The effect of sheephead (*Semicossyphus pulcher*) predation on red sea urchin (*Strongylocentrotus franciscanus*) populations: an experimental analysis

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Summary. An experimental evaluation of the effect of sheephead (*Semicossyphus pulcher*) predation on red sea urchins (*Strongylocentrotus franciscanus*) was initiated at San Nicolas Island, California in Sept. 1980. All sheephead ($N = 220$) were removed from an area of approximately 12,700 m² and subsequent changes in sea urchin numbers and microhabitat utilization were monitored along permanent transects for 24 months. The sea urchins within the transects were also measured in situ to determine changes in the size frequency distribution of the population. Although sea urchins rank only seventh in relative importance in the sheephead's diet at San Nicolas Island, there has been a significant increase in sea urchin numbers in the experimental area (26% increase/year) but there has been no change in the control site. Further, there has been a slight increase in the proportion of sea urchins occupying exposed versus sheltered microhabitats in the removal site. Changes in the size frequency distribution of the urchins were minimal (probably due to an observation period of only one year); the size frequency distribution was unimodal and skewed to the left, indicating weak recruitment of urchins. Comparisons of sheephead densities and the percent of sea urchins in exposed microhabitats (i.e. available to predation by sheephead) were also made at four areas around San Nicolas Island and three areas in Baja California. In areas with low sheephead densities (0–35/hectare) sea urchins were highly exposed, and in areas where sheephead densities were high (200–500/hectare), no urchins were exposed.

This study demonstrates that sheephead are capable of regulating the density and microhabitat distribution of sea urchin populations. These results are discussed in relation to other factors which may affect sea urchin populations.

Introduction

In recent years, much interest has been directed towards the influence of sea urchin grazing on nearshore subtidal communities (see reviews by Lawrence 1975; Lubchenco and Gaines 1981). In several of the areas studied, overgrazing due to high urchin densities has resulted in extensive barren areas (Estes and Palmisano 1974; Breen and Mann 1976; Duggins 1980). Absence of important predators, usually due to human influence, has been implicated as the cause of these urchin outbreaks (Paine and Vadas 1969; Estes and Palmisano 1974). Along the western coast of North America, over-exploitation of sea otters by fur traders in the 19th century drastically reduced the sea otters' range (Kenyon 1969). In many areas where sea otters are absent, high density urchin populations exist. This pattern is seen north of the otters' range in California (Mattison et al. 1977; Pearse and Hines 1979). However, along the coast of southern California and Baja California, relatively few urchin outbreaks have occurred. Historical evidence, as reviewed by Tegner (1980), indicates that where these outbreaks occurred, they did not do so until long after the otters were absent from this area.

Several possible explanations exist for the relative lack of urchin population outbreaks in this sea otter free area. First, urchin recruitment may be minimal and/or extremely patchy south of Point Conception. However, evidence shows that urchins recruit regularly and in high numbers in many areas studied within this region (Tegner and Dayton 1981). Second, additional predators may be present in sufficient numbers to regulate urchin populations (Nelson and Vance 1979; Tegner 1980). Specifically, Tegner (1980) identified the spiny lobster, *Panulirus interruptus* and the sheephead, *Semicossyphus pulcher* (Labridae), as potentially important predators of urchins south of Point Conception. A few areas where dense urchin outbreaks have occurred within this region have also been subjected to extensive fishing pressure by commercial and recreational fisheries (both of the above predators rank high in the take; Tegner 1980).

It has long been known that sheephead eat sea urchins (Limbaugh 1955), however, the extent to which they have been found to do so has varied among studies (Quast 1968; McCleneghan 1968; Winget 1968). Based on patterns observed in the field, a few researchers have argued that sheephead are important predators on sea urchins. For example, Nelson and Vance (1979) observed that the diademid urchin, *Centrostephanus coronatus*, displays a diel activity pattern which is opposite to that of the sheephead. From this observation and the fact that sheephead eat urchins, they inferred that sheephead may have played an important role in the evolution of the behavioral patterns of *C. coronatus*. Additionally, Tegner and Dayton (1977, 1981) attributed the pattern they found of a bimodal size frequency distribution for the red sea urchin, *Strongylocentrotus franciscanus*, to the relative extent of predation by sheephead and lobsters. To date, however, there has been no experi-

mental differentiation of the importance of the roles sheephead or lobster may have as sea urchin predators in nature.

