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## NOTE

# Differential effects of grazing by white sea urchins on recruitment of brown algae

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ABSTRACT: Experiments examined the effects of grazing by the white sea urchin *Lytechinus anamesus*, on microscopic life stages of laminarian algae and on newly recruited *Cystoseira osmundacea* in a Southern California kelp forest. Urchin exclusion experiments and culturing of cobbles from areas with and without urchins indicated that *L. anamesus* inhibited recruitment of laminarian algae by killing gametophyte or microscopic sporophyte life-stages. Newly recruited *C. osmundacea* were less affected and were able to survive in areas where white urchins were abundant. The differential effect of grazing by *L. anamesus* on these algae may lead to the exclusion of kelp by *C. osmundacea*, and may have a profound effect on eventual community composition regardless of the fate of urchins.

Grazing by sea urchins is a major structuring force in subtidal algal communities worldwide (see reviews by Lawrence 1975, Dayton 1985, Schiel & Foster 1986, Harrold & Pearse 1987). The most conspicuous effects of urchins occur when large mobile aggregations graze stands of adult macroalgae and cause abrupt changes in community composition. This results in the formation of so-called 'barren grounds', large expanses of hard substrata with few macroalgae. Scattered populations of urchins may remain in barren grounds eating drift from nearby kelp forests and microflora. As a result of the latter, barren grounds can persist for years as new algal recruits are grazed before they can reach adult size.

In the giant kelp *Macrocystis pyrifera* forests of Southern California there are 3 dominant urchin species: red urchins *Strongylocentrotus franciscanus*, purple urchins *Strongylocentrotus purpuratus* and white urchins *Lytechinus anamesus* (Leighton 1971). Red and purple urchins have received the greatest attention with regard to their effects on kelp (Leighton 1971, Dayton et al. 1984, Ebeling et al. 1985). However, recent studies indicate that grazing by smaller (~1 cm test diameter) but abundant white urchins may be very important in some kelp forests, especially with respect to grazing on juvenile life-stages (Dean et al. 1984).

This investigation of the effects of grazing by *Lytechinus anamesus* was prompted by several observations in the San Onofre kelp forest, 22 km northwest of Oceanside, California, USA (33°225'N, 117°32.5'W). In 1983–1984, we noted few visible recruits of *Macrocystis pyrifera* or other laminarian algae on cobble substrata with high densities of *L. anamesus*. This suggested that white urchins were inhibiting recruitment of kelp by grazing smaller, microscopic life-stages. Also, we observed heavy recruitment of *Cystoseira osmundacea* in offshore portions (depths of 13 to 14 m) of the San Onofre kelp forest in 1984–1985 and unlike *M. pyrifera*, *C. osmundacea* recruited in areas where white urchins were abundant. The latter observations suggested that *C. osmundacea* was less affected by grazing by white urchins than laminarian algae. Preferential feeding by urchins on algal species has been documented elsewhere (Leighton 1966, Vadas 1977) and such interactions have been shown to effect the distribution of algae (Vadas 1977, Lubchenco 1978, Sousa et al. 1981). Therefore, we tested the effects of *L. anamesus* on recruitment of small life-stages of laminarian algae and on the survival of newly recruited *C. osmundacea*.

Six stations were established in the San Onofre kelp forest in areas where *Lytechinus anamesus* were abundant: 3 in the northwest portion of the kelp forest and 3 in the southeast portion. These sites were located off of permanently marked transects that have been used since 1978 to monitor abundances of kelp and sea urchins (Dean et al. 1984). At each site, we erected fenced enclosures designed to exclude urchins. Each fence enclosed an area of 1 m$^2$. Plastic screening (Vexar), with a mesh size of 7 mm, was attached to a

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steel reinforcement bar frame and the frame was secured to the bottom with chain and T-shaped reinforcement bars. To prevent urchins from crawling over the fences, a lip made of sections of 10 cm PVC pipe cut longitudinally was secured to the top of the frame with plastic cable ties. The fences were paired with partially fenced controls at each site. The controls were identical to the fences described above except that the Vexar screen sides were cut off 10 cm above the substrata to allow urchins to crawl freely underneath the fences. The fenced and control pairs were 5 m apart.

