ¹⁾	Denny and Gaylord (1996)
<i>S. droebachiensis</i>	5.0 ¹⁾	Siddon and Witman (2003)
<i>Arbacia lixula</i>	5.5 ²⁾	Santos and Flammang (2007)
<i>Sphaerechinus granularis</i>	4.6 ²⁾	Santos and Flammang (2007)
<i>Paracentrotus lividus</i>	8.2 ²⁾ , 6.1–7.0 ³⁾	Santos and Flammang (2007)

¹⁾ Prediction at which 50% urchins will be dislodged.

²⁾ Prediction for the maximum attachment force which an urchin should achieve by attaching with all their adoral tube feet.

³⁾ Prediction for attachment forces measured in the field.

sites, however, the acceleration force is virtually negligible, because when wave-induced orbital velocity reaches a maximum, water acceleration becomes zero, and because the wave-induced water acceleration is much lower than the gravitational acceleration of 9.81 m s^{-2} (Barber, 1969; Kawamata, 2001b). Thus, an estimate of the dislodgement velocity, defined as the critical velocity at which an organism will be dislodged, is obtained as the velocity at which the velocity-induced force becomes equal to the attachment strength. Dislodgement velocities predicted in this manner for urchin species are summarized in Table 1.

The wave-induced water velocity in subtidal areas is limited by water depth. The maximum water velocity, U_{max} , caused by waves in shallow water is

$$U_{\text{max}} = 0.3 \sqrt{g(H + d)} \quad (1)$$

where g is the acceleration due to gravity ($= 9.81 \text{ m s}^{-2}$), H the wave height, and d the water depth (Denny, 1988). The wave height increases with

decreasing depth but is limited due to the wave breaking. Although the ratio of the wave height to depth at breaking varies in a complex relation with the bottom slope and the steepness of waves,

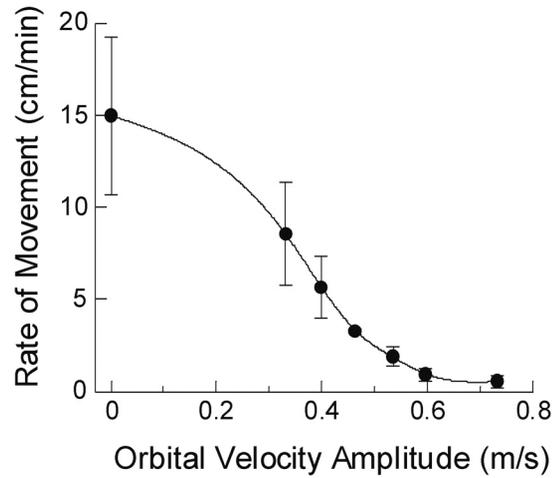


Fig. 1. Maximum rate of movement of *Strongylocentrotus nudus* in oscillatory flow (Kawamata, 1998).

