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HUMAN INFLUENCES ON TROPHIC CASCADES ALONG ROCKY SHORES

David R. Lindberg,[1] James A. Estes,[2] and Kenneth I. Warheit[3]

[1]*Department of Integrative Biology and Museum of Paleontology, University of California, Berkeley, California 94720 USA*
[2]*U. S. Geological Survey, Biological Resources Division and Institute of Marine Studies, University of California, Santa Cruz, California 95064 USA*
[3]*Department of Fish and Wildlife, 600 Capitol Way North, Olympia, Washington 98501 USA, and Department of Zoology, University of Washington, Seattle, Washington 98195 USA*

Abstract. A three-trophic-level interaction among American Black Oystercatchers (*Haematopus bachmani*), limpets (*Lottia* spp.), and erect fleshy algae in rocky intertidal communities of central and southern California was documented via manipulative and "natural" experiments. Removal of the territorial limpet (*Lottia gigantea*) initially caused large increases in the percent cover of erect fleshy algae, followed by a more gradual increase in density of small limpets (*Lottia* spp.) and a decline in algal cover. Algal cover increased following the removal of small limpets at the sites from which *L. gigantea* had been removed earlier, thus demonstrating that the large and small limpets had similar inhibitory effects on plant populations. A comparison of sites with and without oystercatchers showed that *L. gigantea* occupied substrate inclinations in proportion to their availability at sites where oystercatchers were rare, whereas the distribution of *L. gigantea* was skewed toward vertically inclined substrates where oystercatchers were common. Survival rates of limpets translocated to horizontal and vertical substrates were similar in sites lacking oystercatcher predation, but were much lower on horizontal substrates where oystercatchers were common. Our results are consistent with those from several prior studies in demonstrating that shorelines frequented by humans typically lack oystercatchers. Humans also exploit *L. gigantea* and reduce populations to low densities of small individuals. These findings may explain why the midlittoral zone of rocky intertidal communities in western North America are so often dominated by high population densities of small limpets.

Key words: algae; California; grazing; Haematopus bachmani; *historical biology; limpets;* Lottia gigantea; *natural experiments; oystercatchers; predation; refuges; territoriality; human disturbances.*

INTRODUCTION

It is widely believed that human-induced changes to biodiversity are the direct results of exploitation, habitat destruction, and pollution. However, strong linkages often exist among species (Paine 1980); thus, human-induced disturbances may also act on biodiversity through indirect influences on species abundances. Because species vary greatly in the extent to which they influence their component ecosystems (Power et al. 1996), these points suggest that disturbances to the most important players in strongly linked food webs should be of particular concern when assessing the threat of human activities on biodiversity.

Species are linked with other species as their competitors (lateral effects), their food (bottom-up effects), or their predators (top-down effects). Top-down linkages among species and guilds at different trophic levels are known for a variety of ecosystems (Hunter and Price 1992) and, in some cases, high-trophic-level consumers initiate chains of interactions that reach all the way to the base of the food web. Multitrophic-level interactions of this sort have been termed "trophic cascades" (Carpenter et al. 1985). The best documented examples of trophic cascades are from aquatic ecosystems (Strong 1992), including rocky intertidal communities.

From the many studies of rocky intertidal communities at temperate latitudes, two taxa that have been identified repeatedly as important structuring agents are limpets (typically members of the order Patellogastropoda) and oystercatchers (genus *Haematopus*). In these communities, limpets have been shown to have numerous functions, including roles as herbivores, as prey for higher trophic-level consumers, and as space occupiers that limit the recruitment of other invertebrates (Underwood 1979, Branch 1981, and references therein). Some limpet species are territorial (Stimson 1970, 1973, Branch 1981), adding space domination to their role in certain regions. American Black Oystercatchers are important limpet predators in many regions, and flocks of these birds can remove hundreds of limpets from the intertidal zone during a single low tide (Frank 1982, Lindberg et al. 1987). These predation events are known to affect limpet species diversity and abundance patterns (Lindberg et al. 1987, Marsh 1987, Hahn and Denny 1989) and, indirectly, algal cover (Frank 1982, Hockey and Branch 1984). These species often interact via a three-level trophic cascade in which oystercatch-

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ers reduce limpets, thereby enhancing algal populations.

Rocky intertidal communities worldwide have been impacted by human activities such as exploitation and trampling (Liddle 1975, DeVinny et al. 1980, Beauchamp and Gowing 1982, Moreno et al. 1984, 1986, Castilla and Duran 1985, Duran and Castilla 1989, Kingsford et al. 1991, Povey and Keough 1991, Keough et al. 1993, Lasiak and Field 1995). Thus, it is likely that many of these communities are vastly different from what they were even 50–100 years ago. This is surely true of California, a state in which most of the $>20 \times 10^6$ human inhabitants live near the coast. Nonetheless, human influences on the oystercatcher–limpet–algal trophic cascade in California are poorly known because: (1) people occur in large numbers almost everywhere, thus limiting the opportunities for simple comparisons of sites with and without humans; (2) their expected effects on this particular trophic cascade are uncertain because humans disturb oystercatchers and exploit limpets for food; and (3) the influences of both humans and oystercatchers are difficult to assess experimentally.

