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Spatial Patterns in the Life History Characteristics of  
Red Sea Urchins, Strongylocentrotus franciscanus:  
Implications for Recruitment and the California Fishery

By

LAURA ROGERS-BENNETT  
B.A. (University of New Hampshire) 1983  
M.S. (University of Massachusetts, Boston) 1989

DISSERTATION

Submitted in partial satisfaction of the requirements for  
the degree of

DOCTOR OF PHILOSOPHY

in

Ecology

in the

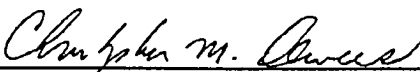


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This thesis is dedicated to my son Brian Robert Bennett for showing me what real life, struggle, and triumph are all about.





Laura Rogers-Bennett  
December 1994  
Ecology

Spatial Patterns in the Life History Characteristics of  
Red Sea urchins Strongylocentrotus franciscanus:  
Implications for Recruitment and the California Fishery

Abstract

I examined habitat specific differences in the morphology, reproduction, and juvenile abundance of red sea urchins, Strongylocentrotus franciscanus. In addition, we conducted a tag-recapture study and examined early growth, to develop an alternative growth model for urchins in northern California. Urchins in shallow habitats encounter high wave energy and drift food such that principle component analysis identified shallow urchins as having large gonads, short spines, and thick tests. Shallow adult urchins also resided in "scars" where they provide spine canopy protection for juvenile urchins. These patterns suggest that not only are shallow urchins important spawners, but they may also act as living nurseries. Since their morphology is unique, shallow urchins could be set aside in harvest refugia offering an alternative urchin fishery management strategy.

The sea urchin fishery is California's largest fishery. Fishery managers are interested in growth models which can predict the time required for urchins to reach the minimum legal size (89 mm). We conducted a tag-rapture study with

wild urchins (N=600) and laboratory cultured juveniles (N=240) in shallow (5m) and deep (15m) subtidal sites. Recapture rates were twice as high in the shallow site (38.5%) compared with the deep site (15%) for wild urchins as well as for outplanted juveniles (20.8% and 10.8%, respectively). We present an alternative growth function with three desirable features 1) infinite growth (lacks asymptotic size), 2) two well defined parameters, and 3) asymmetry about the function's maximum. We obtained parameter values for size at 1 year,  $a = 4.499 (\pm SE 0.207)$ , and growth rate constant  $K = 0.375 (\pm SE 0.003)$ . We estimate red urchins attain harvestable size (89 mm) in 9 years and caution model parameters must be calculated independently in northern and southern California.

Cultured red urchins experienced a lag in growth and jaw emergence immediately post-settlement. Newly settled juveniles (90%) lacked jaws and did not increase in test diameter from size at settlement ( $0.404 \text{ mm} \pm SD 0.038\text{mm}$ , N=10) for 50 days. This period was followed by an exponential growth phase after jaw emergence and the onset of exogenous feeding. Newly settled juveniles also appear to be highly susceptible to mortality in the pre-jaw stage. Therefore, jaw development may encompass a critical stage in urchin recruitment.

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Running Head.- Red urchin ecology and harvest refugia

**Spatial Variation in the Reproduction and Morphology  
of Red Sea Urchins: Implications for Harvest Refugia**

by

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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 (5m) had significantly heavier gonads (mean  $\pm$  1 SD =  $63 \pm 30$ g, N=45) compared with urchins from intermediate (14m) and deep (23m) habitats (mean  $\pm$  1 SD =  $12 \pm 8$ g, N=39). Gonad indices from spring, summer, and fall of 1991 and 1992 show this pattern persisted. Shallow water urchins co-occurred at high densities ( $4.6/\text{m}^2$ ), with seasonally abundant drift algae and wave surge. Juvenile urchin (Strongylocentrotus spp.) recruitment (5-50mm) was highest in association with adults in shallow habitats over a four-year period (Oct. 1988 - Oct. 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.

