

SPATIAL VARIATION IN RED SEA URCHIN REPRODUCTION AND MORPHOLOGY: IMPLICATIONS FOR HARVEST REFUGIA¹

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Abstract. Red sea urchins (*Strongylocentrotus franciscanus*), residing in shallow habitats in Bodega Bay, California are morphologically distinct and possibly enhance recruitment by spawning larvae and sheltering juveniles. This suggests shallow beds of urchins would be ideal candidates for harvest refugia promoting the production of larvae to replenish deeper harvested habitats. Red urchins from shallow beds (5 m) had significantly heavier gonads (63 ± 30 g, $N = 45$, mean ± 1 SD) compared with urchins from intermediate (14 m) and deep (23 m) habitats (12 ± 8 g, $N = 39$, mean ± 1 SD). Gonad indices from spring, summer, and fall of 1991 and 1992 show this pattern persisted. Shallow water urchins co-occurred at high densities (4.6 individuals/m²), with seasonally abundant drift algae and wave surge. Recruitment of juvenile urchins was examined in nine 1-m² quadrats randomly placed in three shallow sites with red urchins and three intermediate depth sites with red urchins in the Bodega Marine Reserve. Juvenile urchin (*Strongylocentrotus* spp.) recruitment (5–50 mm) was highest in association with adults in shallow habitats over a 4-yr period (October 1988–October 1992). Adult red urchins in shallow habitats resided in rock “bowls” where they were 12 times more likely to shelter juveniles than more mobile adults in deep water. Principal component analysis identified five morphological characteristics of shallow water urchins: short spines, large gonads, thick tests, small lanterns, and small peristomial openings. External morphological characteristics (e.g., spine length) could be used to ensure the protection of reproductive urchins in shallow harvest refugia offering an alternative urchin management strategy for northern California.

Key words: echinoderm; fishery management; gonad index; marine reserves; morphometry; Northern California; nursery microhabitat; recruitment; spine canopy protection; *Strongylocentrotus franciscanus*.

INTRODUCTION

Sea urchins are important subtidal herbivores within marine invertebrate and algal communities (reviewed by Lawrence 1975, Harrold and Pearse 1987). Urchins influence the distribution and abundance of algal assemblages, periodically overgrazing kelp forest communities, creating “barren” habitats totally devoid of macroalgae (Harrold and Pearse 1987). Red sea urchins, *Strongylocentrotus franciscanus* (Agassiz), are fished commercially from Mexico to British Columbia (Sloan 1986). In 1991 red urchins became the state of California’s most valuable fishery, worth 34 million dollars ex-vessel price (Kalvass et al. 1991). However, red urchin landings in northern California have declined from 13.8×10^6 kg (30.4×10^6 pounds) in 1988 to 3.2×10^6 kg (7.2×10^6 pounds) in 1993 (P. Kalvass, *personal communications*). Catch per unit effort (CPUE) estimates have also declined by $\approx 40\%$ since

1988. Subtidal transect surveys show a significant reduction in average urchin densities from 1.3 individuals/m² in 1988 to 0.71 individuals/m² in 1991, as well as a reduction in the mean test diameter of urchins from 92 mm in 1988 to 77 mm in 1991 (Kalvass et al. 1991). Lower size limits and season closures are currently in effect, and more regulations have been proposed. This decline in urchin stocks has prompted investigations into the reproductive biology of red urchins in northern California and alternative management strategies.

Habitats where large numbers of juveniles (in excess of local mortality) are generated are called “hot spots” and have been identified for many organisms including butterflies (Harrison et al. 1988), newts (Gill 1978), and spiny lobsters (Davis and Dodrill 1980). Source habitats (*sensu* Pulliam 1988), nursery habitats, or reproductively important habitats could be encompassed within harvest refugia (or fishery refugia) to protect spawners and replenish neighboring harvested habitats with surplus individuals. In the North Pacific fur seal fishery, reproductive bull males and their female harems are protected in rookeries, while immature seals

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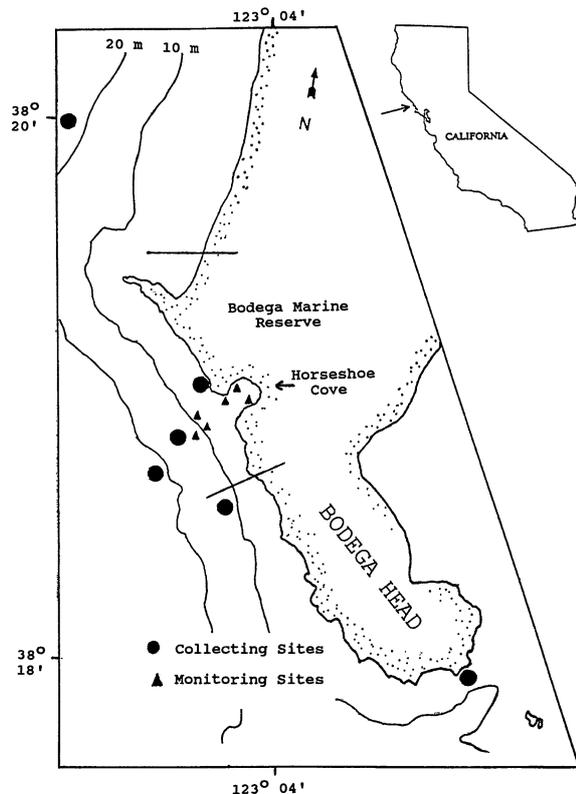