Human exclusion experiments in rocky intertidal communities have shown striking effects (Castilla and Duran 1985, Duran and Castilla 1989, Hockey 1994), although this approach is difficult to implement in most places. Comparing sites of high human use with refuges from human disturbance (e.g., reserves or inaccessible islands) is one way in which the effects of humans on rocky intertidal communities can also assessed. Such refuges, although rare, exist along the coast of central California and can be used to illustrate how rocky intertidal communities in this region were organized prior to the arrival of modern man, demonstrating, in particular, the ecological roles of species that are now reduced or absent because of human activities. By combining results from such a comparative approach with those from manipulative experiments, it is possible to better understand patterns and mechanisms of human influence on coastal ecosystems, even when indirect interactions are an important part of the story. We have employed such a pluralistic approach here by including historical records along with results from natural and manipulative experiments.

Our specific goal was to understand human influences on the trophic cascade among oystercatchers, limpets, and macroalgae in central and southern California. The large territorial limpet *Lottia gigantea* is shown to limit the assemblage of intertidal algae and other smaller limpets (*Lottia* spp.). However, *L. gigantea* has been so depleted by human exploitation that its influence at the community level is no longer observable, except at remote locations. In the absence of *L. gigantea,* smaller limpet species increase in abundance to levels at which they, too, limit intertidal algae. We also consider the influence of American Black Oystercatchers (*Haematopus bachmani*) on limpet populations, and the influence of human activities on both oystercatchers and limpets. We then discuss how variation in the limpet–oystercatcher–human interaction has complex and heretofore unrecognized effects on rocky intertidal communities. We argue that human influences go beyond trampling and exploitation, in that the mere presence of people on a frequent basis constitutes a disturbance to oystercatchers, with important ecological consequences.

METHODS

Species

Lottia gigantea is a large, territorial gastropod that attains shell lengths of >100 mm. It occupies a zone from about mean lower low water (MLLW) to the lower reaches of the high-intertidal zone. Larger individuals maintain territories from which conspecifics and other invertebrate species are excluded (Stimson 1970, 1973). Newly settled sessile organisms are either ingested or dislodged before they are able to achieve a size refuge. The only macroscopic organisms able to persist on *L. gigantea* territories are those finding refuge in substrate irregularities or on the shells of territory holders. Grazing by *L. gigantea* reduces macroalgal cover, particularly of upright species, leaving only crustose forms and a microalgal film on the substratum (Stimson 1970, 1973).

The small limpet guild includes *Lottia digitalis, L. pelta, "Collisella" scabra* (all formerly placed in the genus *Collisella*; Lindberg 1986) and several less common species. These species range from 5 to 25 mm in shell length. Although all of the above-named species overlap and co-occur with *L. gigantea* in the mid-intertidal zone, *"C." scabra* is most common among *L. gigantea* territories. Like *L. gigantea,* these small limpets feed on algal sporelings, blue-green algae, diatoms, and thin algal films and crusts (Castenholz 1961, Craig 1968, Sutherland 1970, Nicotri 1977).

The American Black Oystercatcher (*Haematopus bachmani*) is a territorial shorebird that breeds just above the high-water mark on rocky shores. Oystercatchers feed on a variety of intertidal invertebrates. Between 40% and 50% of the diet of adult birds consists of herbivorous mollusks, mainly limpets (Webster 1941, Hartwick 1976, 1981). In California, *L. gigantea* is a common and preferred prey item (Morrell et al. 1979, Lindberg et al. 1987; K. Warheit, *unpublished data*). Legg (1954), working near Monterey, California, found that 78% of the limpets fed to chicks were *L. gigantea.*

Human exploitation of *L. gigantea* began with the peopling of the west coast of North America ~13 000 years ago and continues today (Vedder and Norris 1963, Abbott and Haderlie 1980). Human exploitation differs from oystercatcher predation, in that humans select the larger individuals and remove limpets from surfaces not accessible to oystercatchers. In the early

1900s, populations of *L. gigantea* were further depleted by commercial fishing (Nelson 1949). Exploitation of *L. gigantea* continues and populations probably have been greatly reduced at most mainland localities (Pombo and Escofet 1996). We are aware of several examples in California in which hundreds of *L. gigantea* were illegally removed during single low tides at Santa Cruz, San Diego (J. Barry and W. G. Wright, *personal communication*), Monterey (T. Hahn, *personal communication*), and Diablo Canyon and Pt. Buchon (G. R. VanBlaricom, *personal communication*).

American Black Oystercatchers are sensitive to human disturbance (Sowls et al. 1980). Their documented disappearance from localities impacted by human activities include: Southeast Farallon Island, California (Ainley and Lewis 1974), Triangle Island, British Columbia, Canada (Carl et al. 1950), and islands off the coast of Baja California, Mexico (Kenyon 1949). Warheit et al. (1984) found an inverse relationship between oystercatcher densities and the amount of human disturbance in the Channel Islands, California; Legg (1954) reported that human disturbance reduced nesting success of oystercatchers at Point Lobos, California; and Hockey (1983*a*) has shown that human disturbance lowers egg and chick survival in the African Black Oystercatcher (*Haematopus moquini*).

Study sites

Limpet removal experiments were conducted at San Nicolas Island, Ventura County, California between April 1980 and June 1984 (Fig. 1). Landels-Hill Big Creek Reserve (Monterey County), Santa Cruz, Año Nuevo Island Reserve (both in Santa Cruz County), and San Nicolas Island were used to determine survival rates of *Lottia gigantea* introduced at sites with and without oystercatchers, and to compare the distribution of *L. gigantea* on substrates of different inclinations.

