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JUVENILE MUSSEL AND ABALONE PREDATION BY THE LINED SHORE CRAB *PACHYGRAPSUS CRASSIPES*

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ABSTRACT Major rocky intertidal predators in the northeast Pacific such as sea stars, whelks, and birds can consume foundation species such as mussels and thereby affect zonation patterns and diversity in these habitats. Predation specifically on juvenile intertidal invertebrates can also substantially impact population dynamics and influence community structure. The lined shore crab *Pachygrapsus crassipes* (Randall, 1840) is an abundant denizen of sheltered and exposed intertidal habitats in the northeast Pacific from Canada to Mexico. This study examined potential *P. crassipes* predation on juvenile mussels (*Mytilus galloprovincialis*), whelks [*Nucella ostrina* (Gould, 1852)], and abalone [*Haliotis rufescens* (Swainson, 1822)] due to conflicting reports on the diet of this species. Crabs consumed more juvenile mussels and abalone than seaweed (*Ulva lactuca*) and fed preferentially on the smallest mussels (6- to 10-mm size class). Further experiments showed that predation on mussels by *P. crassipes* was highly size dependent, with the largest crabs consuming over twenty-five 15-mm mussels per day. Field outplant experiments revealed that *P. crassipes* consumed high numbers of juvenile mussels in a natural setting, meaning that it could substantially affect mussel recruitment. This crab species appears to be an opportunistic predator that could have significant impacts on the recruitment and early life history of several invertebrate prey species.

KEY WORDS: predation, crab, *Pachygrapsus crassipes,* mussel, abalone, juvenile

INTRODUCTION

Predation can play a large role in controlling community structure and is particularly important in the rocky intertidal zone, where predators such as sea stars (Paine 1966) and whelks (Connell 1970, Menge 1976) have pronounced impacts in these space-limited habitats. By consuming competitively dominant mussels, rocky shore predators can mediate competition for space and thus influence community composition. Mussels are consumed by a wide range of predators in the rocky intertidal, including sea stars, whelks, spiny lobsters (Robles et al. 1990, Robles 1997), Asian shore crabs (Kraemer et al. 2007), and several species of birds (Marsh 1986, Wootton 1997). These predators can affect population structure and shape the zonation patterns of their prey, in some cases leading to higher prey densities in high intertidal habitats that serve as a refuge from predation (Paine 1976, Yamada & Boulding 1996).

The impact of predation on juveniles is not as well understood or documented because of the wide range of predators, lack of predator specialization, seasonality of juvenile abundance, and inherent small size of juveniles, but juvenile mortality due to predation can be severe. In a survey of predation on juvenile invertebrates, Gosselin and Qian (1997) found that two-thirds of species studied had over 90% juvenile mortality, with most of this attributed to decapod predation. High rates of early juvenile mortality can affect not only adult abundance and population size, but also population characteristics such as reproductive output and age at maturity (Gosselin & Qian 1997). One small crab species that has been implicated in causing juvenile mortality in snails and urchins is the lined shore crab *Pachygrapsus crassipes* (Armitage & Fong 2006, Clemente et al. 2013).

Although it has been described as ''pugnacious'' by Ricketts et al. (1985) and is highly abundant in exposed and sheltered rocky habitats of the northeast Pacific (Hui 1992, Cassone & Boulding 2006), some studies describe *Pachygrapsus crassipes* as an herbivore or scavenger, consuming primarily diatom films, algae (e.g., *Ulva* spp.), and detritus (Hiatt 1948, Barry & Ehret 1993). More recent studies recognized the predation potential of this species and examined its feeding on juvenile urchins (*Strongylocentrotus purpuratus*) (Clemente et al. 2013) and snails (*Cerithidea californica*) (Armitage & Fong 2006).

The present study focused on potential predation by *Pachygrapsus crassipes* on juvenile rocky intertidal invertebrates, primarily the mussel *Mytilus galloprovincialis*. This mussel is a common invasive species and is the most abundant mussel in the bays and estuaries of southern and central California, where *P. crassipes* is also present (Wonham 2004, Braby & Somero 2005). Because *P. crassipes* can consume juvenile snails and urchins (Armitage & Fong 2006, Clemente et al. 2013), a combination of laboratory and field experiments was used to test the hypothesis that *P. crassipes* was a predator of a range of juvenile invertebrates including abalone, mussels, and whelks.

