Regulation of Keystone Predation by Small Changes in Ocean Temperature

Eric Sanford

Key species interactions that are sensitive to temperature may act as leverage points through which small changes in climate could generate large changes in natural communities. Field and laboratory experiments showed that a slight decrease in water temperature dramatically reduced the effects of a keystone predator, the sea star *Pisaster ochraceus*, on its principal prey. Ongoing changes in patterns of cold water upwelling, associated with El Niño events and longer term geophysical changes, may thus have far-reaching impacts on the composition and diversity of these rocky intertidal communities.

It is predicted that increasing global temperatures will shift species’ geographic ranges to higher latitudes or altitudes (1). On a local scale, communities may undergo gradual changes in composition as species with affinities for warmer temperatures become more abundant. However, temperature changes may have more immediate effects on local populations by altering the interaction between a species and its competitors, mutualists, predators, prey, or pathogens (2). Often a few key interactions contribute disproportionately to maintaining the composition and functioning of a community or ecosystem (3). If these interactions are sensitive to temperature, small climatic changes could generate system-wide ecological changes.

Here I report evidence from experiments in Oregon that slight fluctuations in water temperature regulate the impact of a keystone predator, the sea star *Pisaster ochraceus*, on its principal prey, the rocky intertidal mussels *Mytilus californianus* and *M. trossulus*. Paine’s classic experiments in Washington state demonstrated that without predation on mussels by *Pisaster*, a diverse assemblage of low intertidal algae and invertebrates shifted to a monoculture of the competitively dominant mussel *M. californianus* (4). Densities of *Pisaster* and its effects on intertidal communities are highest during spring and summer in the Pacific Northwest (5, 6). However, preliminary observations suggested that many sea stars became inactive in low zone channels or shallow subtidal waters during periods of upwelling (6). Water temperatures drop 3° to 5°C during these events, which generally last several days to three or more weeks (7). Upwelling is common along the Oregon coast from May to September.

I quantified sea star predation rates at three wave-exposed sites (8) within Neptune State Park (44°15′N, 124°07′W), Oregon, to test the hypothesis that the strength of the *Pisaster-Mytilus* interaction is reduced during periods of cold water upwelling. This 4-km stretch of coastline is composed of extensive rocky benches. The high intertidal zone is characterized by fucoid algae and barnacles, the mid zone by dense beds of *M. californianus*, and the low zone by a diverse mix of algae, sea grass, and invertebrates. At each site, I identified paired reefs (mean area ± SEM = 132.5 ± 49.7 m²) isolated by surge channels. All sea stars were routinely removed from one reef in each pair and allowed to remain at natural densities on the other reef. In April and May 1997, I transplanted 20 clumps of 50 *M. californianus* (shell length, 4.5 to 5.5 cm) to the low intertidal zone on each reef (9).

From June through August 1997, I conducted five consecutive experiments to measure the intensity of sea star predation during periods lasting 14 days each. At the start of each period (10), I randomly selected and uncaged four mussel transplants per reef per site. I then recorded mussel survivorship and local sea star density (the number of sea stars in a 1-m radius around each transplant) on each of the first 6 or 7 days and again on day 14 (11). Temperature data-loggers installed in the low intertidal zone at each site recorded water temperatures when submerged, or air temperatures during low tide, every 30 min. Maximum air temperatures were used as a measure of potential heat stress during aerial exposure (12). Five maximum wave force dynamosmeters (13) at each site recorded variation in wave stress, a factor that can inhibit consumer activity.

The experiments encompassed periods with and without upwelling and thus tested whether per capita interaction strength [the difference in rates of mussel mortality on reefs with and without sea stars, divided by the local sea star density (14)] varied with fluctuations in water temperature. Per capita interaction strength was sharply reduced during a persistent upwelling event (Fig. 1, A and B). During upwelling, there was an even greater proportional drop in the collective impact of *Pisaster* (Fig. 1C) as a result of two effects: Individual sea stars consumed less (lower per capita effects), and the local density of sea stars was reduced (15), presumably as a result of more sea stars remaining inactive in channels or shallow subtidal waters. Both per capita and population interaction strength were significantly correlated with mean water temperature and were unrelated to variation in other environmental factors such as potential aerial heat stress or maximum wave forces (16).