The present study assesses the importance of sheephead predation on the red sea urchin, *Strongylocentrotus franciscanus*, through experimental manipulation. The work was done in an area free of the spiny lobster, *P. interruptus*. Three basic questions were addressed. First, how important are urchins in the diet of sheephead? Second, do sheephead affect sea urchin density? Third, do sheephead affect the microhabitat distribution of sea urchins, i.e., do they restrict the sea urchins to cryptic or protective habitats?

Site description

This study was done in a *Macrocystis pyrifera* forest located at Dutch Harbor on the south side of San Nicolas Island, California, USA (Fig. 1). The kelp forest grows on a bilobed, rocky reef (total area ca. 54,000 m²) surrounded by sand. The reef has extensive vertical relief and deep crevices; depth ranges from 6 to 18 m. The western lobe of the reef (area ca. 12,700 m²) was designated as the experimental site, and the eastern lobe as the control site. Sand separates the two lobes except in the shallow inshore portion of the reef. This shallow portion is composed of small, isolated rocky outcrops separated by sand channels (2–10 m wide). *Egregia menziesii* and *M. pyrifera* grow on these rocky outcrops. Even though the rocks are sparse, the algae were fairly thick, thereby producing a relatively dense canopy which gave the appearance of a continual rocky reef from the surface. *S. pulcher* was observed to be much less common in this inshore area than in the remaining portions of the reef. Lobsters were not present in either site (C. Harrold and D. Reed, unpub. data).

Methods

To test the effects that predation by sheephead have on red sea urchin populations, all sheephead were removed from the experimental site in September 1980 by spearing ($N = 220$). Sheephead are attracted to activities such as divers spearing fish; hence it is likely that most fish were seen and successfully removed. Following the initial removal, all additional sheephead seen in the experimental site were removed at roughly bimonthly intervals (usually 10–20 fish). In addition, sheephead of all sizes were tagged underwater (Matthews and Bell 1979) in the inshore portion of the control site to determine whether these fish were moving into the cleared experimental site. Otherwise, the control site was not manipulated. Some of these tagged fish were occasionally seen near their site of tagging, however, none were ever seen in the experimental site.

To assess changes in the number of sea urchins, five permanent transects were established in each site. The transects were placed along crevices specifically chosen such that the back of each crevice was visible, allowing all adult urchins within the crevice to be seen. Each transect was 5 m long and extended out 1 m from the mouth of the crevice. At bimonthly intervals, total counts were made of all urchins seen in the transects without disturbing any of the urchins.

The microhabitat utilized by each urchin in the transects was also noted. Three microhabitats were designated: (1) *crevice* – urchin within a crevice and/or in contact with two or more planes of the substratum; (2) *pocket* – urchin
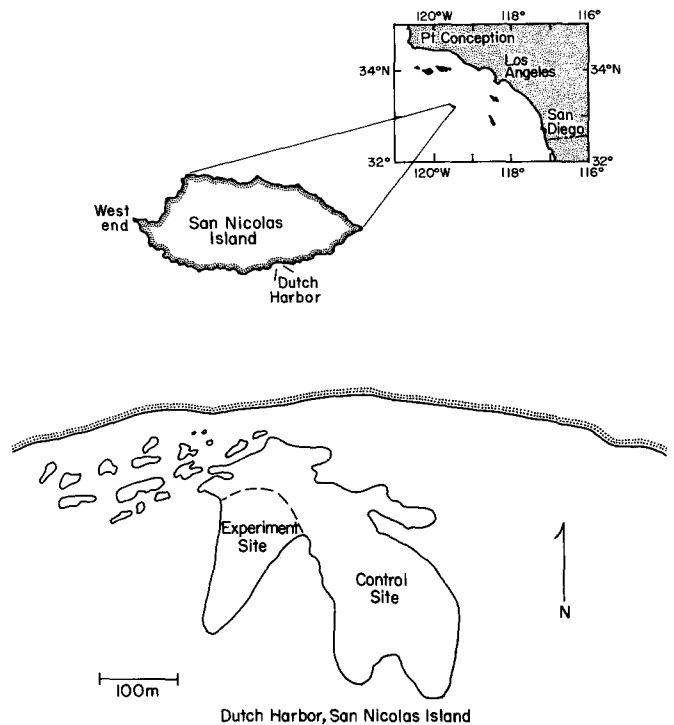

Fig. 1. Map of study site at Dutch Harbor, San Nicolas Island, California. Dashed line approximates the inshore edge of the experimental site

within a rounded depression (typically formed by generations of urchins in relatively soft substrata); (3) *open* – urchin away from any crevice or pocket and in contact with only one plane of the substratum. All urchins within a crevice or pocket microhabitat were considered to be sheltered from sheephead predation even though they could be seen by the investigator (Nelson and Vance 1979; Cowen, pers. obs.).