MATERIALS AND METHODS

Laboratory Experiments

A combination of laboratory and field experiments was conducted with crabs collected in rocky cobble habitats in Moss Landing, CA (36.80715N, –121.78680W), where mussels (*Mytilus galloprovincialis*), algae (*Ulva lactuca*), and whelks (*Nucella ostrina*) were also collected. Laboratory experiments were performed in the flowing seawater laboratory at the Monterey Bay Aquarium Research Institute in Moss Landing, CA, during April 2016. Juvenile abalone (*Haliotis rufescens*) were purchased from the Monterey Abalone Company.

To assess potential predation by *Pachygrapsus crassipes*, crabs were exposed to two ecologically important rocky shore mollusc species with different types of shells: juvenile mussels (*Mytilus galloprovincialis*) and whelks (*Nucella ostrina*), as well as commercially important juvenile red abalone (*Haliotis rufescens*) (Vilchis et al. 2005). Mussels were the primary focus because they are the dominant space competitor in the northeast Pacific

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rocky intertidal (Paine 1966) and are ubiquitous in the range of *P. crassipes*. The bay mussel *M. galloprovincialis* was used because it is a commercially important, broadly distributed invasive species, and because collection and experimental sites were in a protected harbor, where *M. galloprovincialis* is the predominant mussel (Braby & Somero 2005). In Monterey Bay and regions to the south, outer shores are typically dominated by the mussel *Mytilus californianus*, whereas *M. galloprovincialis* is most common in bays, harbors, and estuaries (Wonham 2004, Braby & Somero 2005).

For feeding experiments, 10 replicate square 1-gallon tanks were used, with each tank containing continuously aerated 14°C seawater, a small rock for shelter, one crab, six juvenile mussels [10-mm shell length (SL)], two larger mussels (20 mm SL), two juvenile abalone (15 mm SL), two juvenile whelks (15 mm SL), and a 30 cm^2 piece of *Ulva lactuca*, which is a preferred algal food source for *Pachygrapsus crassipes* (see synonymized *Enteromorpha* in Barry & Ehret 1993). The relative amounts of each species were chosen to make them roughly equivalent in terms of caloric value, with caloric content estimated from published values for each prey item (or a similar species in the same genus) (Paine & Vadas 1969, Okumus & Stirling 1998, Gómez-Montes et al. 2003). All crabs were starved for 5 days prior to feeding experiments. Feeding was checked after 24 h to determine which species and sizes had been eaten, and then the estimated caloric value of the material eaten was calculated for each of the 10 crabs during the experimental period to get an estimate of the feeding capability of *P. crassipes*. The area of *U. lactuca* was measured before and after the experiment to determine how much seaweed the crabs consumed. Seaweed area was used instead of weight because weight is highly dependent on water content and was less reliable (similar methods used in Dick et al. 2005). Additionally, a seaweed growth control under these laboratory conditions showed an increase in size of about 1% per day, a negligible amount over a 24-h experiment. The amount of all prey consumed was tested statistically with a one-way ANOVA for correlated samples.

A controlled tidal system in the laboratory (at 14°C) was used to test *Pachygrapsus crassipes* predation of *Mytilus galloprovincialis* at different tidal levels. This tidal experiment was designed to compare predation rates of *P. crassipes* on mussels that were (1) continuously submerged or (2) only submerged for 6 h at high tide. The seaweed *Ulva lactuca* was provided as a food option in these experiments. A tidal system was built using a solenoid valve to control seawater flow from a header tank at 1 l/min to 10 experimental tanks, which were 3-gallon circular plastic tubs with a wall height of 30 cm. Each tank contained two 5-sided mesh trays with open tops (3 cm × 3 cm × 1 cm) that twenty 1-cm-SL mussels were placed inside at the start of the experiment (to keep them from straying); one cage continuously submerged on the base of the tank, and the other elevated on a PVC stand so that it was submerged only at high tide. After 24 h, the number of remaining mussels in the high and low tidal level cages within each of the 10 tanks was checked to compare feeding rates. Air temperatures were similar to water temperatures in this tidal setup, and crab feeding and respiration rates can vary with air temperature, so this experiment could not assess tidal differences in feeding for situations with different air and water temperatures (Spivak et al. 1996, Stillman & Somero 1996).