San Nicolas Island (SNI) is located ~100 km west of Ventura, California, and is part of the U.S. Naval Pacific Missile Test Center. Because of its location and status, access to SNI is restricted and the intertidal invertebrates there are relatively unexploited by humans. *L. gigantea* numerically dominates the mid-intertidal zones at most locations around the island. American Black Oystercatchers were rare at San Nicolas Island in 1979, when our study began, probably in large part because of the feral cat population. A feral cat removal program was initiated in the early 1980s and the number of American Black Oystercatchers on SNI per kilometer of rocky coast subsequently increased (Lindberg et al. 1987). Even so, oystercatchers were rarely seen at our study sites, and the island-wide population density was remarkably low compared with other California islands (Warheit et al. 1984).

Landels-Hill Big Creek Reserve (SUR) is located ~75 km south of Monterey, California, in the remote Big Sur region, and is part of the University of California Natural Reserve System; human access is restricted and disturbance is minimal. *L. gigantea* dominates the more vertical surfaces in the mid-intertidal zone, and oystercatchers are common along the rocky shores. Much of the horizontal substrate in the intertidal community is dominated by macroalgae (Eernisse 1984).

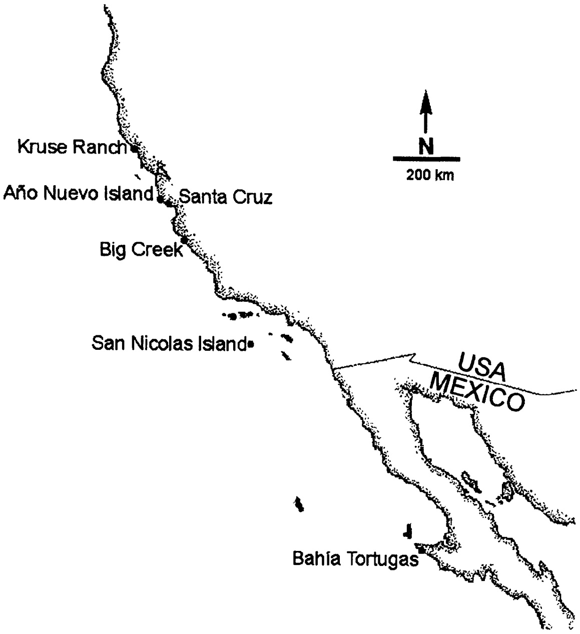

FIG. 1. Sketch map of western North America showing locations of regional study sites referred to in the text. The region in which all of the interacting components have cooccurred for the last 10 000 yr extends from Kruse Ranch, California, USA, in the north to Bahía Tortugas, Mexico in the south.

Although the Santa Cruz (SCZ) site is protected as part of the University of California at Santa Cruz's Long Marine Laboratory, it is adjacent to Natural Bridges State Park, a coastal recreational area with a visitor total of >300 000 people/yr (Beauchamp and Gowing 1982). *L. gigantea* territories dominate most of the mid- and high-intertidal zones on the near-vertical shores immediately south of the marine laboratory. Because of near-constant human disturbance from the adjacent park, oystercatchers are uncommon at this site.

Año Nuevo Island (ANI) is also part of the University of California Natural Reserve System, and is further protected by a 0.8 km wide channel separating it from the mainland. Human access to the island is limited to researchers and occasional other visitors. Limpets occur primarily on vertical surfaces and under edges. Horizontal surfaces not occupied by hauled-out pinnipeds are covered with macroalgae (D. Lindberg and K. Warheit, *personal observations*). The number of American Black Oystercatchers per kilometer of shore at ANI is the highest yet reported in California (Warheit et. al. 1984).

Field techniques

We assessed the ecological role of *Lottia gigantea* in the mid-intertidal zone at SNI by comparing algal cover and small-limpet densities through time between sites in which *L. gigantea* was experimentally removed and unmanipulated control sites. Six sandstone benches were chosen as experimental units. Natural barriers (e.g., sandy beaches, surge channels, unsuitable rocky substrates) surrounded each bench and prevented limpet immigration; all supported similar assemblages of plants and invertebrates prior to our experiments. Small limpets (primarily *Lottia digitalis*) and barnacles were common in the highest zones (~1.5 m above MLLW). The mid-intertidal zones were dominated by *L. gigantea*. "*Collisella*" *scabra* was also common in this zone, and the most abundant macroalgae included *Gelidium* spp., *Gigartina* spp., and *Mastocarpus* spp. The lowest portions of the mid-intertidal zones were covered by the mussel *Mytilus californianus.* Aggregations of the anemone *Anthopleura elegantissima,* the alga *Corallina vancouverensis,* and a marine angiosperm (*Phyllospadix* sp.) were conspicuous in the lowest zones (MLLW and below).

Three permanently marked plots (0.25 m^2 each) were established in the *L. gigantea*-dominated mid-intertidal zones on each bench by securing stainless steel bolts with marine epoxy into holes drilled in the sandstone bench. We sampled the plots in situ with a 0.5 × 0.5 m framer (inside dimensions) that was divided into 25–100 cm^2 subplots with monofilament fishing line. The 32 line intersections (including those with the framer's sides, but not its corners) were used to estimate percent cover of macroalgae. Numbers of limpets were counted within the framer.

L. gigantea was removed from three of the benches in June 1980, and recruits and immigrants were removed at 2-mo intervals thereafter. All plots were sampled once prior to the removals (April 1980), and three times subsequently (October 1980, April 1981, and October 1981).