## 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 million kg (30.4 million pounds) in 1988 to 3.2 million kg (7.2 million pounds) in 1993 (Kalvass personal communications). Catch per unit effort (CPUE) estimates have also declined by about 40% since 1988. Subtidal transect surveys show a significant reduction in average urchin densities from  $1.3\text{m}^{-2}$  in 1988 to  $0.71\text{m}^{-2}$  in 1991, as well as a reduction in the mean test diameter of urchins from 92mm in 1988 to 77mm 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 and bachelor males are harvested (Wilén 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 at least 5mm 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 (Thompson 1982, 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 (1-8km) scales (Sloan et al. 1987). At the microhabitat scale ( $1\text{m}^2$ ) 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 granite walls 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 spring or summer. 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 Dermasterias imbricata.

#### Urchin Study Sites

Three shallow (5m) and three intermediate (11m) study sites each 8x8m (64m<sup>2</sup>) 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 3 additional deeper sites (17m) beyond Horseshoe Cove in fall 1992. The movement of adult urchins

in shallow and intermediate sites was examined in August of 1991. Spines of twenty adult urchins were tagged in situ with individually labelled surgical tubing, lasting 1-2 weeks (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 9 randomly placed 1m<sup>2</sup> quadrats in the six sites quarterly, or as weather permitted from October 1988 to October 1992. Juvenile urchins were measured to the nearest 1mm. Distinguishing between juvenile (5-20mm) red and purple urchins is inconclusive in the subtidal (Rowley, personal communication). Individuals less than 5mm 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 (5m, N=45), intermediate (14m, N=42), and deep (23m, N=39) habitats (Fig. 1). Seven linear and 3 mass characters were measured for each adult urchin.

Linear measures made with vernier calipers include: test diameter, test height, perimeter to top of test (madreporite), perimeter to edge of peristomial opening, diameter of peristomial opening, spine length (mean of 3 longest spines), and test thickness at ambitus (maximum test diameter). Measures of ambitus and test height on 3 live red urchins showed that precision was  $\pm 2.1\text{mm}$  (N=10). All other linear measures were within 0.1mm.

Live urchin body weight (wet) and gonad weight and lantern weight after paper towel drying were determined to within 0.1g. 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 10-100kg. 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 gonad 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 (6 linear measurements, 3 weight measurements; see above). Morphometric characters that exhibited significant differences among depth-groups

using ANCOVA were standardized to 0 mean using Z-scores, and principal components analysis 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 6 multivariate indices differed in discriminant space. Discriminant functions were then calculated based on the 6 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, intermediate, 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 (>50mm test diameter) collected during 8 sampling dates in the spring, summer, and fall of 1991 and 1992. Adult urchins were collected from shallow (3-5m) depths at Bodega Head and from deeper (17m) depths beyond the Bodega Marine Reserve. Gonad index was calculated by multiplying the wet gonad weight by 100 then dividing by the wet weight of the whole urchin (Gonor 1972, Vadas 1977, Carney 1991). At the same



time, drift macroalgae and seagrass were collected from a 2-m x 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 2-3m in one hour.

More adults in shallow habitats sheltered (27.5%) juvenile red and purple urchins (genus Strongylocentrotus) than adults in intermediate habitats (2.2%, Table 2). Overall, there were more juvenile urchins (5-50mm) in shallow habitats than in intermediate habitats over a 4 year period (Table 2). The majority (70%) of the juveniles in the intermediate depth habitats were large (21-50mm), 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 the juveniles at intermediate sites were on

exposed rock surfaces (Table 2).

### Morphometric Analyses

Red urchin morphology differed significantly (ANCOVA,  $P < .001$ , Fig. 2-3) among habitat depths for 5 of the 9 characters measured (spine length, peristomial opening, test thickness, gonad weight, lantern weight). The other measured characteristics (test height, perimeter to top of test, perimeter to edge of peristomial opening) were poor discriminators of depth.