Urchin size frequencies were determined to examine changes in the size structure of the populations in the presence and absence of sheephead. Test diameters were measured in situ with calipers to the nearest 5 mm. With this method some urchins could not be reached, and these were not included in the measurements. Also, some very small urchins (< 30 mm) may have been under the adult urchins or small rocks (see Tegner and Dayton 1977) and this may have resulted in an under-representation of these size classes. Qualitative observations on nearby areas of the reef, however, did not produce any evidence of large recruitment of urchins during the duration of this study.

A representative sample of the sheephead removed from the experimental site was used for diet analysis. (A more extensive analysis of sheephead feeding habits is in preparation). The digestive tracts of these fish were removed and fixed in 4% formaldehyde and then transferred to 70% isopropanol. The prey contents within the tubular digestive tract were removed and identified to the lowest possible taxon. Each prey type was enumerated and the proportion each contributed to the total volume of the gut contents was estimated. Sheephead crush their prey extensively, occasionally requiring the actual number of prey items to be estimated from various identifiable parts (e.g. crab eye stalks and telsons) or their presence as an individual bolus (e.g. urchins).

Sheephead densities were compared with the proportion of sea urchins in the open microhabitat (i.e. those urchins exposed to predation) at four areas around San Nicolas Island and three areas in Baja California, Mexico. These areas were: (a–b) two urchin dominated (kelp free) areas on the west end of San Nicolas Island; (c) a kelp forested area on the west end of San Nicolas Island; (d) East Dutch Harbor (the control site); (e) Isla San Benitos, Baja California (115°34'W, 28°18'N); (f) Isla Guadalupe, Baja California (118°17'W, 29°9'N); and (g) Thurloe Bay Headland, Baja California (114°51'W, 27°37'N). Sheephead densities were estimated from 5 × 50 m transects swum by a diver who recorded all observations on an underwater tape recorder. This method allowed the diver to keep his eye on the fish at all times and swim quickly enough to observe and identify the fish before they could react to his presence, thereby minimizing bias. Urchins were counted, as above, in 5 m transects placed along haphazardly chosen crevices.

Results

Sheephead diet

Sheephead from the experimental site at San Nicolas Island fed on a broad array of prey items (Table 1). The most important prey type, based on index of relative importance values (IRI) (Pinkas et al. 1971), was small brachyuran crabs (carapace length 8–12 mm). Barnacles, primarily *Balanus tintinnabulum*, ranked second. Urchins ranked seventh in importance though they were third overall based on volume only. Usually one urchin bolus (and at most two) was found in the digestive tract of a given sheephead, however, the urchin usually constituted a fairly large proportion of the volume of the food in that fish (range 5–54% of total volume). Many of the least important prey items (e.g. sponge, sipunculids, hydrozoans) were probably taken incidentally with other prey.

Sheephead effect on urchin density

Predation by sheephead appears to have a strong effect on the abundance of *S. franciscanus*. During the 24 months following the removal of sheephead, there was a significant increase in the number of *S. franciscanus* in the experimental site transects (Fig. 2). During the same period, the number of urchins in the control site transects remained the same or decreased slightly. Regressions fitted to each transect and tested with an analysis of covariance (Snedecor and Cochran, 1967) showed no significant differences of slopes and variances within each site, but the slopes between sites were significantly different ($P < 0.01$). This slope represents an approximately 26% annual increase in the number of urchins in the absence of sheephead predation.