The removal of *L. gigantea* was followed by an abrupt flush of algae and, subsequently, by a more gradual increase in small-limpet density and a decline in algal cover. To determine if this algal decline was caused by the increase in the small-limpet population, we established a fourth plot at each bench where *L. gigantea* had been removed. All small limpets were removed from these plots in December 1983 and at 2-mo intervals thereafter. A strip of copper-based antifouling paint was placed around each of the small-limpet removal plots to reduce immigration. Percent cover of macroalgae in the experimental plots was measured in December 1983, before removal of the small limpets, and in the experimental and adjacent control plots at 2-mo intervals thereafter through June 1984.

Our initial observations at SUR and ANI indicated that most oystercatcher foraging occurred on horizontally inclined substrates. To determine how oystercatcher predation on *L. gigantea* might be influenced by different substrate inclinations, we measured the frequency distributions of available substrate inclinations and those occupied by *L. gigantea* at SNI and SCZ (oystercatchers rare) and SUR and ANI (oystercatchers common). These measurements showed striking and consistent differences in microhabitat use by *L. gigantea* between sites where oystercatchers were rare or common. In order to better understand the cause of this pattern, we subsequently translocated marked *L. gigantea* to both vertical and horizontal surfaces at each site and monitored their survival.

The frequency distribution of substrate inclinations was determined by placing a 20 × 2 m transect haphazardly through the mid-intertidal zone. Substrate inclinations on which each *L. gigantea* occurred within the transect were measured to the nearest degree with a Brunton Compass. Available substrate inclinations were determined by contouring the tape over the substrate and measuring the inclination at randomly selected points within the swath. Each point was selected with three random numbers: (1) distance along the tape, (2) direction to the right or left of the tape, and (3) distance perpendicular to the tape.

The limpets to be translocated were marked with a small dab of epoxy or paint, randomly split into two groups, and translocated to either a vertical (>60°) or horizontal (<30°) surface. Initial numbers were determined 24 h after the translocation to allow for mortality from injury or the shock of being moved; losses ranged from 8% to 17% during the first 24 h. We measured the survival of 50–60 translocated *L. gigantea* at each site. Depending on access to the study site and the initial loss rate, follow-up counts were made at varying intervals over the next 2–8 wk.

RESULTS

Lottia gigantea removal experiments

Two months before *Lottia gigantea* was removed (April 1980), erect algal cover was <10% in both the experimental and control plots. By October 1980, 4 mo after *L. gigantea* was removed from the experimental plots, erect algal cover in the removal plots had increased >15-fold, whereas that in the control plots had increased <1.5-fold (Fig. 2). The resulting difference in algal cover between the manipulated and unmanipulated plots was highly significant (Table 1). Thereafter, erect algal cover at the removal plots declined gradually through October 1981, whereas the control plots remained largely unchanged (Fig. 2).

The response of small limpets to removal of *L. gigantea* was equally striking, although the response time was slower. Two months before *L. gigantea* was removed, small-limpet densities in the control plots were >10 times greater than in the experimental plots (Appendix), primarily because the more irregular surface

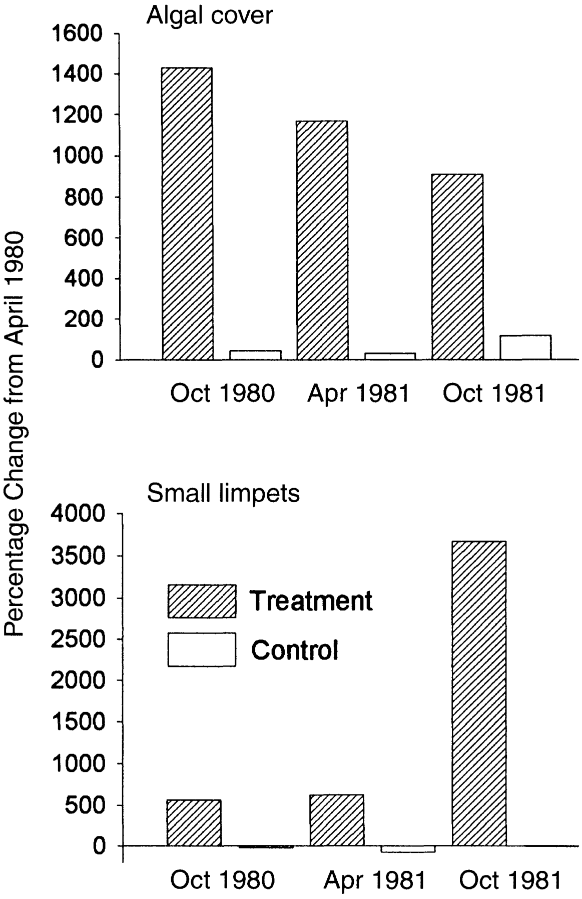

FIG. 2. Percentage change in cover of erect algae and mean small-limpet densities at San Nicolas Island (SNI) experimental sites following the removal of *Lottia gigantea*. Percentage change relative to April 1980 was calculated from pooled means presented in the Appendix.

of the sandstone substrates at the control sites provided more surface area for smaller limpets. Although the number of small limpets increased in the experimental plots after *L. gigantea* removals, these increases did not become statistically significant until October 1981, by which time they were highly significant (Table 1).