Multivariate analysis of variance (MANOVA) using indices composed of 6 variables (test diameter and the 5 from the ANCOVA analysis, see Figs. 2 and 3) also indicated significant differences in the morphology of red urchins among habitat depths ( $F=51.3$ ,  $df=12,234$ ,  $P < .001$ ). 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,

$$\begin{aligned} \text{Canonical score} = & (1.395)\text{PC1 score} + (-1.645)\text{PC2 score} + \\ & (0.190)\text{PC3 score} + (0.624)\text{PC4 score} + (0.283)\text{PC5 score} \\ & +(0.208)\text{PC6 score}. \end{aligned}$$

This indicates that the most important discriminators (coefficients with the largest absolute values) were the

second (PC2) and first (PC1) principal components, respectively. A plot of the factor scores of these 2 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 PC1 and PC2, and the factor score plot in Figure 4b, indicate that urchins from shallow habitats around Bodega Head have short 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 (mean  $\pm$  1 SD=44.6  $\pm$  7.7mm, N=45), compared with intermediate urchins (mean  $\pm$  1 SD=57.2  $\pm$  4.1mm, N=42), and deep urchins (mean  $\pm$  1 SD=65.8  $\pm$  6.5mm, N=39). Red urchins with short blunt spines collected from shallow habitats grew long spines after containment in the laboratory for two months. Shallow urchins had thicker tests (Fig.2, 4b) and withstood greater compression (mean=8) than deep water urchins (mean=6). The highest compression score 10 (corresponding to 100kg) was given to a shallow water urchin.

Gonad weights of urchins from shallow habitats were the largest (Fig. 3). The gonad weight for all shallow-water urchins (mean=63.6g) 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 bimonthly 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 ( $t_{90}=6.93$ ,  $P<.001$ ) than deep water urchins. Gonad index for shallow water urchins varied with drift algae abundance ( $r=0.938$ ,  $N=7$ ,  $P=.002$ ) which included one major drift pulse ( $>1000\text{g}/20\text{m}^2$ ) that appeared in the shallow sample only on 10/10/91. 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 ( $r=.086$ ,  $N=7$ ,  $P=.855$ ). 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, mean  $\pm$  1 SD= $0.472 \pm 0.048$ ,  $N=45$ ; intermediate, mean  $\pm$  1 SD= $0.466 \pm 0.042$ ,  $N=42$ ; deep, mean  $\pm$  1 SD= $0.449 \pm 0.056$ ,  $N=39$ ). However, shallow water urchins had more tube feet pores in the ambitus plates, (mean  $\pm$  1 SD=  $36 \pm 2.69$   $N=13$ ), than deep-water urchins (mean  $\pm$  1 SD=  $29 \pm 1.03$ ,  $N=13$ ). The sex ratio of all mature urchins was 61

female to 62 male (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 gonad 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 (6 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 (LRB and HCF, 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 patterns 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 better hold-on 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 ( $>4/m^2$ ). Field experiments have demonstrated that densities of  $4/m^2$  are required to insure fertilization success of 82% (Levitan et al. 1992). Current velocity also influences fertilization success and velocities greater than 0.2m/sec may decrease fertilization in urchins (Pennington 1985). Shallow habitats periodically experience high velocities (1-5m/sec), 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 where 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 one week. Similarly, red urchins in shallow habitats from southeast Alaska were more sedentary than conspecifics from deeper habitats over a two-month 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 (Davis 1989, Alcala 1988, 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 days in culture (Strathmann 1978, Cameron and Schroeter 1980, 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 shorter than 52mm (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 (>100gm), 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 (<7m) is low indicating a refuge there would affect less than 10% of the catch (Kalvass, personal communication). Harvesting in shallow areas is hindered by near-shore 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 potentially decrease 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 1989) and have been proposed for green abalone (*Haliotis fulgens*) that 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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### Literature Cited

- Alcala, A.C. 1988. Effects of marine reserves on coral fish abundances and yields of Philippine coral reefs. *Ambio A Journal of Human Environments* 12:194-199.
- Andrew, N.L., and J.H. Choat 1985. The influence of predation and conspecific adults on the survivorship of juvenile Evechinus chloroticus (Echinoidea: Echinometridae). *Oecologia* 56:80-87.
- Baker, S.L. 1973. Growth of the red sea urchin Strongylocentrotus franciscanus (Agassiz) in two natural habitats. M.S. Thesis California State University, San Diego, California, U.S.A.
- Black, R., Johnson, M.S., and J.T. Trendall 1982. Relative size of Aristotle's lantern in Echinometra mathaei occurring at different densities. *Marine Biology* 71:101-106.
- Bonnor, W.N. 1982. Seals and Man: A study of interactions. Washington Sea Grant Publication, University Washington Press. Seattle, Washington.
- Booth, J.D. 1979. North Cape - a nursery area for the packhorse rock lobster Jasus verreauxi, New Zealand. *New Zealand Journal of Marine and Freshwater Research* 13:521-528.
- Bradbury, A. 1989. Management and stock assessment of the red sea urchin Strongylocentrotus franciscanus in

