# Do sea urchins and abalones compete in California kelp forest communities?

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## 1 ABSTRACT

Red sea urchins (Strongylocentrotus franciscanus) and red abalones (Haliotis rufescens) live in the same microhabitats, have similar food preferences, and are both nocturnal. Competition for food was analyzed in long-term laboratory experiments comparing growth in mixed and single species groups at three different food levels. Large red abalones depress the growth rates of large red urchins even in the presence of excess food. Red urchins are physiologically and behaviorally better adapted to cope with limited food supplies. These results are discussed in terms of both grazers' use of space, their life table characteristics, and the possibility of historical release from competition. Competition with abalones may have been a more important factor to the regulation of urchin populations in the past, but at today's population levels, predation and environmental factors affecting food supply seem to be the selective factors affecting resource utilization and distribution patterns.

## 2 INTRODUCTION

Sea urchins and abalones are the conspicuous large invertebrate herbivores of southern California kelp forest communities. Of the several species of both groups found in this region, red urchins, Strongylocentrotus franciscanus (Agassiz), and red abalones, Haliotis rufescens (Swainson), are the most prominent in terms of their size, grazing activities and economic importance. Red urchins and red abalones co-occur and share similar life-styles. Both are large, relatively sedentary, nocturnal animals with planktonic larvae. They employ the same primary mode of feeding and show similar food preferences. They are often found close together on the same reefs. There is also some overlap in major predators, including man, although the commercial fishery for abalones predates that for sea urchins by more than a century.

Several recent studies have focused on the question of competition between distantly related taxa and its role in community structure (e.g. Reichman 1979). The ecological similarities between red urchins and red abalones strongly suggest that these taxonomically dissimilar herbivores are competitors. Cox (1962) considered urchins to be "enemies" of abalones in California, that the urchins' more intense grazing would drive abalones out of an area in search of food. Similarly, Shepherd (1973) reported that Centrostephanus rodgersii appeared to have displaced the black-lip abalone H. ruber from extensive areas of Australia. Alternatively, the apparent sea urchin population explosion in southern California, after fishing greatly reduced abalone standing stocks, suggests the possibility that the urchin population growth may have been caused in part by a release from competition with abalones (North and Pearse 1970, Tegner 1980). In view of the importance of sea urchin grazing to the structure of kelp communities here as in many other areas of the world (reviewed by Lawrence 1975), we investigated the role that competition with abalones might play in regulating sea urchin populations. Here we report the results of field and laboratory observations and experiments examining various aspects of the interactions between red urchins and red abalones. These data will be synthesized with other natural history studies to consider the importance of herbivore competition to the structure of southern California kelp forest communities.

## 3 COMPETITION FOR FOOD

We conducted long-term laboratory experiments to examine red urchin and red abalone competition for the giant kelp, Macrocystis pyrifera, the preferred food of both species in southern California (Leighton 1966). Growth was measured in mixed (interspecifically competing) and single (intraspecifically competing) species groups at three resource levels. The experiment was replicated using two size classes: small, faster growing animals (red urchins of 30-60mm test diameters and red abalone of 60-100mm shell length) and larger, slower growing ones (red urchins 50-75mm and red abalones 100-125mm). The experimental design consisted of mixed species tanks with 16 (small) or 14 (large) total individuals and single species tanks of 8 (small) or 7 (large) urchins or abalones. Single species tanks received half the amount of kelp fed to the mixed tanks. Tanks were cleaned, animals were fed, kelp consumption determined and water temperatures monitored every 3-4 days.

The experiments were run over 2-1/2 years at three levels of Macrocystis supply. An initial attempt at food deprivation (~.02 gm kelp/gm animal/day, 2/78 through 6/78) permitted substantial urchin growth and was later designated as "moderate" supply. Kelp supply was then lowered to ~.005gm kelp/gm animal/day for a one-year period (9/78 through 9/79). This is well below the normal laboratory feeding rate of both species (Leighton 1971, this study). Animals which died were replaced with similar sized individuals from 2/78 until the beginning of the "low" food period. For a one-year period following severe food deprivation the experimental animals were offered as much kelp as they could consume (9/79 through 9/80).

Additional abalones and urchins were maintained in two single species control tanks for 1-1/2 years (3/79 through 9/80) to monitor growth rates in the laboratory under conditions of continuous excess kelp supply.