FIG. 1. Map of Bodega Head and the Bodega Marine Reserve, California, showing monitoring and collecting sites.

and bachelor males are harvested (Wilensky 1976, Bonner 1982). Juvenile lobsters in Florida disperse from protected lagoons to deeper fished habitats (Davis and Dodrill 1980). This management strategy can prevent recruitment over-fishing (Davis 1989, Dugan and Davis 1993).

At present, little is known about whether red urchins residing in certain habitats promote recruitment by producing larvae (spawning) or by enhancing the survival of benthic juveniles (sheltering). Red urchin recruitment is defined here as the addition of juveniles ≥ 5 mm in diameter. Habitats that promote recruitment should have (1) abundant algal resources for the development of gonadal tissue in adults, (2) sufficiently high densities of adults to ensure fertilization success, (3) oceanographic features that deliver competent larvae, (4) suitable substrates to attract settling larvae, and (5) sheltered microhabitats that protect newly settled and juvenile urchins from various sources of mortality (e.g., predation).

Some evidence suggests that reproduction, growth, and recruitment in sea urchins may be habitat specific. First, urchins from habitats rich in preferred algal resources often have larger gonads (Vadas 1977), produce more gametes (Keats et al. 1984), and may grow faster than urchins from algae-poor habitats (Ebert 1968, Baker 1973). Second, sea urchins are attracted to abundant

algal resources (Vadas et al. 1986), creating locally dense aggregations within food-rich habitats. Dense urchin aggregations are required for reliable fertilization success (Levitan et al. 1992). Third, sea urchin recruitment appears to be variable spatially (reviewed by Ebert 1983) over continental (Ebert and Russell 1988) as well as local (1–8 km) scales (Sloan et al. 1987). At the microhabitat scale (1 square metre) juvenile red urchins are often spatially distributed under the spine canopy of adults (Tegner and Dayton 1977, Breen et al. 1985, Sloan et al. 1987). In such a microhabitat, juvenile survival may be enhanced by protection from predation and by increased access to macroalgal food resources acquired by adult urchins (Tegner and Dayton 1977). Finally, local environmental conditions are known to influence the morphology of sea urchins (reviewed by Marcus 1983), suggesting that reproductively important urchins might be recognizable.

In this paper, we examine the reproductive potential and sheltering behavior of adult red sea urchins within the environmental regimes found along a depth gradient at Bodega Head, California. We compare red urchins from shallow, intermediate, and deep subtidal habitats for (1) urchin morphology, including gonad index (an indirect measure of reproductive potential), (2) adult urchin density, and (3) the utilization of rock "bowls." We quantify (4) the recruitment of juvenile urchins in the genus *Strongylocentrotus* and, (5) the sheltering behavior of adult red urchins (as defined by Tegner and Dayton 1977). In addition, we report on the environmental conditions associated with shallow and deep subtidal habitats, including food supply (drift algae), wave action, and substrate composition. Finally, we suggest the establishment of shallow harvest refugia to protect potential brood stock, sheltering adults, and newly recruited juveniles, utilizing urchin morphology as a means of identification.

METHODS

Study area

Subtidal studies were conducted along Bodega Head and in the Bodega Marine Reserve (BMR) which extends from Mussel Point south beyond Horseshoe Cove, Bodega Bay, California (38°19'03" N, 123°04'12" W) (Fig. 1). Bodega Head is an exposed headland made up of mostly granitic rock (quartz diorite), and shallow habitats periodically experience intense wave and wind-driven flows. The California Current in this region generally travels from north to south, except when strong north winds blow and upwelling forces surface waters and larvae offshore. Upwelling-relaxation season usually begins sometime in March (spring transition) and lasts into the summer. Some mechanisms have been proposed to facilitate larval transport onshore including cross shelf "fronts" (Roughgarden et al. 1991), internal waves (Shanks 1983), and upwelling shadows (Graham et al. 1992). However, larval transport along

irregular coastlines in northern California is complex and remains unknown.