- Washington state. Washington Department of Fisheries.
- Breen, P.A. 1984. Sea urchins: Suitability of the present minimum size limit. Canadian Manuscript Report of Fisheries and Aquatic Sciences 1174:25-47.
- Breen, P.A., Carolsfield, W., and K.L. Yamanaka 1985. Social behavior of juvenile red sea urchins, Strongylocentrotus franciscanus (Agassiz). Journal of Experimental Marine Biology and Ecology 92:45-61.
- Cameron, R.A., and S.C. Schroeter 1980. Sea urchin recruitment: effect of substrate selection on juvenile distribution. Marine Ecology Progress Series 2:243-247.
- Carney, D. 1991. A comparison of densities, size distribution, gonad and total-gut indices, and the relative movements of red sea urchins Strongylocentrotus franciscanus, in two depth regimes. M.S. Thesis University of California, Santa Cruz, Santa Cruz, California, USA.
- Cowen, R.K. 1983. The effect of sheephead (Semicossyphus pulcher) predation on red sea urchin (Strongylocentrotus franciscanus) populations: an experimental analysis. Oecologia 53:249-255.
- Coyer, J.D., and J.D. Witman 1990. Underwater Catalog: A Guide to Methods and Research. Shoals Marine Laboratory Publishing, New York Sea Grant.
- Davis, G.E. 1989. Designated harvest refugia: the next stage of marine fishery management in California. California

COFI Report 30:53-58.

- Davis, G.E., and J.W. Dodrill 1980. Marine parks and sanctuaries for spiny lobsters, Panularis argus, fisheries management. Gulf Caribbean Fisheries Institute 32:194-207.
- Denny, M.W. and M.F. Shibata 1989. Consequences of surf-zone turbulence for settlement and external fertilization. American Naturalist 134:859-889.
- Dix, T G. 1970. Biology of Evechinus chloroticus (Echinoidea: Echinometridae) from different localities. New Zealand Journal of Marine and Freshwater Research 4:91-116.
- Dugan, J.E. and G.E. Davis 1993. Applications of marine refugia to coastal fisheries management. Canadian Journal Fisheries Aquatic Sciences 50:2029-2042.
- Ebert, T.A. 1983. Recruitment in echinoderms. Echinoderm Studies 1:169-203.
- Ebert, T.A. 1980. Relative growth of sea urchin jaws: an example of plastic resource allocation. Bulletin of Marine Science 30:467-474.
- Ebert, T.A. 1968. Growth rates of the sea urchin Strongylocentrotus purpuratus related to food availability and spine abrasion. Ecology 49:1062-1074.
- Ebert, T.A. and M.P. Russell 1992. Growth and mortality estimates for red sea urchins Strongylocentrotus franciscanus from San Nicolas Island, California.

Marine Ecology Progress Series 81:31-41.

Ebert, T.A., and M.P. Russell 1988. Latitudinal variation in size structure of the west coast purple sea urchin: a correlation with headlands. *Limnology and Oceanography*. 32:286-294.

Edwards, P.B., and T.A. Ebert 1991. Plastic responses to limited food availability and spine damage in the sea urchin Strongylocentrotus purpuratus (Stimpson). *Journal of Experimental Marine Biology and Ecology* 145:205-220.

Estes, J.A., Jameson, R.J. and E.B. Rhode 1982. Activity and prey selection in the sea otter: influence of population status on community structure. *American Naturalist* 120:242- 258.

Fletcher, G.L., Pepper, V.A., and J.C. Kean 1974. A study of the Newfoundland sea urchin with emphasis on aspects important to the development of a fishery. Marine Science Research Laboratory, Memorial University Newfoundland, Technical Report Number 11, pp. 1-41.

Gill, D.E. 1978. The metapopulation ecology of the red-spotted newt, Notophthalmus viridescens. *Ecological Monographs* 48:145-166.