Follow-up feeding experiments were conducted in September 2016 to further parameterize size-dependent feeding rates and preferred prey (mussel) sizes for *Pachygrapsus crassipes*. Mussels and crabs were collected from the same locations as prior experiments and were acclimated to laboratory conditions for 5 days prior the experiments. The effect of *P. crassipes* size on feeding was tested in ten 6-l aerated seawater tanks with crabs ranging from 17 to 36-mm carapace width (CW); thirty 15-mm–SL mussels were provided, and feeding was checked after 24 h at an ambient seawater temperature of 14°C. To examine the impact of mussel size on crab feeding, the same experimental setup was used, with αππρώιμαθηλξ 25-mm-CW crabs and 10 mussels in each of the following size classes: 6–10, 11–15, 16–20, 20–25, 25–30 mm SL. Size preference results were analyzed with a one-way ANOVA for correlated samples. Feeding preference of *P. crassipes* was compared between mussel species using this same 24-h feeding assay with ten 15-mm-SL *Mytilus californianus* and *Mytimohlus galloprovincialis* mussels.

Field Experiments

To test potential predation by *Pachygrapsus crassipes* on juvenile mussels in the field, field outplant experiments were conducted. A preliminary test was performed 1 wk before deployment, with 10 juvenile mussels placed on a submerged rock at the chosen site, and all 10 were eaten by 6 *P. crassipes* within 15 min. Field-collected mussels (10-mm SL) were allowed to attach to 10 cm × 10 cm PVC panels which were covered in 0.5-cm nylon mesh that was attached with cable ties. Forty mussels were placed on each panel (24 panels) in the laboratory seawater system and were given 3 days to attach to the panels with byssal threads. For field deployment, three treatments were used: open (no cage), half cage, and full cage around each panel covered in mussels. Cages were constructed using stainless steel hardware cloth (1-cm openings), with full cages wrapping around all sides of the panel. Half cages had a top and two sides, but the other two sides were left open to allow small crabs (*P. crassipes*) access but block predation from large crabs, large fish, birds, or otters. Open treatments had no cage at all covering the panel.

Experimental panels were deployed in the field in May 2016, with the corners of all panels wedged under rocks at a sheltered location in Moss Landing Harbor with high density of *Pachygrapsus crassipes*. The field site also had a substantial amount of *Ulva* spp. and other drift seaweed, no mussel populations within 100 m, and had insignificant current because it is a dead-end arm with rock walls on three sides. Panels were all arranged haphazardly between +0.5 and +1 m tidal level, and one set was set up in view of a GoPro camera with underwater housing that was used to take photos of the experimental setup every minute to ascertain which species were the primary predators of the provided food platter. Panels were deployed on a –0.15 m (MLLW) low tide at approximately 9 AM on May 14, 2016; the daytime high air temperature was 17°C, and the seawater temperature was 13°C. Panels were retrieved on the morning low tide 24 h after deployment and predation was measured by counting all remaining mussels. A similar experiment was attempted at wave-exposed sites, but the mussels in all cages were washed off of the panels.

RESULTS

Laboratory Experiments

In predation experiments where *Pachygrapsus crassipes* was presented with multiple food choices, crabs consumed the largest amount (by caloric value) of juvenile mussels (0.11 ± 0.021 kcal, x̄ ± SE), followed by juvenile abalone (0.088 ± 0.032 kcal) and seaweed (0.031 ± 0.033 kcal) (Fig. 1) (one-way ANOVA for correlated samples, $F_{(2,18)} = 5.28$, $P = 0.016$). *Post hoc* tests revealed significantly more consumption of mussels than seaweed (Tukey HSD, $P < 0.05$). Crabs did not consume any whelks (*Nucella ostrina*) or large (20 mm SL) mussels in this experiment.

In the tidal experiment, crabs ate a negligible amount of seaweed and displayed little difference in feeding on mussels between the two levels (low = 12.5/day, high = 12.4/day), with a maximum of forty-nine 10-mm mussels consumed by one crab (24.9 ± 4.56 mussels).