Red urchins in shallow habitats aggregate in discrete beds where they reside in scoured rock "bowls." Urchins in deeper habitats remain loosely attached to the substrate. Granite walls are cut by sand channels along the rocky reefs. Further offshore, large granite boulders rise from a sand substrate. Winter storms dominate the region from December through February tearing up much of the attached algae. Red urchin spawning is temporally unpredictable but usually occurs sometime during the winter and/or spring. Late summer and fall are characterized by fog, long periods of calm ocean conditions, and algal growth.

The rank abundance of attached vegetation in the shallow subtidal is (1) short fleshy red algae mostly *Cryptopleura* (= *Botryoglossum*), *Gigartina*, and *Iridaea*, (2) articulated and encrusting coralline algae, (3) seagrass *Phyllospadix*, and (4) the understory kelp *Egregia*. Articulated coralline algae are most abundant in shallow habitats. Deeper depths have lower algal diversity with encrusting coralline algae, and fleshy red algae. There is no surface canopy of large kelps *Nereocystis* on Bodega Head nor extensive subcanopy kelps *Pterygophora*, as at some other sites in northern California. Also absent are many important urchin predators, including sea otters *Enhydra lutris* (Estes et al. 1982), sheephead fish *Semicossyphus pulcher* (Cowen 1983), and spiny lobsters *Panulirus interruptus* (Tegner and Levin 1983). There are many species of sea stars, including the urchin-eating sunflower star *Pycnopodia helianthoides* and the leather star *Derasterias imbricata*.

Urchin study sites

Three shallow (5 m) and three intermediate (11 m) study sites each 8 × 8 m (64 square metres) were permanently marked with stainless bolts inside and beyond the mouth of Horseshoe Cove, in the BMR (Fig. 1). Replicate sites were chosen to maximize habitat uniformity and urchin abundance. In these sites we examined urchin density, behavior, and juvenile recruitment. Urchin density was examined in 1988 at these sites and at three additional deeper sites (17 m) beyond Horseshoe Cove in fall 1992. The movement of adult urchins in shallow and intermediate sites was examined in August 1991. Spines of twenty adult urchins were tagged in situ with individually labelled surgical tubing, lasting 1–2 wk (Coyer & Witman 1990). Twenty "bowls" holding tagged urchins were also labelled with numbered bands in Z Spar epoxy putty. Urchins at intermediate and deep sites were loosely attached to rock walls.

The recruitment of juvenile *Strongylocentrotus franciscanus* and *S. purpuratus* was examined in nine randomly placed 1 × 1 m quadrats in the six sites quarterly, or as weather permitted from October 1988 to October 1992. Juvenile urchins were measured to the

nearest millimetre. Juvenile (5–20 mm) red and purple urchins cannot be distinguished in the subtidal (R. J. Rowley, *personal communication*). Individuals <5 mm could not be accurately sampled using these techniques. Quadrats were searched invasively by removing adults from the substrate to examine the distribution of juveniles in cryptic microhabitats. Canopy-providing adults were defined as urchins with juveniles under their test or in contact with spines.

Urchin morphometrics and biometrics

Red urchins were collected from Bodega Head in the fall of 1990 and 1991 from shallow (5 m, $N = 45$), intermediate (14 m, $N = 42$), and deep (23 m, $N = 39$) habitats (Fig. 1). Seven linear and three mass characters were measured for each adult urchin. Linear measures made with vernier calipers included: test diameter, test height, perimeter to top of test (madreporite), perimeter to edge of peristomial opening, diameter of peristomial opening, spine length (mean of three longest spines), and test thickness at ambitus (maximum test diameter). Measures of ambitus and test height on three live red urchins showed that precision was ± 2.1 mm ($N = 10$). All other linear measures were within 0.1 mm.

Live urchin body mass (wet) and gonad mass and lantern mass after paper towel drying were determined to within 0.1 g. Compression strength was determined by applying weight to the aboral side of a whole urchin, resting on the ground, until the test cracked. Compression strengths were ranked from 1–10 corresponding to 10–100 kg. In addition, tube feet pore pairs from three test plates at the ambitus were counted from a subsample of shallow ($N = 13$) and deep urchins ($N = 13$). Two color variations were recorded: light pink and dark red. Sex was determined by examining the gonads for eggs or sperm.

Urchin samples covered the range of test sizes available at each depth. Each variable was transformed to natural logarithms and analysis of covariance (ANCOVA) among depth-groups using test diameter as the covariate was performed for each of nine variables (six linear measurements, three mass measurements). Morphometric characters that exhibited significant differences among depth-groups using ANCOVA were standardized to zero mean using z scores, and principal components analysis (PCA) was performed to construct components, or multivariate indices, of urchin size and shape (Pimentel 1979, Rohlf 1990).

Multivariate analysis of variance was used to determine if the habitat-groups represented by the six multivariate indices differed in discriminant space. Discriminant functions were then calculated based on the six multivariate indices to group individuals among the habitat-depths. Discriminant scores were plotted to examine similarities among urchin habitat groups. Factor scores for each urchin were examined from the two multivariate indices (from the PCA) that contributed most to the discrimination between shallow, interme-

TABLE 1. Density of adult red urchins inside and beyond the Bodega Marine Reserve. Each depth level represents three 8 m² sites.