Gitschlag, G.R. 1986. Movement of pink shrimp in relation to Tortugas sanctuary. *North American Journal of Fisheries Management* 6:328-338.

Gonor, J.J. 1972. Gonad growth in the sea urchin



Strongylocentrotus purpuratus (Stimpson)

(Echinodermata: Echinoidea) and assumptions of gonad index methods. *Journal of Experimental Marine Biology and Ecology* 10:89-103.

Graham, W.M., Field, J.G. and D.C. Potts 1992. Persistent "upwelling shadows" and their influence on zooplankton distributions. *Marine Biology* 114:561-570.

Harrison, S.D., Murphy, D., and P.R. Ehrlich 1988. Distribution of the bay checkerspot butterfly Euphydryas editha bayensis: evidence for a metapopulation model. *American Naturalist* 132:360-382.

Harrold, C., and D.C. Reed 1985. Food availability, sea urchin grazing, and kelp forest community structure. *Ecology* 66:1160-1169.

Harrold, C., and J.S. Pearse 1987. The ecological role of echinoderms in kelp forests. *Echinoderm Studies* 2:137-234.

Kalvass, P., Taniguchi, I., Buttolph, P., and J. DeMartini 1991. Relative abundance and size composition of red sea urchin, Strongylocentrotus franciscanus, populations along the Mendicino and Sonoma county coasts, 1989. California Dept. Fish and Game. Marine Resources. Administrative Report Number 91-3. 103 p.

Keats, D.W., Steele, D.H. and G.R. South 1984. Depth-dependent reproductive output of the green sea urchin, Stongylocentrotus droebachiensis (O.F. Muller), in

relation to the nature and availability of food.  
Journal of Experimental Marine Biology and Ecology  
80:77-91.

Larkin, P.A. 1978. Fisheries management: an essay for ecologists. Annual Review of Ecology and Systematics 9:57-73.

Lawrence, J.M. 1975. On the relationships between marine plants and sea urchins. Oceanography and Marine Biology Annual Review 13:213-286.

Lees, D.L. 1970. The relationship between movement and available food in the sea urchins Strongylocentrotus franciscanus and Strongylocentrotus purpuratus. M.S. Thesis, San Diego State University, San Diego, California, USA.

Levitan, D.R., Sewell, M.A., and F.-S. Chia 1992. How distribution and abundance influence fertilization success in the sea urchin Strongylocentrotus franciscanus. Ecology 73:248-254.

Lewis, J.B., and G.S. Storey 1984. Differences in morphology and life history traits of the echinoid Echinometra lucunter from different habitats. Marine Ecology Progress Series 15:207-211.

Lissner, A.L. 1983. Relationship of water motion to the shallow water distribution and morphology of two species of sea urchins. Journal of Marine Research 41:691-709.

- Marcus, N.H. 1983. Phenotypic variability in Echinoderms. *Echinoderm Studies* 1:19-38.
- Mattison, J.E., Trent, J.D., Shanks, A.L., Akin, T.B., and J.S. Pearse 1977. Movement and feeding activity of red sea urchins Strongylocentrotus franciscanus in a kelp forest. *Marine Biology* 39:25-30.
- Pennington, J.T. 1985. The ecology of fertilization of echinoid eggs: the consequence of sperm dilution, adult aggregation, and synchronous spawning. *Biological Bulletin* 169:417-430.
- Pimentel, R.A. 1979. Morphometrics. The multivariate analysis of biological data. Kendall and Hunt Publishing Co., Dubuque, Iowa. U.S.A.
- Polacheck, T. 1990. Year round closed areas as a management tool. *Natural Resources Modeling* 4:327-352.
- Pulliam, H.R. 1988. Sources, sinks, and population regulation. *American Naturalist* 132:652-661.
- Quinn, J.F., Wing, S.R. and L.W. Botsford 1993. Harvest refugia in marine invertebrate fisheries: Models and applications to the red sea urchin, Strongylocentrotus franciscanus. *American Zoologist* 33:537-550.
- Roberts, C.M., and N.V.C. Polunin 1991. Are marine reserves effective in management of reef fisheries? *Review of Fisheries Biology* 1:65-91.
- Rogers-Bennett, L. 1989. The spatial association of juvenile green sea urchins. M.S. Thesis University of

Massachusetts, Boston, Massachusetts, USA.