As an independent analysis of the effect of sheephead predation on red sea urchins, an estimate of the *S. franciscanus* standing crop consumed per year by sheephead was calculated (see Paine 1969). To obtain this estimate, the following data were collected. (1) Sheephead density in the experimental site was estimated from the total number removed in the initial clearing. This estimate agrees with transect data on fish densities in the control site (185/hectare and 196 (S.D. = 72)/hectare, experimental and control sites, respectively). (2) The frequency of occurrence of urchins in the diet of sheephead was obtained from the

Table 1. Diet analysis of sheephead from San Nicolas Island (Dutch Harbor). The mean proportionate number, volume, and percent frequency of occurrence of 26 prey items are listed. Index of relative importance values (IRI) are calculated (%N + %V) × %FO. N = 83

| Prey type	%N	%V	%FO	IRI
Crustaceans				
Brachyuran crabs	10.8	43.3	91.5	4950
Barnacles	11.4	7.7	62.6	1196
Mole crabs	0.6	14.7	24.1	369
Gammarid amphipods	5.8	1.1	53.0	366
Decapod shrimp	2.5	2.9	42.2	228
Isopods	0.7	0.7	14.4	20
Molluscs				
Bivalves	3.5	2.9	67.5	432
Gastropods	3.4	1.6	56.6	283
Chitons	0.4	1.1	16.9	25
Echinoderms				
Urchins	0.7	8.5	36.1	332
Brittlestars	0.7	0.6	19.3	25
Sand dollars	0.5	0.5	9.6	10
Sea stars	0.02	0.2	1.2	1
Cucumbers	0.08	0.05	2.4	1
"Worms"				
Polychaetes	3.9	3.9	61.4	479
Nemerteans	0.4	0.01	1.2	1
Sipunculids	0.4	0.05	2.4	1
Miscellaneous				
Eggs	47.8	0.6	6.0	290
Algae	1.7	1.5	39.8	127
Polychaete tubes	2.5	2.7	21.7	113
Tunicates	1.0	2.4	22.9	78
Bryozoans	1.1	1.0	26.5	56
Fish	0.2	0.9	13.2	15
Hydrozoans	0.2	0.5	7.2	5
Anemone	0.4	0.2	1.2	1
Sponge	0.1	0.1	7.2	1
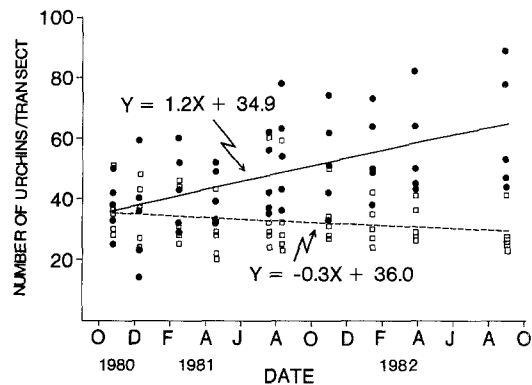
Fig. 2. Changes over-time in *S. franciscanus* abundance in the presence and absence of sheephead. The data are presented as the number of urchins per transect: solid circles are experimental site, open squares are control site. The regressions are of all five transects in each site: solid line is experimental site, dashed line is control site

diet analysis. When sheephead feed on *S. franciscanus*, portions of the test are consumed. This allows for easy identification of an urchin "meal", however, it is not clear whether this represents a whole urchin or if the urchin was ultimately shared with other sheephead. (3) To clarify this point, individual urchins (90–130 mm test diameter) were placed in the open and the number of sheephead actually taking bites

of the test were counted. (4) The number of meals each sheephead ate per day was estimated by both field observations and by examining the degree of gut fullness of sheephead collected at various times of the day. (5) Finally, urchin densities were estimated with randomly placed 1 m² quadrats.

Sheephead density, diet analysis and feeding observations were integrated to estimate the annual consumption of urchins by sheephead (Table 2). Of the sheephead digestive tracts examined, 36% contained remains of sea urchins. Feeding trials in the field showed that an average of 3 (S.D. = 2) sheephead consumed portions of the urchin's test during the attack on a single urchin. Hence, for the purpose of the estimation of predation rate, the occurrence of sea urchin parts in the digestive tracts of three sheephead are assumed to represent a single urchin. Other fish, including smaller sheephead, will also take bites of the urchin, but they only obtain such soft, quickly digested parts as gonads, which are not recognized in the diet analysis. Since 36% of the fish examined had urchins in their digestive tracts and the density of sheephead is 185 per hectare, I estimate that 22 urchins are consumed in one hectare per day. Over a year, that estimate becomes 8030 *S. franciscanus* eaten by sheephead per hectare.