Depth	Year	Total no. (no./m ² ± 1 SD)	Density
			(no./m ² ± 1 SD)
Shallow (5 m)	1988	879	4.58 ± 2.66
Intermediate (11 m)	1988	414	2.16 ± 0.41
Deep (17 m)	1992	45	0.23 ± 0.00

iate, and deep water urchins. All statistical analyses were performed with SYSTAT (Wilkinson 1987).

Seasonal gonad index and drift algae

Gonad indices of shallow and deep water urchins were determined for samples ($N = 10$) of adult red urchins (>50 mm test diameter) collected during eight sampling dates in the spring, summer, and fall of 1991 and 1992. Adult urchins were collected from shallow (3–5 m) depths at Bodega Head and from deeper (17 m) depths beyond the Bodega Marine Reserve. Gonad index was calculated by multiplying the wet gonad mass by 100, then dividing by the wet mass of the whole urchin (Gonor 1972, Vadas 1977, Carney 1991). At the same time, drift macroalgae and seagrass were collected from a 2 × 10 m transect (Harrold and Reed 1985). Transects were oriented perpendicular to shore in areas inhabited by red urchins. *Phyllospadix* spp. and algae (identified to phylum) were wet weighed.

RESULTS

Urchin density, behavior, and sheltering

Shallow habitats had adult urchin densities twice that of intermediate and twenty times that of deep habitats (Table 1). Urchins in the shallow habitats were densely packed, within rock "bowls." Tagged individuals ($N = 10$) in shallow habitats were observed in their home "bowls" for six consecutive days. In contrast, tagged urchins in deep water ($N = 12$) were highly mobile, moving 2–3 m in 1 h.

More adults (27.5%) in shallow habitats sheltered juvenile red and purple urchins (genus *Strongylocentrotus*) than adults in intermediate habitats (2.2%, Table 2). Overall, there were more juvenile urchins (5–50 mm) in shallow habitats than in intermediate habitats over a 4-yr period (Table 2). The majority (70%) of

the juveniles in the intermediate depth habitats were large (21–50 mm), compared with shallow juveniles (21%) (Table 2). Juveniles in shallow habitats occurred in cryptic microhabitats (98%), most often under the spines and test of adult red urchins (Table 2). In contrast, 60% of juveniles at intermediate sites were on exposed rock surfaces (Table 2).

Morphometric analyses

Red urchin morphology differed significantly (ANCOVA, $P < 0.001$, Figs. 2 and 3) among habitat depths for five of the nine characters measured (spine length, peristomial opening, test thickness, gonad mass, and lantern mass). The other measured characteristics (test height, perimeter to top of test, and perimeter to edge of peristomial opening) were poor discriminators of depth.

Multivariate analysis of variance (MANOVA) using indices composed of six variables (test diameter and the five from the ANCOVA analysis, see Figs. 2 and 3) also indicated significant differences in the morphology of red urchins among habitat depths ($F = 51.3$, $df = 12, 234$, $P < 0.001$). Discriminant analysis correctly classified 95.6% of shallow urchins, 92.7% of intermediate urchins, and 84.6% of deep urchins into the depth habitat where they originated. A plot of discriminant scores clearly shows separation of urchin depth-groups in multivariate space (Fig. 4A), and shows that the discriminant axis provided most of the discrimination. The coefficients of the first discriminant function are,

$$\begin{aligned} \text{Canonical score} = & (1.395) \text{ PC 1 score} + (-1.645) \text{ PC 2 score} \\ & + (0.190) \text{ PC 3 score} + (0.624) \text{ PC 4 score} \\ & + (0.283) \text{ PC 5 score} + (0.208) \text{ PC 6 score.} \end{aligned}$$

This indicates that the most important discriminators (coefficients with the largest absolute values) were the second (PC 2) and first (PC 1) principal components, respectively. A plot of the factor scores of these two components (Fig. 4B) shows that the second principal component provides the majority of morphometric separation in the discriminant analysis (Fig. 4A). The signs (+ or -) of the factor loadings for PC 1 and PC 2, and the factor score plot in Fig. 4B, indicate that urchins from shallow habitats around Bodega Head have short

TABLE 2. Percent of adult red urchins (>50 mm) providing canopy shelter and the total number of adults. Microhabitat distribution (UT = under test, US = under spines, RC = rock crevice, UCA = upright coralline algae, Exp. = exposed) of juvenile urchins (5–50 mm), *Strongylocentrotus* spp., within 1 m² quadrats in shallow and intermediate depth sites ($N = 3$) in the Bodega Marine Reserve, from October 1988 to October 1992.