Rohlf, F.J. 1990. Morphometrics. Annual Review of Ecology and Systematics 21:299-316.

Roughgarden, J.J., Pennington, T., Stoner, D., Alexander, S., and K. Miller 1991. Collisions of upwelling fronts with the intertidal zone: cause of recruitment pulses in barnacle populations of central California. Acta. Oecologia 12:35-51.

Rowley, R.J. 1989. Settlement and recruitment of sea urchins Strongylocentrotus spp. in a sea-urchin barren ground and a kelp bed: are populations regulated by settlement or post-settlement processes? Marine Biology 100:485-494.

Russo, A.R. 1979. Dispersion and food differences between two populations of the sea urchin Strongylocentrotus franciscanus. Journal of Biogeography 6:407-414.

Shanks, A.L. 1983. Surface slicks associated with tidally forced internal waves may transport pelagic larvae of benthic invertebrates and fishes shoreward. Marine Ecology Progress Series 13:311-315.

Sloan, N.A. 1986. World jellyfish and tunicate fisheries and the Northeast Pacific echinoderm fishery. Canadian Special Publications Fisheries Aquatic Sciences 92:23-33.

Sloan, N.A., Lauridsen, C.P., and R.M. Harbo 1987.  
Recruitment characteristics of the commercially

- harvested red sea urchin Strongylocentrotus franciscanus in southern British Columbia, Canada. Fisheries Research 5:55-69.
- Strathmann, R.R. 1978. Length of pelagic period in echinoderms with feeding larvae from the northeast Pacific. Journal Experimental Marine Biology and Ecology 34:23-27.
- Tegner, M.J. 1993. Southern California abalones: can stocks be rebuilt using marine harvest refugia? Canadian Journal Fisheries and Aquatic Sciences 50:2010-2018.
- Tegner, M.J., and P.K. Dayton 1977. Sea urchin recruitment patterns and implications of commercial fishing. Science 196:324-326.
- Tegner, M.J., and L.A. Levin 1983. Spiny lobsters and sea urchins: analysis of a predator-prey interaction. Journal of Experimental Marine Biology and Ecology 73:125-150.
- Vadas, R.L. 1977. Preferential feeding: An optimization strategy in sea urchins. Ecological Monographs 47:337-371.
- Vadas, R.L., Elnor, R.W., Garwood, P.E. and I.G. Babb 1986. Experimental evaluation of aggregation behavior in the sea urchin Strongylocentrotus droebachiensis: A reinterpretation. Marine Biology 90:433-448.
- Wilens, J.E. 1976. Common property resources and the dynamics of overexploitation: The case of the North Pacific Fur

Seal. University of British Columbia, Research Paper 3  
Vancouver, Canada.

Wilkinson, L. 1987. SYSTAT: The System for Statistics.

Systat Inc., Evanston, Illinois

Yamasaki, A. and A. Kuwahara 1990. Preserved area to effect  
recovery of overfished Zuwai crab stocks off Kyoto  
Prefecture, p. 575-585. In Proceedings of the  
International Symposium on King and Tanner Crabs. 28-30  
November 1989, Anchorage Alaska. Alaska Sea Grant  
College Program, University of Alaska, Fairbanks,  
Alaska.

Table 1. Density of adult red urchins in shallow, intermediate, and deep sites, (3 sites/depth, each 8x8m), inside and beyond the Bodega Marine Reserve.

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

Table 2. Percent of adult red urchins (>50mm) 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 (5-50mm), Strongylocentrotus spp., within 1m<sup>2</sup> quadrats in shallow and intermediate depth sites (n=3) in the Bodega Marine Reserve, from October 1988 to October 1992.

Percent Adults		Juvenile Microhabitat Distribution						
Depth	No. Quad. % Canopy	No. Juv.	Size Juv. (mm)	UT	US	RC	UCA	Exp.
Shallow (5m)	138 27.5(737)	379	5-20	229	88	31	28	3
		103	21-50	52	15	29	1	6
Inter. (11m)	158 2.2(755)	20	5-20	10	4	3	2	1
		47	21-50	1	3	4	0	39



### Figure Legends

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

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.