Growth, monitored monthly for all individuals, was measured as change in test or shell diameter and change in wet weight after the animals were blotted dry. We assessed both parameters, as diameters are unlikely to accurately reflect losses, while wet weight is apparently susceptible to fluctuations in water content (Leighton & Boolootian 1963). Because of the extreme variability observed, especially among abalone, experimental results were interpreted in terms of species total weights and diameters in each tank. Test diameter and wet weight turned out to be well correlated growth indicators for urchins. Abalone shell diameters changed little throughout

the experimental period and did not increase even under excess food availability. This may be an artifact of the laboratory conditions. Wet weight was used as the more realistic growth indicator.

Red urchin and red abalone feeding rates varied in a similar fashion with temperature and the time of year (Figure 1). Both animals fed at higher rates when the temperature was below 18°C, the period from October through March. Prolonged elevated temperatures (>21°C, unusually high temperatures for the depths at which these animals live) caused a decline in abalone feeding rates not exhibited by the urchins, but generally these herbivores are making the same temporal use of a common food resource.

Figure 1. Variation of feeding rates with temperature and time of year.
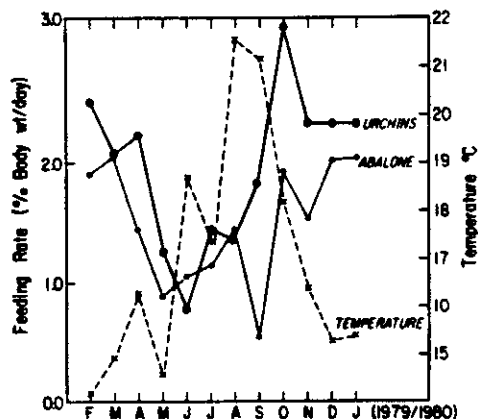


Red urchins, however, are about 1.5 times more efficient than red abalones at converting Macrocystis to body weight. Control urchins maintained in a single species tank under conditions of excess food supply gained .036gm body weight/gm wet weight Macrocystis vs. .024gm body weight/gm wet Macrocystis for abalones raised under the same conditions for a one-year period.

The results of the food competition experiment are presented as the treatments exhibiting higher growth (Table 1) and in terms of the total growth of all individuals in each treatment (Table 2). Individual variability was unaccountably high. For example, some months intraspecifically competing animals (both urchins and abalones) grew more and some months less than interspecifically ones of similar size even under conditions of excess food supply. Analysis of individuals matched by size and of tank totals with paired t tests showed no significant differences. The trends (Table 1)

Table 1. Apparent outcome of food competition experiment. Treatments exhibiting higher growth rates in inter- vs intraspecific competition.

| | Food availability | | |
| --- | --- | --- | --- |
| | Low | Moderate* | Excess |
| Small animals | | | |
| Sea urchins | No effect | No effect | No effect |
| Abalones | No effect | Interspecific | Interspecific |
| Large animals | | | |
| Sea urchins | Intraspecific | Intraspecific | Intraspecific |
| Abalones | Intraspecific | Interspecific | Interspecific |

Table 2. Total growth (%Δbody weight/%Δdiameter) of all individuals in each treatment of the food competition experiment.

| | Treatment (food supply) | | | | | |
| --- | --- | --- | --- | --- | --- | --- |
| | Low | (n) | Moderate* | (n) | Excess | (n) |
| Small sea urchins | | | | | | |
| Interspecific | +16.6/+6.3 | (8) | +38.4/+12.6 | (8) | +23.7/+8.2 | (8) |
| Intraspecific | +15.4/+3.3 | (8) | +37.0/+13.9 | (8) | +21.9/+5.6 | (6) |
| Large sea urchins | | | | | | |
| Interspecific | +1.9/+2.6 | (7) | +2.4/+3.3 | (7) | +18.5/+2.6 | (4) |
| Intraspecific | +5.3/+3.1 | (7) | +4.8/+2.9 | (7) | +28.4/+4.8 | (6) |
| Control sea urchins (mixed sizes) | | | | | +40.1/+10.0 | (4) |
| Small abalones | | | | | | |
| Interspecific | -7.8/0.0 | (8) | +6.4/+4.7 | (8) | +45.8/+2.1 | (7) |
| Intraspecific | -7.8/-1.6 | (5) | +0.8/+3.2 | (8) | +16.2/-0.9 | (3) |
| Large abalones | | | | | | |
| Interspecific | -11.9/-2.1 | (7) | +3.0/+3.1 | (7) | +19.1/-1.4 | (6) |
| Intraspecific | -6.8/-1.0 | (7) | +1.6/+0.1 | (7) | +8.6/-1.6 | (2) |
| Control abalones (mixed sizes) | | | | | +7.4/+0.9 | (7) |

*Note this period covers only 5 months and does not include summer when weight losses may occur

suggest that small urchins are unaffected by the presence of abalones. Large urchins consistently did better in intraspecific competition, even under conditions of excess food supply, suggesting that abalones in some way interfere with their growth.