I also examined *Pisaster* feeding rates in the laboratory (17) under three temperature regimes: constant 12°C, constant 9°C, and a...
treatment that simulated episodic upwelling by alternating between 12°C and 9°C every 14 days. Sea stars were fed *M. trossulus* (18 shell length, 3.0 to 4.0 cm) ad libitum. The number of mussels consumed per tank was recorded every 14 days. Sea stars in 9°C tanks consumed, on average, 29% fewer mussels than those at 12°C (Fig. 2). As predicted, sea stars in the alternating treatment fed intensely at 12°C, more slowly at 9°C, then faster again at 12°C (19).

These results suggest that interannual variation in the frequency and intensity of coastal upwelling could alter the dynamics of these intertidal communities through strong effects on keystone predation. In recent decades, upwelling patterns in the California Current have changed substantially in response to more frequent and intense El Niño–Southern Oscillation (ENSO) events, interdecadal regime shifts in the North Pacific, and perhaps global warming (20). During ENSO years, warm water accumulates in the eastern Pacific, the thermocline is depressed, and upwelled waters are drawn from shallower, warmer layers. These effects were apparent at my field sites during the 1997–98 ENSO. Only 6.3% of the high tides during May through August 1997 had mean water temperatures below 9.5°C, whereas 36.7% of the high tides fell below this mark during the same period of 1996. It remains to be determined whether such variation is sufficient to alter community composition. Systematic changes in cold water upwelling, which may accompany global warming (20), would be expected to modify predation intensity by *Pisaster* during the summer, when sea star densities and effects are the highest. This change might alter both the vertical extent of mid zone mussel beds and the species composition of the low intertidal zone.

This study demonstrates that the local strength of a keystone interaction can be altered by slight temperature shifts and changes in the timing and intensity of seasonal events. At larger spatial scales, *Pisaster*’s per capita impact on prey may decrease with increasing latitude (21), although this response could be modified by acclimatization or local adaptation to temperature and sea star–mussel interaction strengths (IS) during consecutive 14-day periods (x axis). All data are means (= SEM) of values recorded at three study sites. (A) High tide water temperatures (the mean from 2 hours before to 2 hours after each high tide). Temperatures above the x axis are the overall means for the 27 high tides of each period. (B) Mean per capita IS of sea stars on transplanted mussels during each 14-day period. (C) Mean per population IS of sea stars during each period. Both per capita and per population IS were significantly lower during upwelling than during the other four periods [ANOVA, contrast the third period (middle bars) with the other four; F_{1,53} = 10.03, P = 0.003 (per capita); and F_{1,53} = 11.10, P = 0.002 (per population)].

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**Fig. 2.** Sea star feeding rates in three laboratory treatments: 12°C (solid bars), 9°C (open bars), and alternating (hatched bars) (for periods 1 through 3: 12°C, 12°C, and 12°C, respectively). Bars are mean consumption rates (= SEM) in treatments (n = 4 tanks per treatment) during three consecutive 14-day periods. Data were analyzed in a repeated measures ANOVA. Treatment F_{2,9} = 59.81, P < 0.001; time F_{2,18} (36.99, P < 0.001), and time x treatment F_{3,18} = 5.70, P = 0.004 were all significant. Within each time period, horizontal lines above bars indicate groups whose means do not differ (Tukey-Kramer, P > 0.05).

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**References and Notes**


6. E. Sanford, unpublished data.


8. Replicate sites (Strawberry Hill, Pigeon Reef, and Bob Creek Wayside) were several hundred meters apart. Water temperatures generally varied < 0.2°C over these distances.

9. Mussels from a common source were transplanted under plastic Vexar mesh cages that allowed mussels to reach to the rock and shielded them from foraging sea stars until cages were removed. Mussels reattached securely. Mean percent survivorship (= SEM) 14 days after cages were removed was 97.4 ± 0.45% on reefs without sea stars (n = 60 transplants).

10. Starting dates were set as the first day of each spring tide series.

11. Sites were inaccessible during the neap tides, days 8 through 13.

12. Temperatures recorded by the data-loggers at low tide predicted *Pisaster* body temperature. On 20 dates, I used a digital thermohypodermic probe to measure the body temperatures of 10 randomly selected sea stars at Strawberry Hill, 20 to 30 min before they were resubmerged by the incoming tide. Mean body temperature was significantly correlated with the maximum air temperature recorded by the data-logger during that low tide (y = 0.76x + 2.75, R² = 0.85, P < 0.001).