Feeding rate of *Pachygrapsus crassipes* was positively and significantly correlated with crab size (CW), as the largest crabs consumed over twenty-five 15-mm mussels per 24 h (linear regression, $F = 10.0$, $P = 0.02$, $R^2 = 0.625$) (Fig. 2). Mussel size was also important, as size preference experiments revealed significantly higher predation on 6- to10-mm mussels than any other size class (one-way ANOVA for correlated samples, $F_{(4,36)} = 53.2$, $P < 0.0001$) (Fig. 3). Crabs strongly preferred *Mytilus galloprovincialis* over *Mytilus californianus* in choice experiments, as they consumed solely *M. galloprovincialis* at the 15-mm size that was provided.

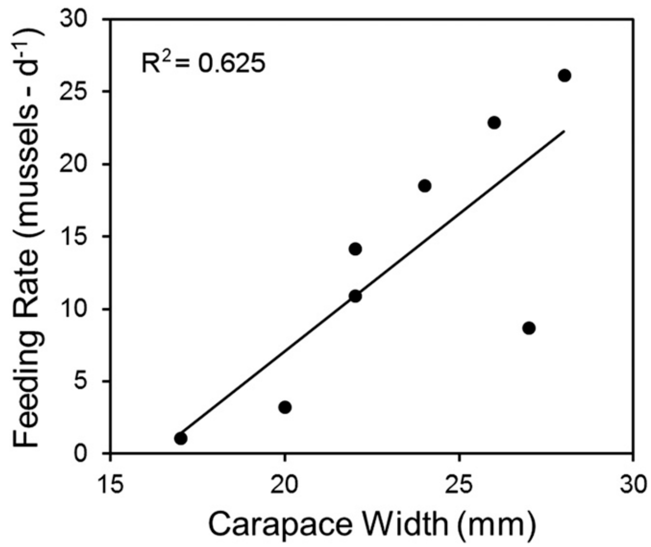

Figure 2. Feeding rate of *Pachygrapsus crassipes* on juvenile mussels. Crab size (CW) was positively correlated with the number of 15-mm mussels consumed per 24 h.

Field Experiments

Field outplant experiments showed strikingly high field predation rates on juvenile mussels that were placed in areas of high *Pachygrapsus crassipes* density. After 24 h in the field, only 3 of the 480 juvenile mussels on open panels (0.20 per panel) or in half cages (0.25 per panel) remained, whereas the vast majority of the 40 initial mussels were still present on the full cages (34.4 ± 2.87 per panel) (Fig. 4). This indicated that although approximately 5 mussels per panel were either washed away, crawled away, or were eaten through the cage, there was a high level of predation—no open or half-caged panel had more than 2 out of 40 mussels remaining, and even those were wedged under the cable tie holding the mesh to the panel. Furthermore, time-lapse photography on one set of panels revealed little to no predation during the low tide of deployment, but all 40 mussels on the open and half-cage panels were eaten by *P. crassipes* within 1 h of panels being submerged by the rising tide. The photos also showed the pattern that was visually observed in the field; *P. crassipes* consuming algae at low tide, then the mussels at high tide. As many as six *P. crassipes* crabs were observed in photos feeding on experimental mussels at once; no other predators were observed on camera. Although the field site had very low flow, the photos verified (for one set of panels) that the mussels in the open and half cages were eaten by crabs (not washed away).

DISCUSSION

The central finding of this study was that the lined shore crab *Pachygrapsus crassipes* can be a major predator of several juvenile rocky intertidal invertebrates, especially mussels (*Mytilus galloprovincialis*). Previous studies included conflicting reports of herbivory (Hiatt 1948, Barry & Ehret 1993) and predation (Armitage & Fong 2006, Clemente et al. 2013), but

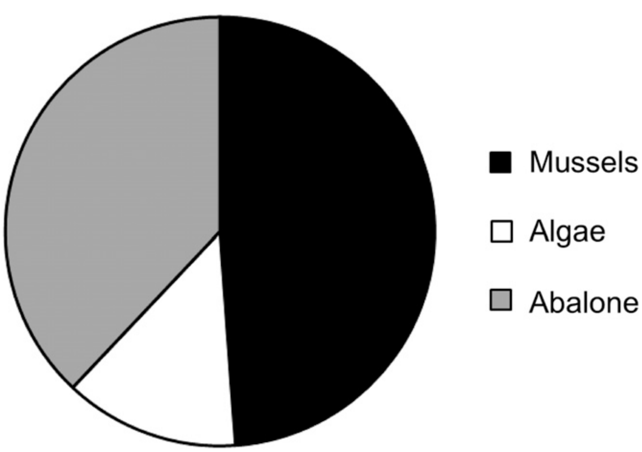

Figure 1. Pie chart showing relative caloric values of prey items consumed by *Pachygrapsus crassipes* in laboratory food preference experiments. Crabs ate the most juvenile mussels (*Mytilus* spp.), followed by juvenile abalone (*Haliotis rufescens*) and algae (*Ulva lactuca*).