The number of *Lytechinus anamesus,* laminarian algae, and *Cystoseira osmundacea* were counted after fences were erected on 2 April 1985. There were no other urchin species present. We then removed all white urchins from the exclusion areas and from a 1 m perimeter outside the fences. Twice weekly thereafter, through 31 May 1985, we visited each site and removed any urchins that had gotten into the cages (usually 1 to 6 individuals) and again cleared the area within a 1 m perimeter of the cages.

On 31 May 1985, we counted the number of *Lytechinus anamesus,* laminarian algae, and *Cystoseira osmundacea* within each exclusion and control plot. This was after the last clearing of urchins from the exclusion fences on 27 May 1985. We classified laminarian blades as such because *Macrocystis pyrifera* were indistinguishable from *Pterygophora californica* and other laminarian algae at this early stage of development. Later surveys at these sites indicated that all recognizable survivors were *M. pyrifera.*

Differences in the net change in densities of sea urchins and algae at test and control sites were examined using paired *t*-tests (Sokal & Rohlf 1969). In all cases, densities were log-transformed (log [density + 1]).

There was a significant change in densities of *Lytechinus anamesus* among fenced and control areas as a result of the exclusion of urchins. Densities of *L. anamesus* ranged from 59.5 to 30.8 $m^{-2}$ in fenced and control plots in our initial survey of 2 April 1985 (Table 1). Eight wk later, white urchin densities averaged 2.7 $m^{-2}$ in the exclusion and 56.0 $m^{-2}$ in the control area.

There were no visible laminarian algae in any of our plots on 2 April, but after 6 weeks small blade stages began to appear in the urchin exclusion areas. After 8 wk, densities of blades in the 1 $m^2$ fenced areas averaged 12.3 $m^{-2}$ compared with 1.8 $m^{-2}$ in the control. The increase in density was significantly greater in the exclusion area than in the controls (Table 1).

In contrast to the laminarian algae, changes in densities of *Cystoseira osmundacea* did not differ significantly among urchin exclusion and control plots (Table 1). However, mean densities decreased slightly in the control area and increased slightly in the exclusion sites, suggesting a possible effect of grazing by urchins.

We further examined the effects of grazing on microscopic life-stages of kelp by collecting cobble substrata from areas with high densities of *Lytechinus anamesus* (>10 $m^{-2}$) and from nearby 'control' areas without urchins. These cobbles were cultured in the laboratory for 3 wk to determine the number of gametophyte or microscopic sporophyte stages present. Three cobbles were collected from the downcoast (southeast) portion of the kelp forest where white urchins were abundant and 5 cobbles were collected from a control site ca 15 m away where there were no urchins. Both sets were collected from within 1 m of a adult *Macrocystis pyrifera* that had sporophylls with sori present, and that were presumably fertile.

The cobbles were placed in plastic buckets, covered, and brought to the surface. In the laboratory, cobbles were placed in filtered seawater containing $GeO_2$ (1 µg $l^{-1}$) overnight to prevent diatom contamination. The next day, the cobbles were placed in plastic culture containers with 8 l of Provasoli's enriched seawater Cultures were kept at 15°C and 45 µE $m^{-2}$ $s^{-1}$ irradiance levels (12 h photoperiod). These represent optimum conditions under which settled gametophytes develop into sporophytes within 10 to 21 d (Deysher & Dean 1986). After 3 wk in culture, the cobbles were examined under a dissecting microscope and the number of laminarian sporophytes were counted. The perimeter of each cobble was then traced and the surface area determined using a planimeter. Student's