14. Interaction strengths were calculated according to the method of S. A. Navarrete and B. A. Menge [Ecol. Mon. 66, 409 (1996)]. I used the discrete time version of the Losa-Volterra equation: M_{t+1} = M_t e^{xP_{t+1}} where M is the number of mussels at time t, M is the number of mussels when the transplant was first uncaged, e is the natural logarithm, y describes the per capita rate of change for mussels in the absence of *Pisaster*, x is the per capita interaction strength of *Pisaster* on the per capita rate of change of mussels, and P is local sea star density. I estimated survival rates for each mussel transplant from the slope of the linear regression of ln(M_t/M_o) over time [days 1 through 14]. Population interaction strengths (µP) were estimated by subtracting the mean mussel survival rate (the slope of the log regression) on reefs without *Pisaster* from the survival rate observed in mussel transplants on reefs with *Pisaster*. Dividing by the mean local sea star density for that transplant and time period gave per capita interaction strength (µ). This procedure gave four independent estimates of interaction strength per site x time period combination.

15. Local sea star density differed among time periods and sites [two-way analysis of variance (ANOVA), F_{4,53} = 2.80, P = 0.035 (time period); and F_{2,53} = 6.79, P = 0.002 (site)]. Sea star density during the
upwelling period (17 July through 1 August) was 31.6% lower than during the other four periods (mean ± SEM = 2.48 ± 0.32 sea stars/m², n = 12 versus 3.63 ± 0.26 sea stars/m², n = 48) and was consistently higher at Pigeon Reef than at the other two sites (mean ± SEM = 4.36 ± 0.38 sea stars/m², n = 20 versus 2.92 ± 0.25 sea stars/m², n = 40).

16. I used multiple regressions to test whether variation in mean interaction strength among time periods and sites was associated with (i) water temperature (the mean during 27 high tides per period), (ii) potential heat stress (the mean of maximum low tide air temperature on the five warmest days per period), or (iii) wave stress (the mean of maximum force per day on 5 to 7 days per period). Per capita interaction strength was associated with water temperature (P < 0.001) but was unrelated to potential heat stress (P = 0.18) or wave stress (P = 0.53). Similarly, population interaction strength was correlated with water temperature (P < 0.001) but not with potential heat stress (P = 0.13) or wave stress (P = 0.74). Site variables were significant in both models because both per capita and population interaction strength were consistently higher at Pigeon Reef, the site with higher sea star density (15). Together, water temperature and site explained 80.9% of the variation in mean population interaction strength.

17. In early June 1996, 48 sea stars (wet weight, 118 to 138 g) were collected from Neptune State Park. Four individuals were randomly assigned to each of 12 closed 110-liter tanks held in a cold room, and heat- ers with controllers self-regulated treatments to ±0.1°C. Water was circulated by two pumps in each tank, and water quality was maintained by filters and weekly water changes. Salinity was maintained at 36 ± 1 parts per thousand, and the experiments were conducted under a schedule of 12 hours of light and 12 hours of darkness. All sea stars were initially acclimated without food at 11°C for 10 days, and then treatments were randomly assigned (n = 4 tanks per treatment).

18. Mytilus trossulus was used because this species is the most common prey item in Pisaster’s diet at these sites. I quantified the diet of actively feeding sea stars (n = 1664) on 14 dates during the summer of 1995 and 1996. The percent of individuals feeding on a given prey species was as follows: mussels (M. trossulus, 56.0%; M. californianus, 5.0%), barnacles (Pollicipes polymerus, 41.8%; Balanus glandula, 6.0%; Semibalanus cariosus, 3.2%; Chthamalus dalli, 1.4%; B. nubilus, 0.7%), whelks (Nucella spp., 1.5%), and limpets (Lottia spp., 0.5%). The total exceeds 100% because P. ochraceus often feeds on several prey species at a time.

19. Results are presented for the first three periods of the experiment. Thereafter, sea stars became temporarily satiated on the ad libitum diet, and feeding rates declined sharply in all treatments. After 4.5 months, sea stars used in the experiment had energy stores (polaric cells) much larger than that of field animals.
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