The trends for both sizes of abalones were a function of food supply. All abalones at moderate and excess food levels grew better in interspecific competition but under severely food-limited conditions, large urchins apparently outscrambled the abalones. Both size groups of abalones lost weight under severely food-limited conditions, both size groups of urchins gained. Abalone mortalities observed during the last 2 years of the experiment supported these trends; 10 out of 15 intraspecifically competing abalones died vs 3 out of 15 interspecifically competing abalones. No such difference was observed with the urchins;

3 animals were lost from each treatment.

The change in the outcome of the interspecific competition experiments under conditions of low food supply and the urchins' superior food-conversion efficiency suggest the hypothesis that red urchins are better adapted to surviving food shortages in the wild. If the maintenance threshold for red abalones is higher than that for red urchins, episodes of reduced food availability could lead to decreases in abalone populations under conditions where urchin populations manage to subsist. To compare these herbivores' abilities to withstand food stress, red urchins, red abalones and purple urchins (S. purpuratus, a co-occurring urchin about half the size of S. franciscanus) were starved in separate aquaria supplied with coarse-filtered circulating sea water. The aquaria were scrubbed about every three days to prevent the buildup of edible

Table 3. Food stress experiments

|  | S. purpuratus | S. franciscanus | H. rufescens |
|---|---|---|---|
| N (# alive after 50 days) | 10 | 9 | 8 |
| $LD_{50}$ (days) | 175 | 221 | 203 |
| $LD_{90}$ (days) | 232 | 328 | 324 |
| Average % weight loss (± 2 S.D.) at time of death | 21.3% (±11.1) | 31.3% (±11.1) | 35.2% (±16.4) |

microorganisms. Only animals which survived a minimum of 50 days and thus were presumed to be free of disease or capture-associated injury were used.

When the results (Table 3) for weight loss are corrected for species differences in the ratio of inorganic material (shell or test) to tissues and body fluids, S. purpuratus remains the least tolerant to food deprivation, dying at a 48% organic weight loss. H. rufescens showed a 55% organic weight loss, while S. franciscanus lost almost 80% of its organic weight before dying. There was a strong tendency for smaller animals to die before the larger ones, -both within and between species, which probably reflects increased relative gonad production with size. It is known for urchins (Lasker & Giese 1954), and may be true for abalones as well, that the gonads are resorbed in times of food stress to provide metabolic energy.

While this experiment showed no difference in time to starvation for red urchins and red abalones, the animals do exhibit different behavioral adaptations for coping with food stress. We repeated Leighton's (1968) observations of the behavior of starved animals when the scent of Macrocystis is introduced into their water. Abalones assumed feeding posture, raising the anterior portion of their shell and body in position to snare the algae when it drifted by. Red urchins moved actively toward the source of the scent.

Differences in food preferences and grazing patterns further suggest that red urchins are better adapted to dealing with periods of reduced food supply and thus utilize food resources differently than red abalones. Leighton (1966) carried out extensive studies of the common kelp forest grazers' food preferences among seven species of algae. Both red urchins and red abalones strongly preferred Macrocystis of the seven algal species and consumed at least some of each of the other species. The urchins, however, showed a wider range of acceptance of algal species of intermediate preference (Leighton 1966), a more generalist feeding strategy. In times of adequate food supply, both red urchins and red abalones feed primarily on algal drift,

fragments of plants moved by currents and surge. Time-lapse photography and zones free of macroalgae up to about 0.5m around reefs where these grazers live indicate that they also undertake limited nocturnal foraging (Tegner et al. unpublished data). Once the drift food supply becomes limiting, however, red and purple urchins will leave their normal protected habitat and attack attached plants. In severe cases, urchin fronts form which move through stands of Macrocystis, consuming all living macroalgae with the exception of encrusting coralline algae (Leighton 1971). This behavior has not been observed in abalones, and Leighton (1968) reports observations of abalones starving to death after high densities of urchins destroyed algal beds.