Table 1. Mean densities (no. $m^{-2}$) and net change in densities of *Lytechinus anamesus,* laminarian blades, and newly recruited *Cystoseira osmundacea* in urchin exclusion and control areas. 'Before' means were from a sampling prior to the removal of urchins and 'after' means were from a sampling at the conclusion of the experiment 8 wk later

| | Mean before | | Mean after | | Net change | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | Excl. | Contr | Excl. | Contr | Excl. | Contr. | Paired *t* | df | *p* |
| *Lytechinus anamesus* | 59.5 | 30.8 | 2.7 | 56.0 | −56.8 | +25.2 | −9.70 | 5 | < 0.01 |
| Laminarian blades | 0 | 0 | 12.3 | 1.8 | +12.3 | +1.8 | −2.66 | 5 | 0.04 |
| *Cystoseira osmundacea* | 13.3 | 8.5 | 18.0 | 7.0 | +4.7 | −1.5 | −2.39 | 5 | 0.06 |

*t*-tests (Sokal & Rohlf 1996) were used to compare densities of sporophytes on cultured cobbles collected from urchin areas and from control sites.

Cobbles collected from areas with high densities of *Lytechinus anamesus* produced average sporophyte densities of 11 per 100 $cm^2$ after 3 wk in culture. This was significantly fewer than the 118 per 100 $cm^2$ on cobbles collected from a nearby site without urchins ($t = -3.26$, df = 6, $p = 0.02$).

The results of these experiments indicated that *Lytechinus anamesus* inhibited recruitment of laminarians by killing small sporophyte or gametophyte life-stages. Whether urchins were actively grazing laminarian sporophytes is in question. It seems likely that the urchins were grazing on the microflora of which small laminarian life-stages were a part. It may also be that many of the laminarians were abraded as the urchins moved across the substratum.

Unlike the laminarian algae, small *Cystoseira osmundacea* appeared to be relatively unaffected by white urchins. We observed urchins crawling over the small *C. osmundacea* and some fronds showed signs of being grazed. However, this did not have a significant effect on abundances of *C. osmundacea*, at least for the 8 wk experimental period.

Most of the *Cystoseira osmundacea* in our experimental plots were less than 10 cm in height at the outset of our study, and from the observations of Schiel (1985), we suspect that these individuals were recruited during the previous 2 to 3 mo. Thus, experiments were not conducted during a time when most *C. osmundacea* were developing from microscopic embryonic stages. However, new recruits were observed at one site where *Lytechinus anamesus* had persisted in high densities since 1978 (Dean et al. 1984, S. Schroeter & J. Dixon unpubl.) indicating that embryos developed and survived for several months where there were urchins.

Recruitment of *Cystoseira osmundacea* at depths greater than 10 m is unusual. Previous studies in the San Onofre kelp forest (T. A. Dean unpubl.) and elsewhere (Schiel 1985) indicate that *C. osmundacea* is seldom found at high densities ($> 1$ $m^{-2}$) at depths greater than 10 or 11 m. The recruitment of *C. osmundacea* in deeper parts of the San Onofre Kelp forest began in mid-1984, coincident with the El Niño of 1983 to 1984, and may have been the result of thinning of the *Macrocystis pyrifera* canopy, and increased water clarity that occurred during this time (Dean & Jacobsen 1986, Tegner & Dayton 1987). This extension of *C. osmundacea* into deeper waters plus the differential effect of grazing by *Lytechinus anamesus* on *C. osmundacea* and laminarian algae may have profound effects on future community composition. If *C. osmundacea* are able to escape grazing pressures of urchins, they may eventually dominate the community to the exclusion of laminarians such as *M. pyrifera* and *Pterygophora californica*. Established stands of *C. osmundacea* are resistant to invasion by laminarians (Dayton et al. 1984) and adult *C. osmundacea* have low rates of mortality (Dayton et al. 1984, Schiel 1985, Gunnill 1986). Thus, the effect of grazing on early life-stages may have a long-lasting influence on the community regardless of eventual changes in the abundance of white urchins.

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