Fig. 3. Frequency distributions of gonad weight, Aristotle's lantern weight, and diameter of peristomial opening, for red sea urchins from shallow, intermediate, and deep sites along the Bodega Head, California.

Fig. 4. Plots of discriminant scores, and factor scores for the 2 components (PC2 and PC1) contributing most to the discrimination among depth habitat groups of red sea urchins.

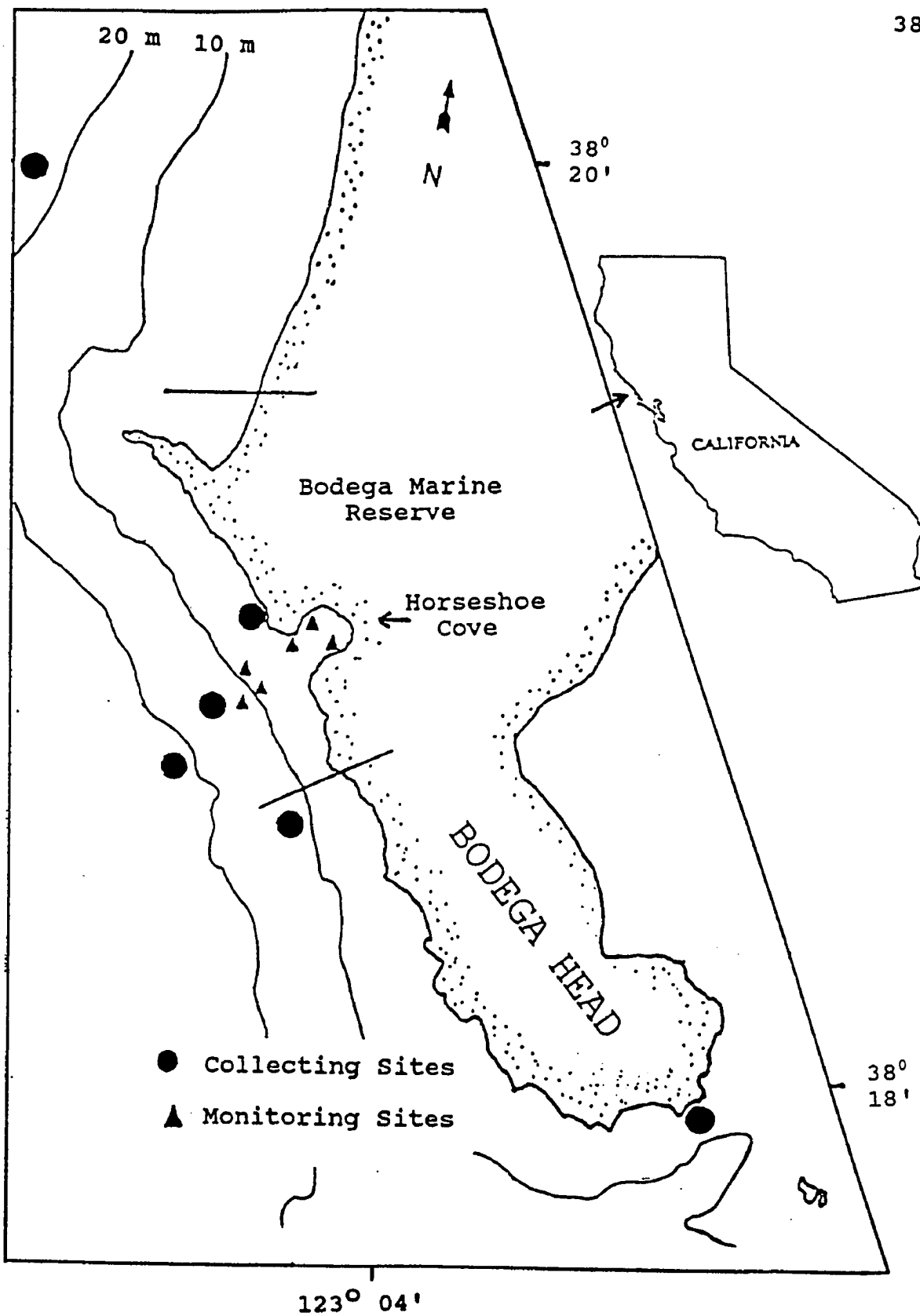


Figure 1.