Urchin populations may persist for considerable periods of time after macroalgae have disappeared from an area, subsisting on drift and fine-grained grazing which does not allow algal spores to become established or grow (Shepherd 1973). The presence of intact diatom frustules in sea urchin guts illustrates the efficiency of this mechanism (Leighton 1968). Sea urchins have also been reported to be capable of capturing large zooplankton (Leighton 1968), to take up and incorporate dissolved organic material from sea water (Pearse & Pearse 1973), and to utilize nitrogen fixed by bacteria in their gastrointestinal tracts (Guerinot and Patriquin 1981): such mechanisms would allow these grazers to persist under conditions of greatly reduced macroalgal food supply.

4 UTILIZATION OF SPACE

Food and space resources for abalones and sea urchins are closely linked because their primary method of feeding, the capture of drift algae, is strongly influenced by the physical structure of the habitat. While commonly co-occurring on the same reefs, red urchins and red abalones use space somewhat differently. Juvenile red urchins occur almost exclusively under the spine canopies of conspecific adults, a microhabitat offering protection from predators and a share of the drift food snared by the adult urchin

(Tegner & Dayton 1977). Once too large to fit under the spine canopy, intermediate-size urchins cluster close to adults or seek shelter under rocks or in crevices. Adult red urchins tend to be less cryptic, clustering at the base of reefs, under ledges or large rocks. Despite these variations, all size classes of red urchins can be found in the same general area, which is not the case for red abalones. We have most commonly found juvenile red abalones under rocks of less than 0.1m$^2$ bottom surface area or under the spine canopies of adult red urchins. Adult red abalones, requiring approximately planar surfaces large enough to accommodate diameters exceeding 200mm, are typically found under ledges, on the sides of reefs or under "table" rocks (>0.5m$^2$ bottom surface area), habitats which do not appear to offer adequate protection to juvenile abalones. Thus habitat where juveniles are abundant often will not physically support adults and vice versa. Intermediate-size abalones are found under intermediate-size rocks and in crevices. For all size classes of both herbivores, small-scale distribution patterns appear to reflect differential susceptibility to predation. Both are subject to a wider variety of predators when they are small and both attain a partial refuge in size as adults (Tegner & Dayton 1981, Tegner et al. unpublished data).

While behavioral interactions between red urchins and red abalones over the use of space may occur between any size classes, that between juvenile abalones and adult urchins may be the most important. In addition to the benefits of protection from predators and a food supply, adult urchins often maintain a patch of encrusting coralline algae free from overgrowth by other organisms. Encrusting coralline algae is a potent stimulus for red abalone veligers to settle and undergo metamorphosis (Morse et al. 1979). Juvenile red abalones up to about 20mm are common under urchins, but we have observed abalones of up to 50mm in the spine canopy nursery. The importance of the spine canopy nursery to abalones varies with the habitat; in areas where there is little to no turnable rock, successful abalone recruitment may depend completely on the presence of urchins. The benefits of the spine canopy association to both juvenile abalones and urchins also appears to be a function of food supply. In extensive barren areas where little or no drift macroalgae is available, the urchins scrape the substrate for microflora, a process which seems to interfere with the settlement or survival of juveniles, since none are found in extreme cases (Tegner et al. unpublished data). While the potential benefits of the spine canopy nursery to abalones is obvious,

the impact of this association on the urchins is not clear. We have observed adult urchins unsuccessfully attempting to keep juvenile abalones out and juvenile abalones displacing juvenile urchins from the cover of the canopy in the field.

The abalones' larger size, heavy shells and superior strength suggest that they would win interference contests for space, but such interactions may not be of importance to the structure of southern California kelp communities today. First, coexistence is common: animals can often be found side by side. Secondly, given the intensity of today's commercial fisheries, it is unlikely that space is ever limiting in southern California, although the quality of space must vary. Certain spots on the reef probably facilitate the capture of drift algae or are less accessible to predators. The quality of space may become critical with intense sea otter predation in central California (Lowry & Pearse 1973) or rougher sea conditions in northern California. Finally, small-scale distribution patterns of both species appear to reflect predation pressure.