This estimate would be conservative if there are multiple feeding periods by sheephead in one day. Several lines of evidence, however, indicate that this is not the case. First, sheephead appear to have a single peak feeding period in the morning hours with a much lower rate of feeding occurring through the remainder of the day. Of 131 digestive tracts collected at different times of the day, only those collected within 1.5 h of sunrise were consistently empty (or at least the posterior portion). During all other periods of the day, the digestive tracts were relatively full. Sheephead are strictly diurnal animals which retreat to holes and crevices in the reef at night (Ebeling and Bray 1976; Nelson and Vance 1979; Hobson et al. 1981); hence, they do not feed during the night. In addition, at no time has any sheephead been observed to defecate in the water, thereby emptying part of its digestive tract for further feeding (pers. obs.). This suggests that sheephead may only be defecating at night. The pattern of feeding during the day and defecating at night has been found in other reef fishes (Bray et al. 1981). From these data and observations, I consider sheephead to be consuming only one main meal per day.

Densities of sea urchins in the control and experiment sites were highly variable ($X \pm$ S.D.: $2.4 \pm 3.3/m^2$, $N = 50$ and $3.9 \pm 5.1/m^2$, $N = 37$, respectively), reflecting a patchy distribution within a high relief reef. Therefore, the standing crop of *S. franciscanus* is given as a range (24,000–39,000 urchins/hectare) to cover some of the possible urchin densities sheephead are likely to encounter. Dividing the number of *S. franciscanus* eaten in one year by the standing crop provides the final estimate of the percentage of the *S. franciscanus* standing crop that are consumed annually by sheephead, 20.5–33% (Table 2). The observed annual increase in urchin numbers in the experimental site, 26%, falls within this estimated range.

Effect of sheephead on urchins' spatial distribution

Concomitant with the increase in the abundance of urchins, utilization of the open microhabitat by *S. franciscanus* increased along the experimental site transects (Fig. 3). Prior

Table 2. Estimate of the percent of the urchin standing crop eaten by sheephead at Dutch Harbor, San Nicolas Island. See text for details

A.[a]	Sheephead density (number/hectare)	185
B.[b]	Number of urchins eaten by sheephead per day per hectare	22
C.	Number of urchins eaten by sheephead per year per hectare	8030
D.[c]	Urchin standing crop (number/hectare)	24,000–39,000
E.	Resulting percent of the standing crop consumed by sheephead per year	20.5–33%

[a] Based on the actual clearing of sheephead
[b] Based on: 1) 36% of sheephead with urchin remains in diet; 2) 3 (SD = 2) sheephead sharing an urchin; 3) one feeding per day per sheephead
[c] Range based on mean estimates ($\pm$ SD) of $2.4 \pm 3.3/m^2$ (control site) and $3.9 \pm 5.1/m^2$ (experimental site)
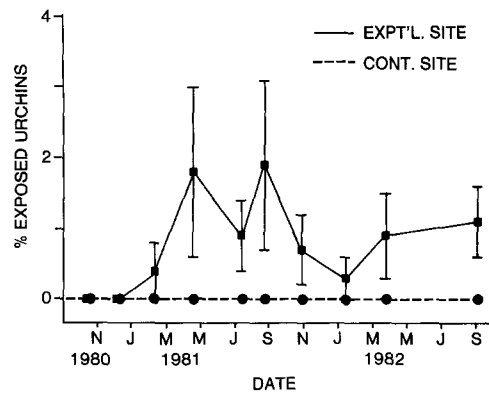

Fig. 3. Changes over time in the percent of *S. franciscanus* in the open (i.e. exposed) microhabitats in the presence and absence of sheephead (control and experimental sites, respectively). Data are presented as $\bar{X} \pm$ S.E. ($n = 5$ transects)

to the removal of sheephead no urchins were found in the open in either site. Throughout this study, all urchins observed in the control site were in sheltered microhabitats (i.e. crevices and pockets). In the experimental site, a low percentage of the urchins were found in the open microhabitat, beginning about six months after the initial clearing. Although relatively few urchins were in the open in the experimental site, their presence there indicates a lack of predation. All urchins placed in the open in the control site either quickly moved to shelter or were attacked by sheephead. No urchins placed in the open in the experimental site were ever attacked.