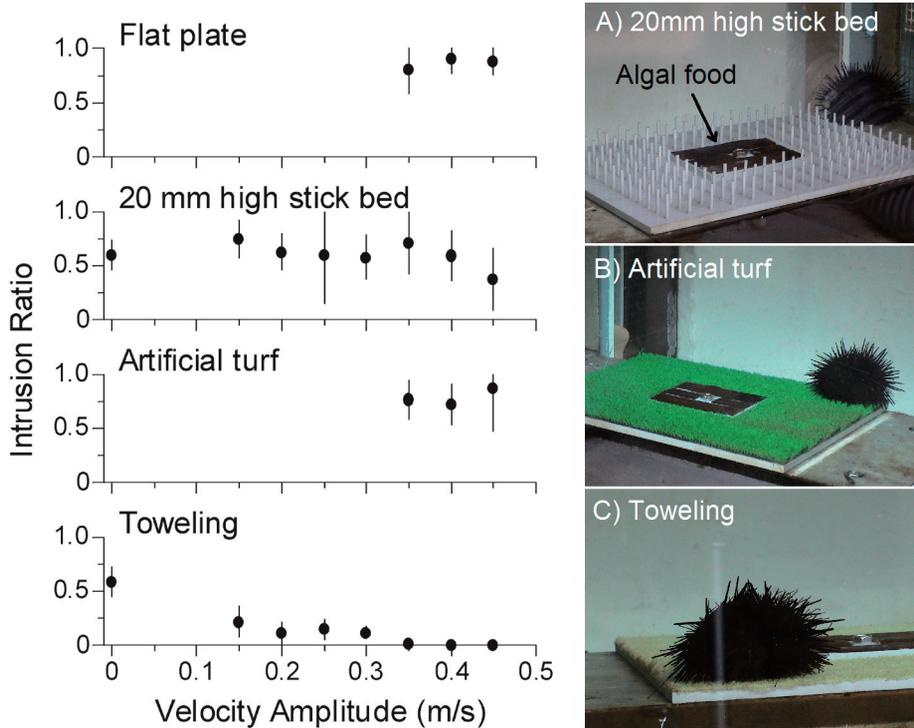


Fig. 2. Intrusion ratios of *Strongylocentrotus nudus* for the control flat plate and experimental substrata in different velocity amplitudes (Kawamata and Furuhashi, unpublished data). Error bars indicate 95 % confidence intervals.

possible ratios are limited to as high as 1.4 for steep slopes (Denny, 1988). Thus, the maximum possible water velocity is

$$U_{\max} = 0.46 \sqrt{g d} \quad (2)$$

It is predicted from Eq. 2 that the dislodgement velocity of sea urchins is very unlikely to occur in subtidal areas. For example, when $d = 4$ m, U_{\max} is only 2.9 m/s. Taking into account the additional attachment strength due to bracing of spines, the distributional area of sea urchins generally cannot be limited by the wave-induced dislodgement while being stationary.

Benthic movement

During movement, urchins are much more subject to the effects of water motion than when attached while being stationary. Fig. 1 shows the maximum rate of movement by *Strongylocentrotus nudus*, which was stimulated with a spot light in oscillatory flows. The urchins showed minimal ability to move at about 0.7 m/s. Attachment to the substratum by tube feet is a primary factor affecting the mobility of sea urchins. This was found by the oscillating-flow-tank experiment (Kawamata and Furuhashi, unpublished data) which tested the inhibitory effects on sea urchin invasion over several types of substrata, including a stick bed, artificial turf and toweling (Fig. 2A, B and C). Contrary to initial speculation, only toweling had a clear effect on urchin invasion, as shown in Fig. 2. The ordinate

represents the intrusion ratio, defined as the ratio of the number of the 'intrusion successes' (mounting a test substratum entirely) to that of the 'intrusion trials' (contact with the edge of the substratum). The intrusion ratio remained as high for the stick bed and for the artificial turf as for the control flat plate at a velocity amplitude of 0.35 m/s. In contrast, the ratio was significantly lower for toweling than for the stick bed even at as low as 0.15 m/s. The mechanism for toweling to inhibit urchin invasion is very simple. Tube feet attach to the substratum with their distal suckers. On toweling, however, the suckers fail to achieve an effective attachment to the fabric texture of the toweling, so that urchins cannot easily move in moving water.

A good example of such substratum effect in nature is the colonization of barren substratum by rapid-growing turf algae prior to the formation of kelp *Laminaria religiosa* stands on the Sea of Japan coast of Hokkaido, northern Japan. The kelp generally dominates the wave-exposed shallow area from mid winter to early summer, while after summer *Strongylocentrotus nudus* denude the substratum of erect macroalgae up to the upper limit of the subtidal area forming extensive barrens. In the absence of non-crustose algae, sea urchins forage even to the uppermost part of the subtidal zone exposed to surging waves (Fig. 3A). When an algal carpet is formed, however, then sea urchins are excluded from the area, even at calm sea conditions (Fig. 3B).