Depth	No. of quadrats	% of adults providing canopy	No. urchins			Juvenile microhabitat distribution				
			Adults	Juveniles	Size juv. (mm)	UT	US	RC	UCA	Exp.
Shallow (5 m)	138	27.5	737	379	5–20	229	88	31	28	3
				103	21–50	52	15	29	1	6
Inter. (11 m)	158	2.2	755	20	5–50	10	4	3	2	1
				47	21–50	1	3	4	0	39

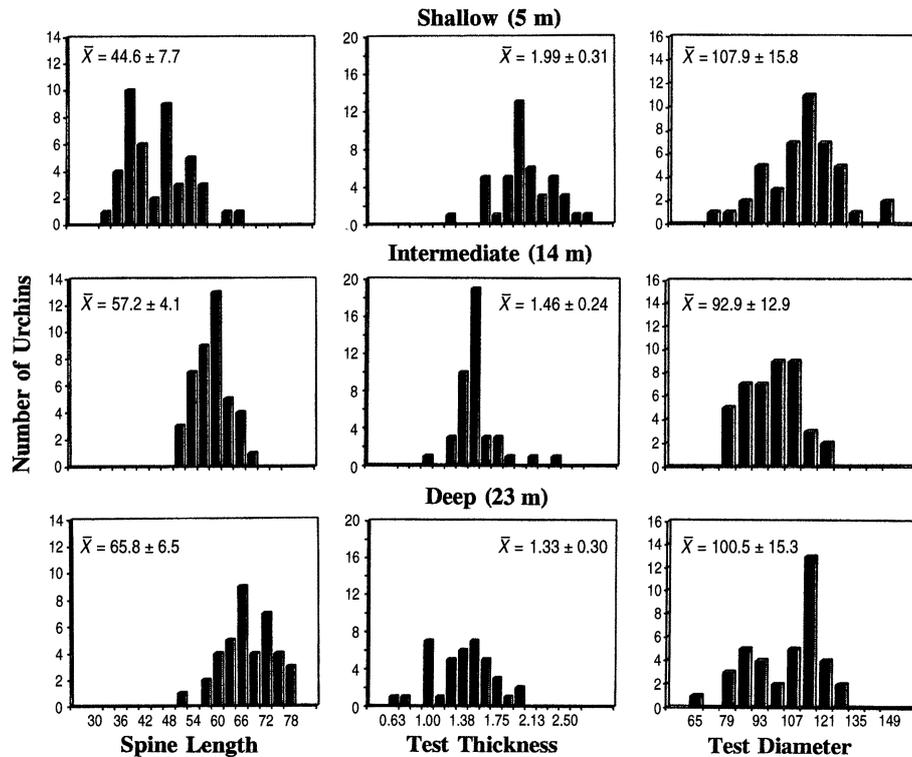


FIG. 2. Frequency distributions of spine length, test thickness, and test diameter, for red sea urchins from shallow, intermediate, and deep sites along Bodega Head, California. The mean \pm 1 SD is given for each distribution.

spines, thick tests, large gonads, and small peristomial openings and lanterns, compared with urchins from intermediate or deep habitats.

Spine length was the best visual discriminator of shallow-water urchins (Fig. 2), shallow-water urchins had the shortest spines (44.6 ± 7.7 mm, $N = 45$, mean \pm 1 SD), compared with intermediate urchins (57.2 ± 4.1 mm, $N = 42$, mean \pm 1 SD), and deep urchins (65.8 ± 6.5 mm, $N = 39$, mean \pm 1 SD). Red urchins with short blunt spines collected from shallow habitats grew long spines after containment in the laboratory for 2 mo. Shallow urchins had thicker tests (Figs. 2 and 4B) and withstood greater compression (mean = 8) than deep water urchins (mean = 6). The highest compression score 10 (corresponding to 100 kg) was given to a shallow water urchin.

Gonad mass of urchins from shallow habitats were the largest (Fig. 3). The gonad mass for all shallow-water urchins (mean = 63.6 g) was 4 times that of the intermediate and deep-water samples (Fig. 3). Gonad index samples of shallow ($N = 80$) and deep ($N = 80$) urchins were taken every two months during the spring, summer, and fall of 1991 and 1992 in conjunction with drift algae samples. Shallow water urchins had significantly higher gonad index values ($t_{80} = 6.93$, $P < 0.001$) than deep water urchins. Gonad index for shallow water urchins varied with drift algae abundance ($r = 0.938$, $N = 7$, $P = 0.002$) which included one major

drift pulse (>1000 g/20 m²) that appeared in the shallow sample only on 10 October 1991. Excluding this major drift event, the relationship between drift algae and gonad index in shallow urchins is weakened ($r = 0.799$, $N = 6$, $P = 0.056$). Drift algae were scarce in deep habitats and were not significantly related to gonad index in deep water urchins ($r = 0.086$, $N = 7$, $P = 0.855$). Shallow habitats had the highest abundance of drift algae among all collection dates. Drift algae were most abundant in the fall and least abundant in the spring following the winter storms.