Comparison of the proportion of urchins in exposed microhabitats with sheephead densities in different geographical locations supports the experimental conclusions that sheephead affect the spatial distribution of sea urchins (Fig. 4). For example, one of the areas on the west end of San Nicolas Island had absolutely no sheephead and the entire area was an urchin "barrens" with almost every urchin exposed. The two other areas examined on the west end of San Nicolas Island had relatively low densities of sheephead and a fairly high proportion of the urchin population in exposed microhabitats. All of these areas also had very low lobster densities. To the contrary, the control site at Dutch Harbor, San Nicolas Island, had relatively high
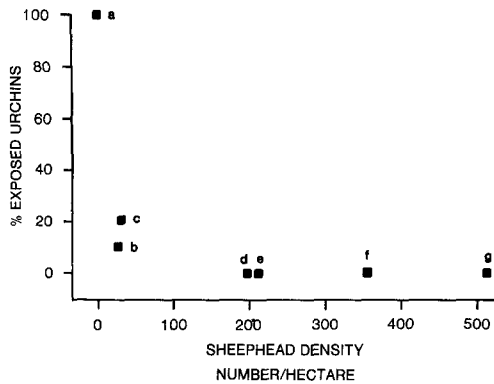
Fig. 4. Comparison of the percent of *S. franciscanus* in open (i.e. exposed) microhabitats versus the density of sheephead at seven different sites. The letters refer to the sites listed in the text (methods).

sheephead densities and, as shown above, no urchins were ever found in exposed microhabitats. The Thurloe Bay, Baja California site had extremely dense sheephead and lobster populations. This site also had no urchins in the open. In fact, the urchin population at Thurloe Bay was very sparse (pers. obs.). The same trends are present at both Isla San Benitos and Isla Guadalupe (Fig. 4).

Size frequency of urchins

No significant changes were seen in the urchin size frequencies in either site over the period they were examined (Nov. 81–Sept. 82; Fig. 5). The size frequency of both the control and experimental site urchins was basically unimodal and skewed to the smaller size classes. There was no indication of a large scale recruitment during this study. However, there is evidence of a weak recruitment by September, 1982, in both sites, though it was stronger in the experimental site.
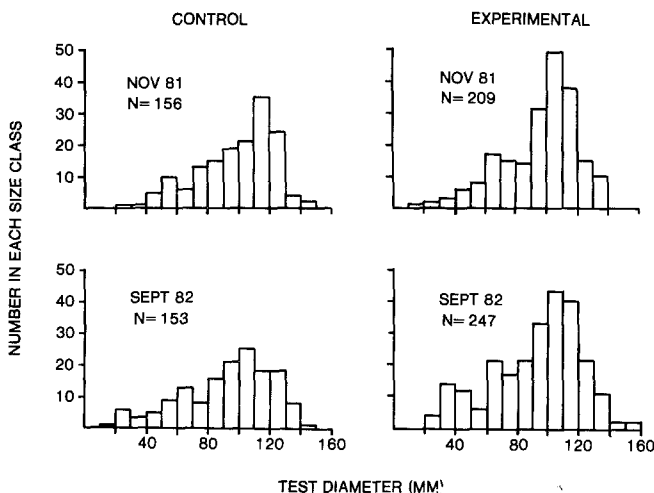

Fig. 5. Size frequency distribution of *S. franciscanus* test diameters sampled on both sites on November, 1981 and September 1982. The change over time within each site was non-significant at $\alpha = 0.05$ (Median test, $\chi^2_{(1)} = 2.9$ and 0.2, control and experimental sites, respectively)

Discussion

This study demonstrates that sheephead are capable of affecting the density and microhabitat distribution of sea

urchin populations. By eating only exposed sea urchins, sheephead successfully restrict urchins to crevice and pocket microhabitats and limit their densities. Following the removal of sheephead from the experimental site, the number of urchins increased at a fairly rapid rate (26%/year). For the purpose of examining whether this rate of increase could be accounted for by the absence of sheephead predation, I estimated a potential predation rate. The resulting estimate indicates that the observed increase of urchin numbers in the absence of sheephead is realistic (Table 2).

This is interesting in light of the finding that, at San Nicolas Island, *Strongylocentrotus franciscanus* do not dominate the diet of sheephead. Their generalized diet is important in two respects. First, considering their impact on urchin populations, sheephead may also be important predators on a variety of other invertebrates within the reef system that are also included in their diet. Second, such a broad diet may provide sheephead with valuable flexibility when they are in a potentially competitive situation. In the past, when sea otters co-occurred with sheephead, it is likely that urchins were infrequently eaten (if at all) by sheephead. By reaching within crevices (Lowry and Pearse 1973), sea otters are capable of preying on urchins which were unavailable to sheephead. Since sheephead eat a wide array of prey, the loss of urchins from their diet should not seriously affect their survival.