Small-limpet removal experiments

The percent cover of erect, fleshy algae at the *L. gigantea* removal plots continued to decline through April 1982, reached minima of 9.3% to 12.9% from June through December 1982, and thereafter remained largely unchanged through 1983 (Fig. 2; D. R. Lindberg and J. A. Estes, *unpublished data*). Following removal of the small limpets from plots within the three experimental sites in December 1983, the erect algal cover increased to ~75% by February 1984 and remained at roughly this level through June 1984 (Fig. 3), when the experiment was concluded. Significant differences in algal cover between experimental (*L. gigantea* and small limpets removed) and control (*L. gigantea* only removed) plots existed throughout this period (*t* tests, all *P* values $\ll 0.01$). Erect algal cover remained unchanged at ~10% in the control plots (those plots in the experimental sites from which small limpets were not removed) during this same time period (Fig. 3).

TABLE 1. Results of one-way ANOVAs testing the effects of *Lottia gigantea* removal on small-limpet densities and algal cover. The analyses all are based on measurements taken from three permanently marked plots at each of six intertidal benches located around the perimeter of San Nicolas Island.

	Algae			Small limpets		
Date	*F*	*P*	R^2	*F*	*P*	R^2
Oct 1980	37.00	0.004	0.90	2.63	0.180	0.40
Apr 1981	6.72	0.061	0.63	4.25	0.110	0.52
Oct 1981	2.30	0.204	0.37	853.96	0.000	1.00

Note: Lottia gigantea was removed from three of the benches in June of 1980 and these removals were maintained throughout the experiment. Separate ANOVAs were done on differences between measurements made in April 1980 (just before the removal of *L. gigantea*) and those made on each of the three listed dates. Data were summed among plots within benches, and the sums among benches were used to compute experimental errors. Thus, all of the *F* statistics have 1 and 4 degrees of freedom. Algal cover data were not arcsine-transformed because the lower end of difference measurements is not constrained to end at zero (see Appendix).

In summary, results from these two experiments demonstrated that: (1) *L. gigantea* limits erect, fleshy algae and smaller limpets in the mid-intertidal zone; (2) algal cover increased soon (<2 mo) after the removal of *L. gigantea,* and increases in the abundance of small limpets occurred after 1–2 yr; (3) the small limpets that replaced *L. gigantea* limited erect algae in a manner similar to *L. gigantea*; and (4) without limpet grazing, erect algae became the dominant space occupiers.

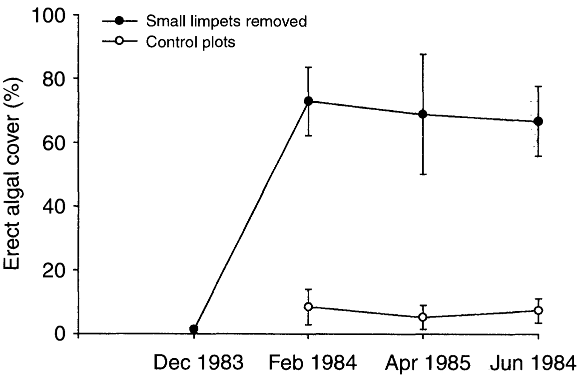

FIG. 3. Pooled mean percentage of erect algal cover for three experimental sites, from which small limpets were excluded, and from four control sites, in which small limpets were present. Vertical bars represent ±1 SE. All pairs are significantly different from one another (*t* test; $P < 0.01$) following the exclusion of small limpets from the experimental plots.