Test shape is often described using a ratio of height : diameter (Marcus 1983). This ratio did not differ with depth (shallow, 0.472 ± 0.048 , $N = 45$, mean \pm 1 SD; intermediate, 0.466 ± 0.042 , $N = 42$, mean \pm 1 SD; deep, 0.449 ± 0.056 , $N = 39$, mean \pm 1 SD). However, shallow water urchins had more tube feet pores in the ambitus plates (36 ± 2.69 , $N = 13$, mean \pm 1 SD), than deep-water urchins (29 ± 1.03 , $N = 13$, mean \pm 1 SD). The sex ratio of all mature urchins was 61 ♀ to 62 ♂ (1:1), and the color ratio was 91 dark red to 31 pink (3:1). Sex and color morphology ratios were not influenced by depth.

DISCUSSION

Brood stock morphology

Our investigations indicate that shallow-water urchins along Bodega Head have heavy gonads, high go-

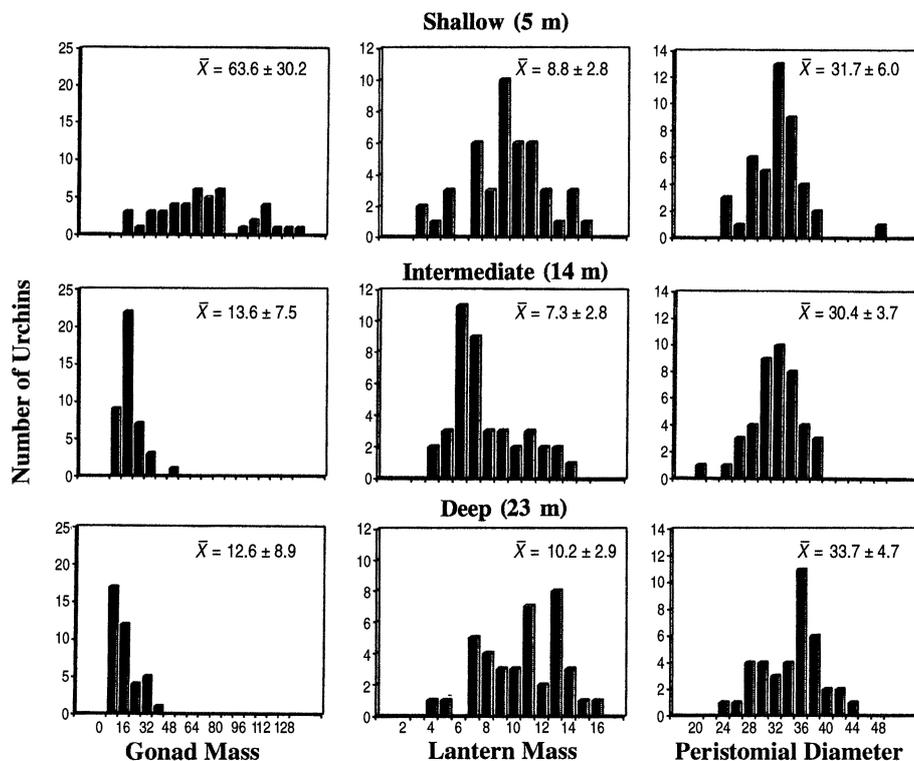


FIG. 3. Frequency distributions of gonad weight, Aristotle's lantern mass, and diameter of peristomial opening, for red sea urchins from shallow, intermediate, and deep sites along the Bodega Head, California. The mean \pm 1 SD is given for each distribution.

nad indices (Fig. 3), and occur in dense aggregations, suggesting they have greater reproductive success than urchins in deeper habitats (Larkin 1978, Keats et al. 1984, Levitan et al. 1992). Larger gonads, which histological examination revealed were more reproductively active, were also found in red urchins from shallow habitats in southeast Alaska (Carney 1991). Similarly, larger gonads were also found in green urchins from shallow water in Newfoundland, Canada (Fletcher et al. 1974, Keats et al. 1984), suggesting this pattern is not unique to northern California.