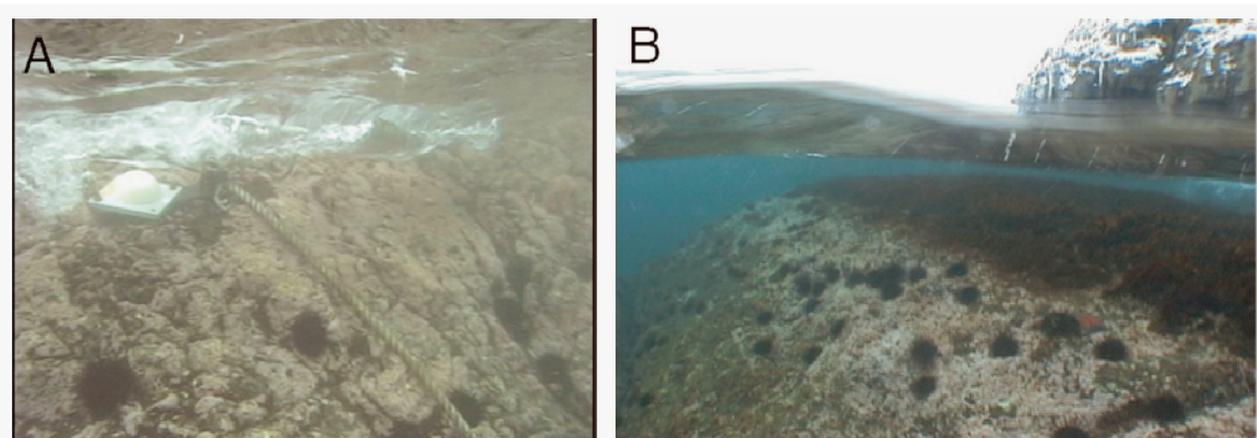


Fig. 3. The uppermost part of the subtidal on the Sea of Japan coast of Hokkaido immediately before (A; 27 December 1999) and after early colonization of algae (B; 4 January 2000) (Kawamata, 2001a).

Vertical movement

Little was known about vertical movement in sea urchins, and line cultivation methods have been used in urchin barrens without much consideration for the climbing ability of sea urchins. Actually, however, sea urchins climb even thin vertical ropes as long as food is limited on the seabed (Fig. 4). A recent laboratory study (Kawamata, 2008) showed the high climbing performance of *Strongylocentrotus nudus* in oscillatory flows using upright rods of 10 and 3 mm diameters with algal food items attached at 2.5 cm intervals. In this case, sea urchins climbed the rods to graze on food items from the bottom one by one although they did not always reach the top food item. In the absence of oscillatory flows, urchins readily climbed and grazed on almost all the food items even for thin rods. Urchin climbing was reduced in height and in frequency as the velocity amplitude increased. However, the animals were able to climb even at 0.4 m/s regardless of the rod diameter.

A flume tank experiment was also conducted

on the climbing performance of *S. nudus* for swingable and fixed columns covered by microalgae in oscillatory flow (Fig. 5). Contrary to initial speculation, sea urchins also climbed the swaying upright objects if food was un available elsewhere.

Feeding

Feeding is even more susceptible to water motion than movement because the mechanical instability of sea urchins increases during feeding as follows. Sea urchins have their mouth at the center of their attachment base so that they must detach more than half the number of their tube feet used to cling to the substratum while feeding. At the same time, the animals must overcome the additional drag on algae. Therefore, the upper velocity limit for feeding on foliose macroalgae is lower than that for movement (Kawamata, 1998). Oscillating-flow-tank studies (Kawamata, 1998; 2001a) indicated that the velocity limit for feeding may somewhat vary with animal size and algal morphology but is limited to less than ca. 0.4 m/s.