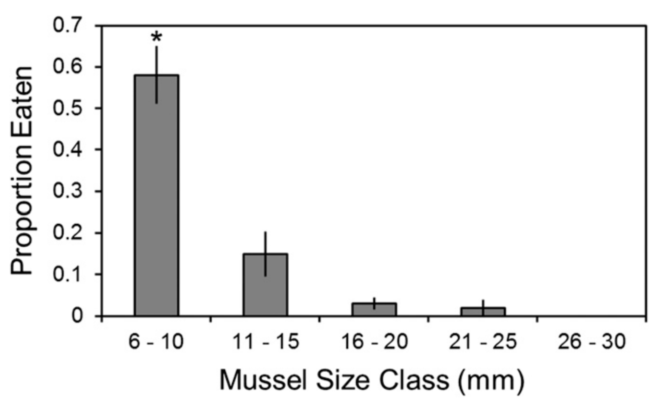

Figure 3. Prey size preference for *Pachygrapsus crassipes*. Crabs clearly preferred smaller mussels (SL) during the 24-h feeding trial (±SE).

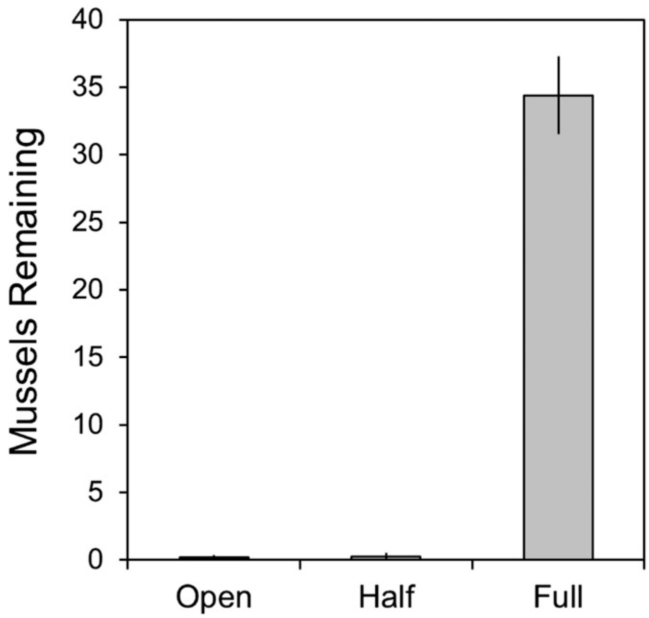

Figure 4. Mussels remaining after field experiments that exposed 40 juvenile (10-mm SL) mussels per experimental panel to predation in an intertidal location with a high density of *Pachygrapsus crassipes*. Mussels on open panels with no cage and half-cage panels were almost all consumed, whereas approximately 35 of 40 mussels remained after 24 h in the full cage treatment ($n = 8$) ($\pm$SE).

this study was the first to describe predation on juvenile mussels, abalone, and whelks. This is not the first study to find that *P. crassipes* can be a predator, but they are commonly spotted consuming macroalgae or scraping algae off rocks at low tide (Ricketts et al. 1985). Nevertheless, they may just exhibit this behavior at low tide and in situations when higher quality food such as juvenile invertebrates is not readily available, as experiments in the present study showed higher consumption of juvenile mussels and abalone compared with the seaweed *Ulva lactuca* (Fig. 1).