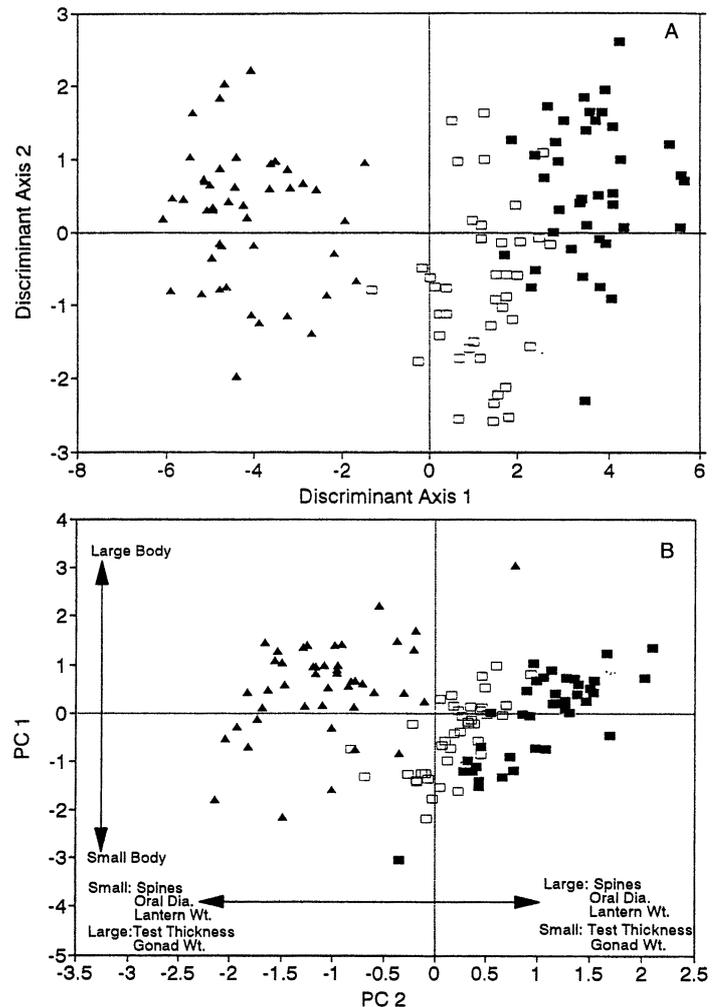
Additional observations suggest that the differences in reproductive potential, morphometry, and behavior we have quantified for urchins along Bodega Head can be extrapolated to other areas in the northern California fishery. We have conducted numerous surveys encompassing the fishery grounds (six locations from Bodega Bay to Fort Bragg over a six-year period) that indicate shallow habitats contain intermittent beds of red urchins at high densities often residing in "bowls" exhibiting the short-spine morphology (L. Rogers-Bennett and H. C. Fastenau, *personal observations*). Moreover, commercial divers suggest such patterns are easily recognizable and widespread (Directors Sea Urchin Advisory Committee, *personal communications*). Therefore, it is not unreasonable to suggest these pat-

terns are typical throughout the northern California fishery grounds.

Wave exposure and food availability influence several morphometric characters in addition to gonad size. Our results and those of others (Ebert 1980, Black et al. 1982) suggest urchins in food-poor habitats compensate by increasing lantern size and peristomial opening. Also, urchins in shallow-exposed and food-rich habitats typically have short spines and thick tests (Ebert 1968, Dix 1970, Lewis and Storey 1984). Since short-spined urchins grew long spines in the laboratory, spine length may be primarily influenced by wave action. Edwards and Ebert (1991) have shown that breaking spines (simulating wave action) stimulates calcification, increasing test and spine thickness but not spine length. In addition, urchins in exposed habitats can also have flat tests (Marcus 1983, but see Dix 1970); however, in this study urchin test shape was similar among depths. Red urchins apparently increase the density of tube feet and scour rock "bowls" to enhance attachment in exposed habitats.

While urchin beds in shallow habitats are intermittently dispersed along Bodega Head and in Horseshoe Cove, individuals are highly aggregated in these beds (>4 individuals/m²). Field experiments have demonstrated that densities of 4 individuals/m² are required

FIG. 4. Plots of discriminant scores, and factor scores for the two components (PC 2 and PC 1) contributing most to the discrimination among depth habitat groups (\blacktriangle = shallow, 5 m; \square = intermediate, 11 m; \blacksquare = deep, 23 m) of red sea urchins.



to insure fertilization success of 82% (Levitan et al. 1992). Current velocity also influences fertilization success and velocities >0.2 m/s may decrease fertilization in urchins (Pennington 1985). Shallow habitats periodically experience high velocities (1–5 m/s); however, calm ocean conditions prevail about a quarter of the year. Shallow subtidal habitats, coves, and areas protected by headlands experience lower velocities than surf-zone (intertidal) habitats in which models suggest fertilization may be low (Denny and Shibata 1989).

Nursery microhabitats

Urchins in food-rich habitats are more sedentary than urchins in food-poor habitats (Lees 1970, Mattison et al. 1977, Russo 1979, Harrold and Reed 1985). In this study, red urchins from shallow habitats remained within individual “bowls” for 1 wk. Similarly, red urchins in shallow habitats from southeast Alaska were more sedentary than conspecifics from deeper habitats over a 2-mo period (Carney 1991). Increased water motion in shallow habitats may bring drift food to urchins,

reducing the need to forage beyond their “bowls.” In addition, high wave action may also interfere with urchin mobility (Lissner 1983).