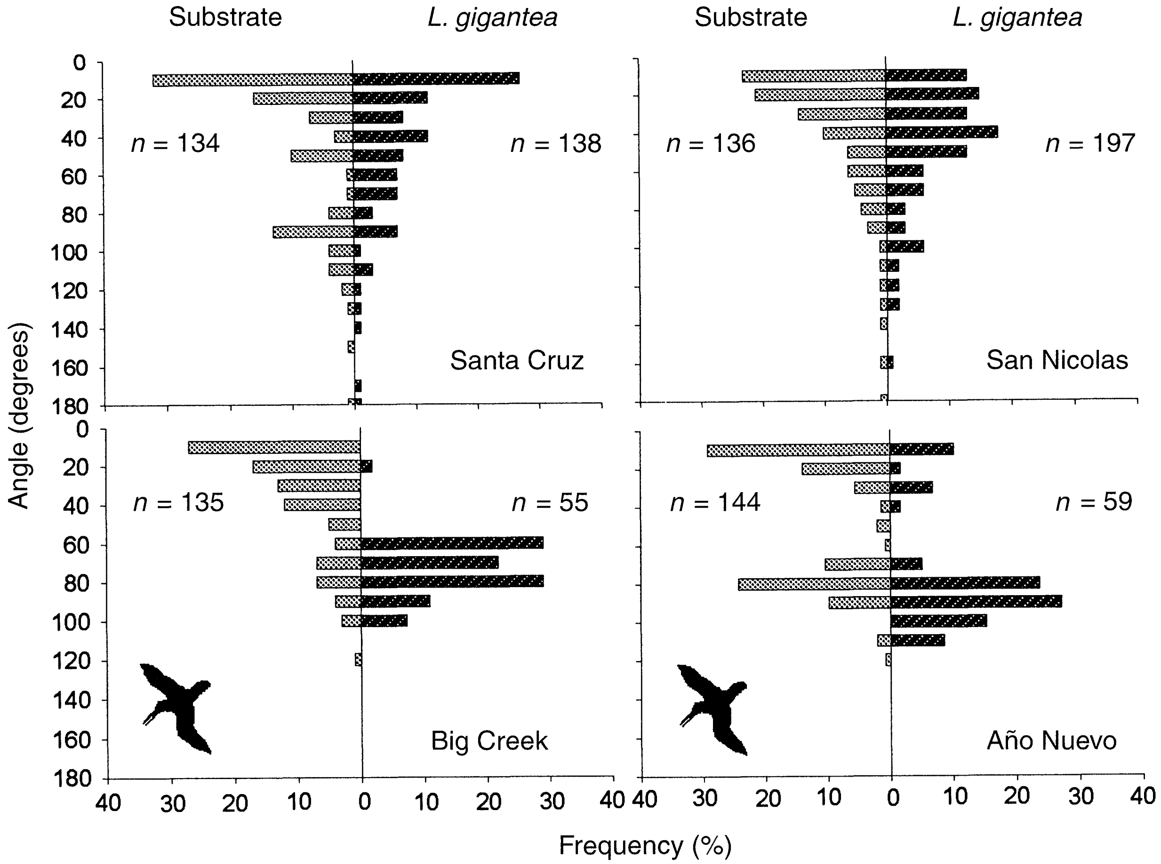

FIG. 4. Frequency distributions of available substrate angles and substrate angles occupied by *L. gigantea* at four study sites in central and southern California (angles were measured from horizontal). Oystercatchers were present at Big Creek and Año Nuevo and absent at Santa Cruz and San Nicolas. Areas surveyed ranged between 30 m^2 and 35 m^2; *n* indicates the number of individual limpet and substrate measurements.

Oystercatcher predation patterns

The microhabitat utilization of *L. gigantea* differed markedly between sites where oystercatchers were either rare or common. At the sites where oystercatchers were rare, there was no significant difference between the frequency distribution of available substrate inclinations and those occupied by *L. gigantea* (SNI; $\chi^2 = 6.28$, $P > 0.05$), or where there was a significant difference, the *L. gigantea* occurred more frequently than expected on horizontally inclined substrates (SCZ; $\chi^2 = 12.21$, $P < 0.05$; Fig. 4). At SUR and ANI, where oystercatchers were common, the *L. gigantea* occurred significantly more often than expected on vertically inclined substrates ($\chi^2 = 431.88$ and 79.63, respectively, $P < 0.005$ for both; Fig. 4).

Translocations of *L. gigantea* to vertically and horizontally inclined substrates demonstrated the speed with which such distribution patterns can be created. Survival of the translocated *L. gigantea* throughout the experiment was relatively high (67–95%) on vertically inclined surfaces at all four sites and on the horizontally inclined surfaces at SCZ and SNI (Fig. 5). Although the experiment at SCZ was complicated by human exploitation of the translocated limpets, survival rates before and after this event were about equal. In contrast, almost none (0–4%) of the *L. gigantea* translocated to horizontal surfaces at SUR and ANI survived >2 wk. A single limpet did survive for >2 wk on a horizontal surface at ANI periodically covered by elephant seals (*Mirounga angustirostris*). Although it is possible that these patterns were caused by some factor besides oystercatcher predation, we spent hours observing the SUR and ANI study sites from a distance, and all observed *L. gigantea* losses were due to oystercatchers. At SUR, five *L. gigantea* translocated to a horizontally inclined surface were located and eaten by oystercatchers within 4 h of being put there.

Human predation

The human exploitation event accidentally documented at SCZ (Fig. 5) was probably typical of human predation on *L. gigantea* at other locales. The limpets were taken during a low tide (probably on one day), near dawn, on or about 14 August 1981. Pry bar marks were common on the substratum. In addition to the limpets we had marked for the translocation experi-