Tegner's (1980) contention that sheephead (and lobster) predation has been important south of Point Conception since the demise of sea otters is supported, at least for sheephead. Wherever sheephead are abundant throughout the main part of their range (Pt. Conception, California to Punta Abreojos, Baja California), urchins are restricted to protective microhabitats and presumably their numbers are restricted. This appears to be the case whether lobsters are present or not. In tropical regions, a wide variety of fishes forage on urchins, and the urchins have demonstrated a host of adaptations to this predation pressure (Randall et al. 1964, Randall 1967; Snyder and Snyder 1970; Fricke 1971). However, within temperate areas, the importance of fish predation is only recently becoming understood (Bernstein et al. 1981; Andrew and Choat 1982). In both of these studies, fish were shown to be important urchin predators, but they were not capable of regulating the urchin populations because of only a seasonal presence of the fish (Bernstein et al. 1981) or their inability to prey on all urchin size classes (Andrew and Choat 1982). The present study has shown that sheephead can successfully regulate sea urchin abundance. Their success may arise from the fact that sheephead at San Nicolas Island are permanent residents of the community and exposed urchins have little, if any, refuge in size.

A question that remains unanswered at this point is: where are the additional urchins coming from? There are several possibilities. First, in the absence of a large, consistent recruitment, there may still be a sufficient number of urchins recruiting to maintain the urchin population. To obtain the increase of urchins found in this study, only 12 recruits/transect/year are needed. Considering the weak recruitment as seen in the size frequency distribution of the urchins (Fig. 5), this may be partially realized. Second, urchin recruitment may occur as an occasional pulse, as was found in areas off Oregon and central California (Ebert 1967). However, in the absence of such a pulse, one would have expected to see the number of urchins in the control

site to continuously decrease while those in the experimental site would have remained constant. Since this is opposite to the present findings, this possibility can be discounted. Finally, there may be a "pool" of urchins throughout the reef that is moving from one crevice to another. The rate of movement would be determined by the quality of the crevice, i.e. amount of drift algae available. Urchins within a crevice with a sufficient food supply would remain there (Russo 1979). All of the transects in this study were along the lower edge of the reef's rocky outcrops. It is possible that, by being closest to the bottom, more drift is available to urchins in these crevices than those in crevices along rocky faces or on top of the reef. Urchins would not be expected to leave these lower crevices. In the absence of sheephead, the urchins moving into (and remaining) in higher quality crevices would not be eaten (either in transit, or as the crevices become crowded and urchins are forced into the open).

Another question of interest is: what mechanisms would cause the proportion of urchins in the open microhabitat to increase? Throughout this experiment at San Nicolas Island only a very low proportion of the urchin population was exposed in the absence of sheephead. However, as shown in this study, there are areas where a large proportion of the urchin population is exposed where sheephead densities are low (Fig. 4). An increase in the proportion of exposed urchins may occur in two ways. First, over time, the urchin population continues to build up in the absence of extensive predation pressures and eventually both fills the available crevices and overexploits the available drift for food. As the population continued to grow and drift food became in short supply, more and more urchins would be required to move into the open to find food. Urchins have been shown to increase their movement in the absence of adequate food supply (Mattison et al. 1977; Russo 1979; C. Harrold and D. Reed, unpubl. data). Second, the source of drift material could be significantly reduced following an extensive local disturbance. As above, in the absence of drift algae, the urchins would have to move from the crevices in order to find another food source. An example of this appears to have occurred on Naples Reef, Santa Barbara, Calif. where sheephead are relatively rare (78/hectare; Ebeling et al. 1980) and extensive storm waves severely reduced the *Macrocystis pyrifera* canopy in the area (A. Ebeling and D. Laur, pers. comm.).

Finally it appears that a threshold exists in relation to sheephead density and their effect on urchin populations. In areas with sheephead densities above this threshold, urchins are completely confined to protective microhabitats as a result of predation by the sheephead. Where sheephead densities are below this threshold, the urchin populations respond directly to other regulating mechanisms such as food shortages and storms. From the results of this study, this threshold appears to be somewhere between 100–150 sheephead per hectare. However, the exact determination of the threshold is difficult, since it is likely to vary between sites in relation to such factors as urchin recruitment rates, food and crevice availability, lobster density and storm intensity.

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