Crabs may prefer juvenile invertebrates to seaweed in some settings because of the higher caloric value of animal tissue (Paine & Vadas 1969, Okumus & Stirling 1998, Gómez-Montes et al. 2003). They may have evolved an innate preference for high-calorie prey when these prey are available, but this is purely speculative, as little is known about the mechanism underlying crab feeding preference. Seaweed was more abundant in Moss Landing harbor where the present study was conducted, so the mussel consumption was not likely due to higher availability of invertebrates. Crabs ate little seaweed in feeding experiments when an excess of juvenile mussels was also provided. This is not to suggest that *Pachygrapsus crassipes* does not consume algae in the field, but it appears that juvenile invertebrates like mussels and abalone are a preferred option when they are available. Observations and time-lapse photos in the field suggested that most mussel predation by *P. crassipes* occurred at high tide, which may be because the water protects them from the threat of bird predation (Marsh 1986, Wootton 1997). As such, a more ubiquitous and easy to handle food source such as algae may be preferred in the field at low tide, when handling mussels or abalone could lead to greater exposure to predators. Laboratory tidal experiments in the present study did not reveal a difference in crab feeding by tidal level, but the timing of feeding (at high versus low tide) was not observed and air temperature was similar to water temperature, so the applications to field intertidal habitats were limited. The tidal and diurnal phasing of crab feeding deserves far greater study, as feeding assumptions are largely based on what researchers observe during daytime low tides.

There may also be a strong wave exposure gradient in *Pachygrapsus crassipes* predation, as feeding on wave-exposed shores likely only occurs at low tide because moving around in a wave-swept environment increases the chances of being washed off of rocks (Stutz 1978, Lau & Martinez 2003). In addition, the preference of *P. crassipes* for *Mytilus galloprovincialis* over *Mytilus californianus* at 15-mm SL suggests that crab impacts would be larger in protected areas where thinner-shelled mussel species are more abundant. If crabs consume mussels primarily when they are submerged in calm water conditions (as observed in this study), then the effect of *P. crassipes* predation on juvenile mussels would be strongest in sheltered habitats such as estuaries, bays, and harbors. Nevertheless, crabs may be able to consume smaller, newly settled mussels of any species at high rates even at low tide, which would increase their potential impact in wave-exposed areas.

High levels of predation on juvenile mussels by *Pachygrapsus crassipes* in laboratory and field (Figs. 2–4) experiments suggest that *P. crassipes* may not only be a major predator of juvenile mussels, but that it could have enough of a predation effect to shape ecological patterns on rocky shores. The high density of *P. crassipes* (PISCO surveys found 58 rocky intertidal sites with at least 10 *P. crassipes* per m^2, without even sampling harbors and estuaries) combined with its relatively high feeding rates could decimate newly settled mussels. Crabs in the present study consumed approximately twenty-five 10-mm-SL mussels per day, and this number is likely far higher for mussel recruits which would have a smaller size, shorter handling time, and weaker attachment strength than the experimental mussels in the present study. Mussel recruitment rates can approach 100,000-m^{-2}-day on the outer shores of the northeast Pacific (Broitman et al. 2008) so may overwhelm predators at some sites on a seasonal basis, but sites with intermediate levels of recruitment could experience substantial predation effects of *P. crassipes*. The results of this study cannot provide accurate estimates of predation rates on mussel recruits, but the characterization of *P. crassipes* as an opportunistic predator of juvenile invertebrates suggests that newly recruited mussels could be a significant (though temporally patchy) component of its diet.

Predation on ubiquitous mussels has a been a major focus of intertidal ecology for over 50 years (Paine 1966, Menge 1976, Connell 1970, Robles et al. 1990), but predation on small juvenile invertebrates is not as well documented (Gosselin & Qian 1997). Even large invertebrates are susceptible to a wide range of predators as juveniles and this can lead to predation-related mortality of over 90% in many species, so predators that focus on juveniles and new recruits could have broad impacts on ecological communities. Along these lines, Robles et al. (1990) highlighted the ability of a relatively novel intertidal predator (spiny lobsters) to prey heavily on juvenile mussels and cause shifts in population size structure. Lined shore crabs have not been considered an important predator due to their high level of algae consumption (Hiatt 1948, Barry & Ehret 1993) and limited studies of its predation rates. The finding that *Pachygrapsus* *crassipes* is a voracious predator on juvenile mussels in the laboratory and the field suggests that this crab species is an opportunistic predator that could play a major ecological role in rocky intertidal habitats in the northeast Pacific, affecting recruitment and juvenile mortality of mussels and other invertebrates.

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