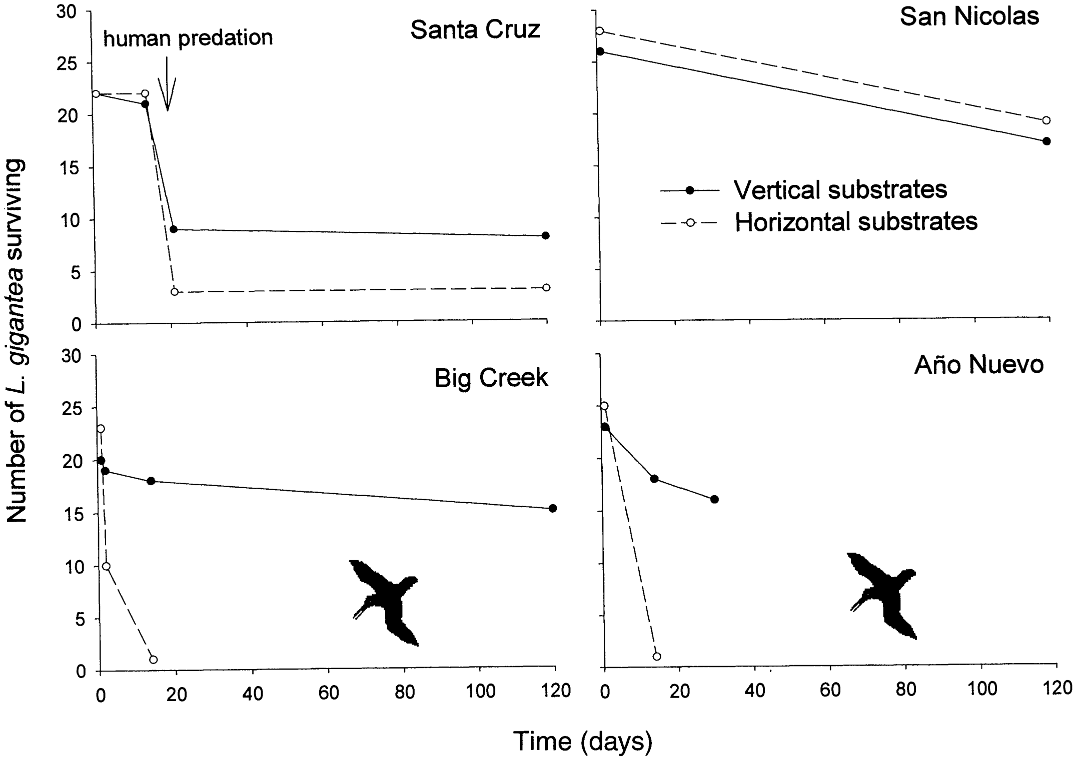

FIG. 5. Survival of *L. gigantea* translocated to vertical and horizontal substrates. Oystercatchers were present at Big Sur and Año Nuevo, and absent at Santa Cruz and San Nicolas. Translocated limpets were 35–60 mm in length.

ments, >125 unmarked individuals were taken from the area in which we had previously recorded substrate inclinations. In total, >300 limpets were removed from this area. The only remaining limpets were those in the smaller size classes (<25 mm) and individuals on near-vertical substrates that were inaccessible to people.

DISCUSSION

Results from the manipulative and natural experiments reported show that some rocky intertidal communities in central and southern California are organized around a complex of cascading influences produced by interactions among algae, limpets, oystercatchers, and humans. We have created a hierarchical view of the system's behavior by amalgamating all the individual interactions (Fig. 6), and the resulting model can be used to make qualitative predictions of the effects of various perturbations. However, even with such a model, the predictions are uncertain. For example, removal of *Lottia gigantea* has two expected effects: the enhancement of macroalgae and the enhancement of small limpets. Our experiments showed that both occur. Yet, the enhancement of small limpets is also detrimental to the algae, and a priori one could not determine how this negative effect on the algae compares in importance with the positive effect of removing *L. gigantea.* Our results indicate that removal of *L. gigantea* ultimately is of little consequence to the algae, because the guild of small limpets that subsequently develops is comparable to *L. gigantea* in grazing effectiveness.

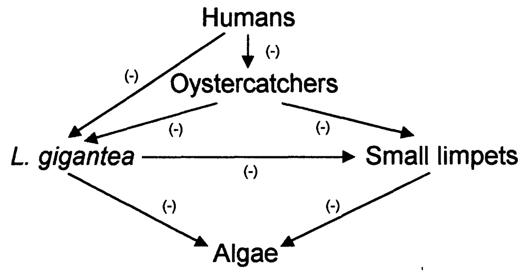

FIG. 6. Hierarchical model of algae–limpet–oystercatcher–human interactions in California mid-intertidal zones. Negative arrows indicate detrimental effects; although all modeled interactions are shown as negative, the effects between levels are multiplicative. For example, by removing the small limpets, oystercatchers have a positive effect on the algae.

Dense populations of small limpets occupy horizontal and vertical surfaces on many of California's rocky shores (e.g., Ricketts et al. 1985). Our findings indicate that this situation exists, at least in part, because modern humans have heavily exploited *L. gigantea* and have disrupted the predatory influences of oystercatchers. In sites protected from human disturbance, such as ANI and SUR, limpets are mainly restricted to vertical substrates where they are beyond the reach of foraging oystercatchers (Hahn and Denny 1989; Fig. 4), and algae dominate horizontal surfaces. At other sites (SNI and SCZ) where human exploitation of *L. gigantea* was typically low, but human disturbance disrupts the predatory influences of oystercatchers, *L. gigantea* dominated both vertical and horizontal surfaces (Fig. 4).

Humans first arrived in California ~13 000 yr BP (Nilsson 1983). Early aboriginals frequented rocky shores, exploited *L. gigantea,* and probably disrupted oystercatchers. Thus, we envision that these early humans drove rocky intertidal communities toward an organizational state dominated by small limpets on both horizontal and vertical surfaces. Modern-day human use of the nearshore environment also results in communities that are organized in this way. However, in areas where human activity is high, but human predation on limpets is absent or minimal (e.g., refuges and parks, such as our study sites SNI and SCZ before the poachers struck), rocky intertidal communities are dominated by *L. gigantea* on both vertical and horizontal surfaces. These latter states of community organization probably are very recent, accounting for <0.3% (~40 yr) of the evolutionary history of the complete system.

Interactions among the taxa and guilds considered in our study are not unique to California shores, but also occur in England (Lewis and Bowman 1975), Chile (Castilla 1981), the Pacific Northwest of North America (Frank 1982, Marsh 1987), Australia (Parry 1982), southern Africa (Hockey and Branch 1984), and Panama (Levings et al. 1986). Similar interactions among limpets, oystercatchers, and humans have been described in Chile (Castilla 1981) and South Africa (Hockey and Branch 1984). However, previous studies have not focused on the complete cascade as a functioning unit. Instead, the components have been individually studied and then the scope and strength of the interactions have been inferred (see the South African example that follows). In addition, past studies have not recognized the significant effects within a trophic level (e.g., small vs. big limpets) or the resulting horizontal/vertical community organization driven by oystercatcher predation.