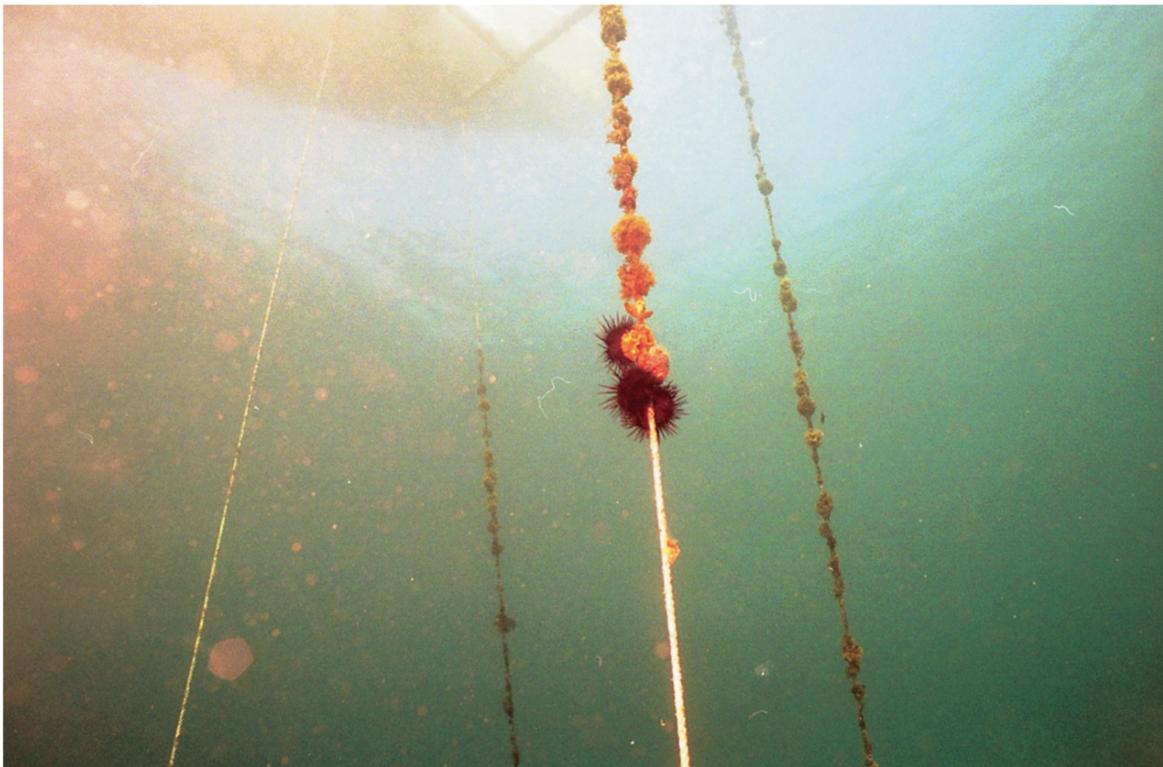


Fig. 4. Sea urchins (*Strongylocentrotus nudus*) climbing anchor ropes to feed on algae in an urchin barren of Miyagi, Prefecture northeastern Pacific coast of Honshu.

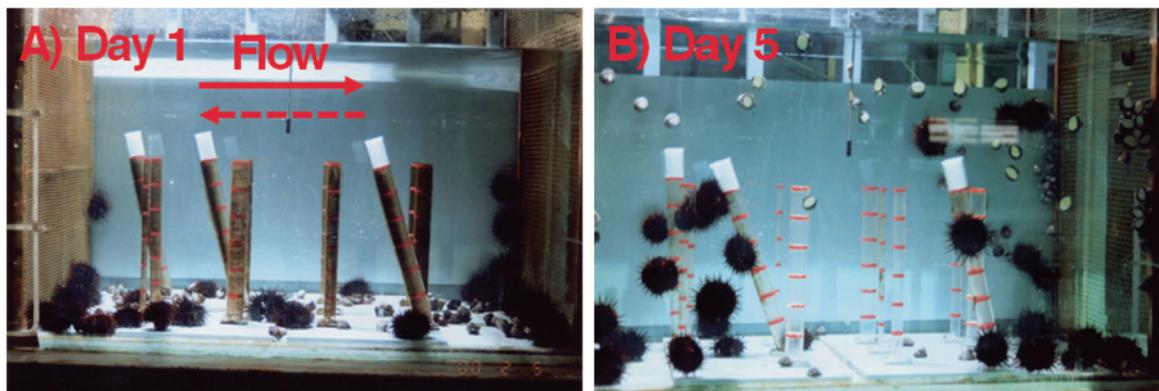


Fig. 5. Sea urchins (*Strongylocentrotus nudus*) climbing on swingable as well as fixed rods in the oscillatory flow with the velocity amplitude of 0.15 m/s (Kawamata unpublished data). The microalgae had initially covered the entire surface of both kinds of rods (A) and then were almost completely grazed by climbing urchins on day 5 (B).