Sedentary behavior may render shallow urchins more suitable as canopy providers for juveniles. Our data indicate that shallow adults were more likely to shelter juvenile *Strongylocentrotus* (Table 2) and that adult size alone was a poor predictor of sheltering behavior. Sheltering behavior described by Tegner and Dayton (1977) for red urchins in southern California has been observed for red urchins in British Columbia (Breen et al. 1985), purple urchins in Oregon (Ebert 1968), and green urchins (*S. droebachiensis*) in Massachusetts (Rogers-Bennett 1989), but not for urchins (*Evechinus chloroticus*) in New Zealand (Dix 1970, Andrew and Choat 1985). Sloan et al. (1987) have demonstrated the importance of the spine canopy for red urchin recruitment in British Columbia. They showed harvested areas contained fewer juveniles than unharvested areas and suggest that decreasing spine canopy microhabitat reduces juvenile urchin survival.

Implications for refuge management

Harvest refugia can be set aside to protect optimal reproductive habitats, allowing natural dispersal of new recruits to replenish harvested habitats (Davis 1989, Polacheck 1990, Dugan and Davis 1993). Models of harvest refugia suggest this management strategy yields substantial increases in spawning stock (Polacheck 1990). Other potential benefits include protecting brood stock while harvesting only surplus recruits from productive areas (Davis and Dodrill 1980), increases in the mean size and age of individuals in a population, and maintenance of genetic and species diversity (Dugan and Davis 1993). Refuges appear to be highly effective at increasing densities within their borders (Alcala 1988, Davis 1989, Roberts and Polunin 1991), and several examples indicate refuges can increase fish catch in nearby harvested habitats (Booth 1979, Davis and Dodrill 1980, Acala 1988). Tag and recapture studies of invertebrate fisheries show dispersal into adjacent fished areas for snow crabs (Yamasaki and Kuwahara 1990) and pink shrimp (Gitschlag 1986); however, research on the benefits of refuges is just beginning.

We suggest the unique reproductive biology of short-spined red urchins warrants the establishment of shallow harvest refugia. Harvest restrictions in shallow water or other habitats with abundant drift and wave action (e.g., seamounts, wash-rocks) that contain beds of densely aggregated urchins with short spines and large gonads could be implemented to help protect brood stock and maintain spine canopy to increase juvenile survival. Shallow refugia could supply deeper harvested habitats with larval recruits as settlement does not appear to be habitat specific (Cameron and Schroeter 1980, Rowley 1989). While little is known about the dispersal ability of larval urchins, they can potentially travel great distances since the planktonic stage lasts 23–70 d in culture (Strathmann 1978, Cameron and Schroeter 1980; L. Rogers-Bennett et al., *unpublished manuscript*). Results from models of red urchin refugia support the preservation of multiple reserves within the larval dispersal range (Quinn et al. 1993). This could be accomplished by protecting many discrete urchin beds in shallow habitats.

We propose that this management strategy can be successfully implemented. First, easily recognizable differences in spine length among urchins at various depths (Table 4) facilitates the creation of a gauge to identify reproductively important urchins from protected areas. Simple spine-length gauges could be easily inscribed onto harvesting rakes. Our data indicate that prohibiting the harvest of urchins with spines <52 mm (2") would protect 82% of the shallow-water urchins while allowing 90% of intermediate and 97% of deep urchins to be harvested. Second, large red urchins with very large gonads (>100 gm), typical in shallow habitats (called "bombers" in the industry), have a poor market value once processed (D. Rudie, Catalina

Offshore Products, Inc., *personal communication*). Finally, commercial catch in shallow habitats (<7 m) is low, indicating a refuge there would affect <10% of the catch (P. Kalvass, *personal communication*). Harvesting in shallow areas is hindered by nearshore wave action and the difficulty in dislodging urchins from "bowls."

The harvest refugia strategy appears to have several advantages compared with other management options. Upper-size limits protect only large individuals, so that intermediate-size urchins are harvested, reducing local densities and potentially decreasing fertilization success. In addition, upper-size limits may be inadequate since harvest rates are high, urchins are spatially clumped, and growth is slow (Ebert and Russell 1992), suggesting few individuals will escape into the protected class (Breen 1984). Area rotations are currently employed in Washington state (Bradbury 1991) and have been proposed for green abalone (*Haliotis fulgens*), which appear to have limited larval dispersal (Tegner 1993). If dispersal rates of larval and juvenile urchins in northern California are found to be low, fished zones should be rotated. However, while habitat rotations appear to be successful in Washington, this strategy requires real-time monitoring, and continually shifting the location of fishing zones adds transportation costs for divers and processors. With these caveats in mind, fishery managers should consider the reproductive importance of short-spined red urchins in shallow habitats when devising management plans to sustain red urchin resources in northern California.

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