The South African cascade is very similar to that in California. *African* Black Oystercatchers (*H. moquini*) feed on a diverse assemblage of limpets belonging to the genus *Patella* (Hockey and Underhill 1984), and densities may be as high as 75 oystercatchers/km of rocky coastline on offshore islands (Hockey 1983*b*). Hockey and Branch (1984) estimated that oystercatchers removed 2.8 × 10^6 limpets/yr from one 2.5-km stretch of coastline, and showed that removal of these limpets enhanced macroalgal cover. Human disturbance has negative effects on South African Black Oystercatcher populations (Hockey 1983*a*), and human predation reduces both maximum and mean limpet size at some localities (Hockey and Bosman 1986). Although the limpet and oystercatcher species are different, and humans have occupied the South African system for substantially longer than its California analogue (150 000 yr BP vs. ~13 000 yr BP), the species interactions and influences of human disturbance appear to be similar in both regions.

Today, much of the rocky shore of central and southern California is influenced by human disturbance. We have argued that the prevailing pattern of community organization in this area differs from the setting in which the key interacting species originated or lived for at least the last 3.5 × 10^6 yr. However, it is in this altered setting that most ecological work on California rocky shores has been done. Human disturbances (i.e., exploitation of large limpets and reduction of shore bird populations) tend to drive rocky intertidal communities to an organizational state dominated by small limpets, and several well-known papers have been published on the ecology of these species (e.g., Frank 1965, Sutherland 1970, Dayton 1971, Haven 1973, Nicotri 1977). Few studies have been conducted in areas with large populations of both oystercatchers and *L. gigantea*; thus, relatively little attention has been given to how these two important species mediate interactions between other invertebrates and algae. Moreover, studies seldom have been replicated on both horizontal and vertical substrates, microhabitats indicated by our data to have supported different biotas, and consequently may have experienced different selective pressures.

In our study, several approaches were necessary to tease apart the various components of a trophic cascade. Replicated and controlled manipulations were used to clarify the outcomes of interactions among the plants and herbivores, whereas natural experiments (we could not manipulate populations of humans or birds, for obvious reasons) were used to understand how higher trophic-level consumers mediate these interactions. The strength of conclusions from manipulative and natural experiments necessarily differs, but the joining together of these techniques provided insights that otherwise would not have been obtained. We believe that this approach also holds promise elsewhere for understanding the rapidly growing influence of humans on natural communities and ecosystems.

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APPENDIX

Percent cover of erect, fleshy algae and abundance of *Lottia gigantea* and small limpets from three experimental (*L. gigantea* removed) and three control (*L. gigantea* present) rocky intertidal benches at San Nicolas Island, California, USA. Data are from three 0.25-m^2 quadrats on each bench. *L. gigantea* was removed from the experimental benches in June 1980. April represents spring, and October represents fall.

	Lottia gigantea		Small limpets		Algae	
	Mean	1 SE	Mean	1 SE	Cover (%)	1 SE
Experimental 1						
Apr 1980	3.33	0.33	2.67	1.67	2.08	1.37
Oct 1980	0.03	0.33	3.67	1.20	87.50	3.10
Apr 1981	0.00	0.00	10.00	3.22	72.92	5.63
Oct 1981	0.00	0.00	114.67	6.23	62.50	1.79
Experimental 2						
Apr 1980	9.67	0.88	5.33	1.85	0.00	0.00
Oct 1980	0.67	0.33	48.67	31.92	60.42	12.68
Apr 1981	0.00	0.00	54.33	18.67	32.29	16.37
Oct 1981	0.33	0.33	124.67	25.14	59.38	10.02
Experimental 3						
Apr 1980	1.00	0.00	1.33	0.66	12.50	6.51
Oct 1980	0.00	0.00	9.00	5.57	75.00	2.00
Apr 1981	0.00	0.00	3.33	3.53	79.17	12.28
Oct 1981	0.00	0.00	112.00	25.51	25.00	13.63
Pooled experimental benches						
Apr 1980	4.67	1.32	3.11	0.95	4.86	2.76
Oct 1980	0.33	0.17	20.44	11.75	74.31	5.72
Apr 1981	0.00	0.00	22.56	9.70	61.46	9.53
Oct 1981	0.11	0.11	117.11	10.67	48.96	7.76
Control 1						
Apr 1980	7.00	1.15	8.33	3.29	2.08	1.37
Oct 1980	7.67	0.88	9.67	6.77	12.50	3.60
Apr 1981	10.00	1.00	4.33	2.19	5.21	1.07
Oct 1981	6.67	1.77	2.33	1.20	27.08	2.76
Control 2						
Apr 1980	7.70	2.90	35.00	4.04	8.30	4.63
Oct 1980	10.30	1.45	33.30	9.53	6.00	3.05
Apr 1981	9.00	2.00	22.70	5.36	3.30	2.40
Oct 1981	11.00	3.79	33.70	7.22	9.30	1.33
Control 3						
Apr 1980	12.00	2.89	62.70	33.03	19.00	10.69
Oct 1980	9.00	2.08	43.00	11.00	23.70	13.04
Apr 1981	8.30	2.03	32.70	12.78	30.00	15.01
Oct 1981	9.00	2.08	66.70	14.75	27.00	13.50
Pooled control benches						
Apr 1980	8.78	1.42	35.33	12.43	9.81	4.22
Oct 1980	9.00	0.87	28.67	6.78	14.06	4.76
Apr 1981	9.11	0.90	19.89	5.80	12.85	6.15
Oct 1981	8.89	1.49	34.22	10.43	21.14	4.97