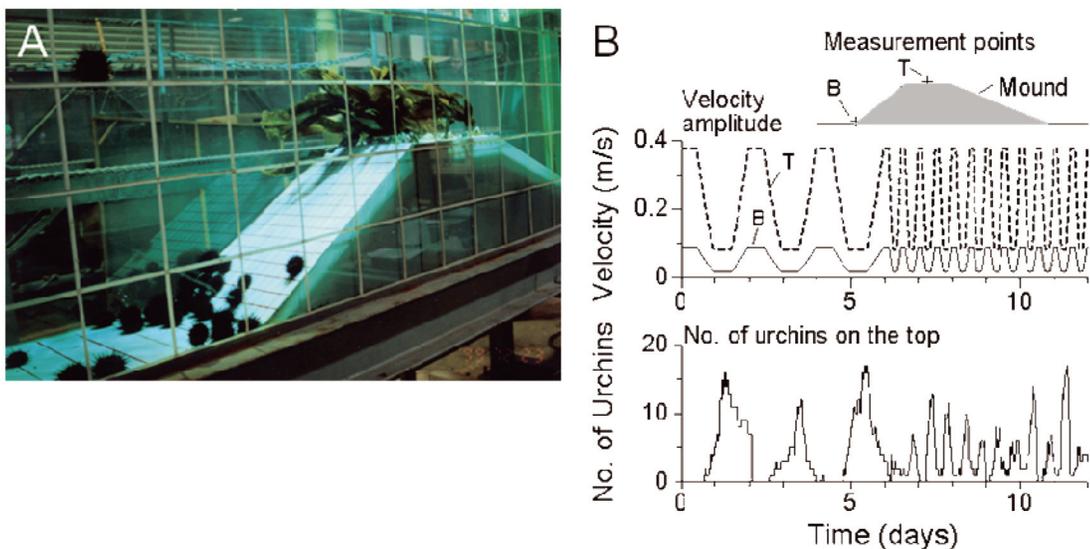


Fig. 6. A flume tank experiment on the foraging behavior of the sea urchin *Strongylocentrotus nudus* in the vicinity of a *Laminaria* bed placed on the top of a mound (Kawamata, 2001a).

In addition, the wave-induced movement of macroalgal fronds, called the “whiplash” effect, may repel urchins away from macroalgal stands. Although many studies described the importance of the whiplash effect in the survival of algal stands in dense urchin barrens (e.g. Velimirov and Griffiths, 1979; Himmelman, 1984; Dayton, 1985; Konar, 2000; Gagnon *et al.*, 2003; Konar and Estes, 2003), few studies have quantitatively assessed the water motion which cause the movement of algal fronds (Kawamata, 1998; 2001a; Gagnon *et al.*, 2006). Kawamata (2001a) conducted a flume tank experiment on the behaviors of *S. nudus* around a

Laminaria bed placed on the mound under waves (Fig. 6). In the experiment, strong and weak wave periods were repeated over a 12 day period in the pattern shown in Fig. 6. The velocity amplitude at the top of the mound where kelp plants were placed was higher than that at the bottom of the mound. The movement of the urchins up and down the slope in response to the change in water velocity was clear from the results aggregated at the edge of the kelp stands as the water motion decreased. On the contrary, they began to move back away from the stands when the velocity amplitude increased beyond only 0.1 m/s.

Conclusion

Foraging activity of sea urchins is greatly affected by wave action through limiting movement and feeding rather than through dislodgement. The effects of waves on urchin behaviors can be quantitatively understood by laboratory flow-tank experiments, while wave-induced water motion is too complex to readily assess in nature. Such quantitative information coupled with the assessment of water motion will provide insights not only into urchin-kelp interactions but also into useful methods for kelp restoration in urchin barrens.

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