5 POPULATION ECOLOGY

Natural history considerations are also relevant to the question of competition between sea urchins and abalones. Life history traits suggest that red urchins are a "weedier", more opportunistic species than red abalones. While some female red abalones mature earlier, Giorgi & DeMartini (1977) did not observe 100% sexual maturity until the abalones were larger than 100mm or about their fourth year. Red abalones produce a relatively large, lecithotrophic egg (170μ) and adult female fecundities are on the order of 10$^6$ (Georgi & Martini 1977). The larvae are planktonic for a short period, about 7 to 8 days at 15°C (Morse et al. 1979), and, once competent to settle, show less than a day's variation in time of settlement (Leighton pers. comm.). In contrast, red urchins become sexually mature by about 50mm (Bernard & Miller 1973, Tegner et al. unpublished data), which is during their second year of life. The planktotrophic eggs of S. franciscanus are about 120μ and adult fecundities are on the order of 10$^8$ (V.D.Vacquier pers. comm.). Red urchin larvae are planktonic for a minimum of 40 to 62 days (Strathmann 1978, Cameron & Schroeter 1980) and, once competent to settle, may delay settlement for up to two months (Strathmann 1978). Clearly, red sea urchins have a greater capacity for extensive dispersal than red abalones. This plus their more generalist feeding strategy

and their behavioral and physiological adaptations for coping with food stress indicate red urchins have a more opportunistic life-style than red abalones.

# 6 CONCLUSIONS

The importance of competition between the two largest herbivores to the structure of southern California kelp forest communities seems questionable today. Generally Macrocystis resources are abundant, and human exploitation now maintains populations of both grazers well below their carrying capacities. However, large-scale disappearances of Macrocystis standing stocks are a well-known feature of the recent history of this community (e.g. Leighton 1971, Tegner 1980) and continuing small-scale disruptions associated with grazing pressure, environmental fluctuations or Macrocystis life cycles (Tegner 1980, Tegner & Dayton 1981, Dayton Ms) suggest that competition between red sea urchins and red abalones may be important under some conditions. The apparent sea urchin population explosion, starting in the 1950's after intensive fishing greatly reduced abalone standing stocks, supports the hypothesis that interactions with abalones helped control urchin populations (North & Pearse 1970, Tegner 1980), ecological release being one of the more compelling sorts of evidence for competition (Wiens 1977).

Our data do not indicate that competition with red abalones is likely to be a major factor regulating red urchin populations. However, the consistency of trends in the laboratory growth experiments argue that weak competitive interactions are real. This is seen in the growth inhibition of large urchins in competition with abalones under all conditions of food supply, in superior growth of abalones in competition with urchins except when food was severely limiting (which is supported by different behavioral responses to food deprivation), and in more abalone deaths in the intraspecific competition experiments. Abalones may be able to decrease the urchins' relative fitness when food supplies are adequate through interference competition. Williams (1981) recently reported a case where interference competition between mobile herbivores mediates food and space utilization and may reduce destructive echinoid grazing pressure in a coral reef environment. Yet even with greatly increased abalone standing stocks, competitive exclusion would be unlikely because of the red urchins' opportunistic characteristics: better abilities to cope with food stress, higher reproductive rates and wider dispersal. While the abalones appear to exert a negative impact

on the urchins, the frequency of abalones in the spine canopy nursery and the apparent beneficial influence of sea urchins on the growth of both small and large abalones under conditions of excess food supply in the competitions experiment (Table 2) indicate that the presence of urchins is of positive value to the abalones.

These results have several implications for the structure of southern California kelp forest communities. Red urchins and red abalones both prefer Macrocystis, but abalones are not known to destructively overgraze their food resource as has been documented for sea urchins (Leighton 1971, Lowry & Pearse 1973, Shepherd 1973, Lawrence 1975, Tegner 1980, and references cited in these papers). In times of abundant food supply, the apparent interference abalones exert over urchin growth rates may help control urchin populations and hence their grazing, but we have no evidence that urchins could drive abalones from an area (or decrease their relative fitness) until food becomes limiting. Fluctuations in resources thus have a major potential for changing the outcome of any interactions.

The apparent urchin population explosion along the coast of southern California in the 1950's and '60's (North & Pearse 1970) was associated with major declines in Macrocystis beds but also with decreases in landings of both abalones and spiny lobsters, Panulirus interruptus, a major urchin predator (Tegner 1980, Tegner & Dayton 1981). It has recently been shown (Tegner & Dayton 1981) that red urchin population size structure, small-scale distribution patterns, and associated grazing damage to Macrocystis are strongly correlated with the presence of two major predators, the spiny lobster and the California sheephead, Semicossyphus pulcher. In contrast with the relatively weak effects competition with abalones appears to exert on red urchins, these predators, both of which are exploited, appear capable of regulating urchin populations.

Competition may have been more important in the past when larger standing stocks of both of the herbivores and their predators limited both food and space resources and made foraging tactics and habitat selection more critical. At today's population levels, predation and environmental fluctuations affecting food supply seem to be the selective forces affecting resource utilization traits and small-scale distribution patterns.

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