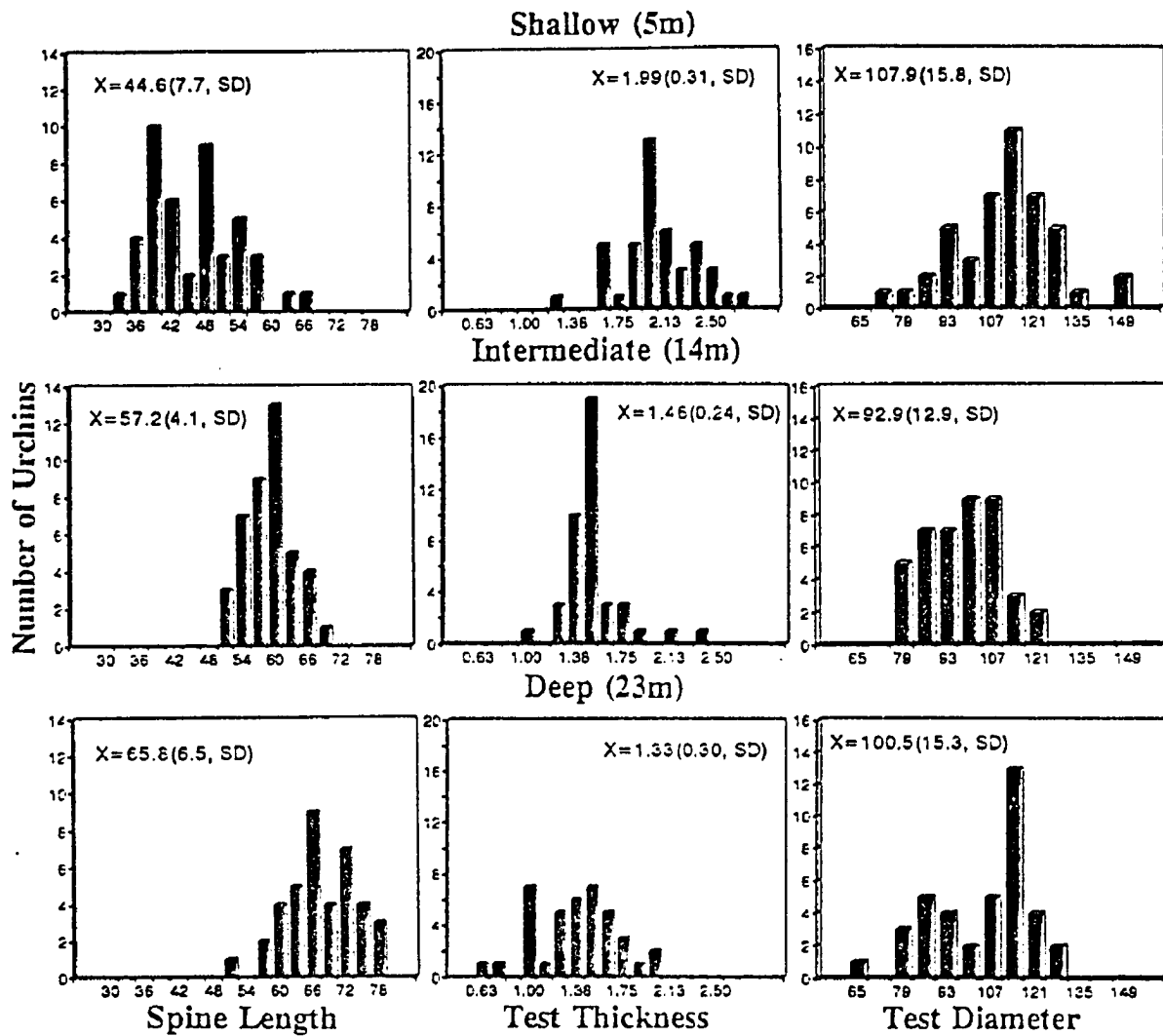


Figure 2.

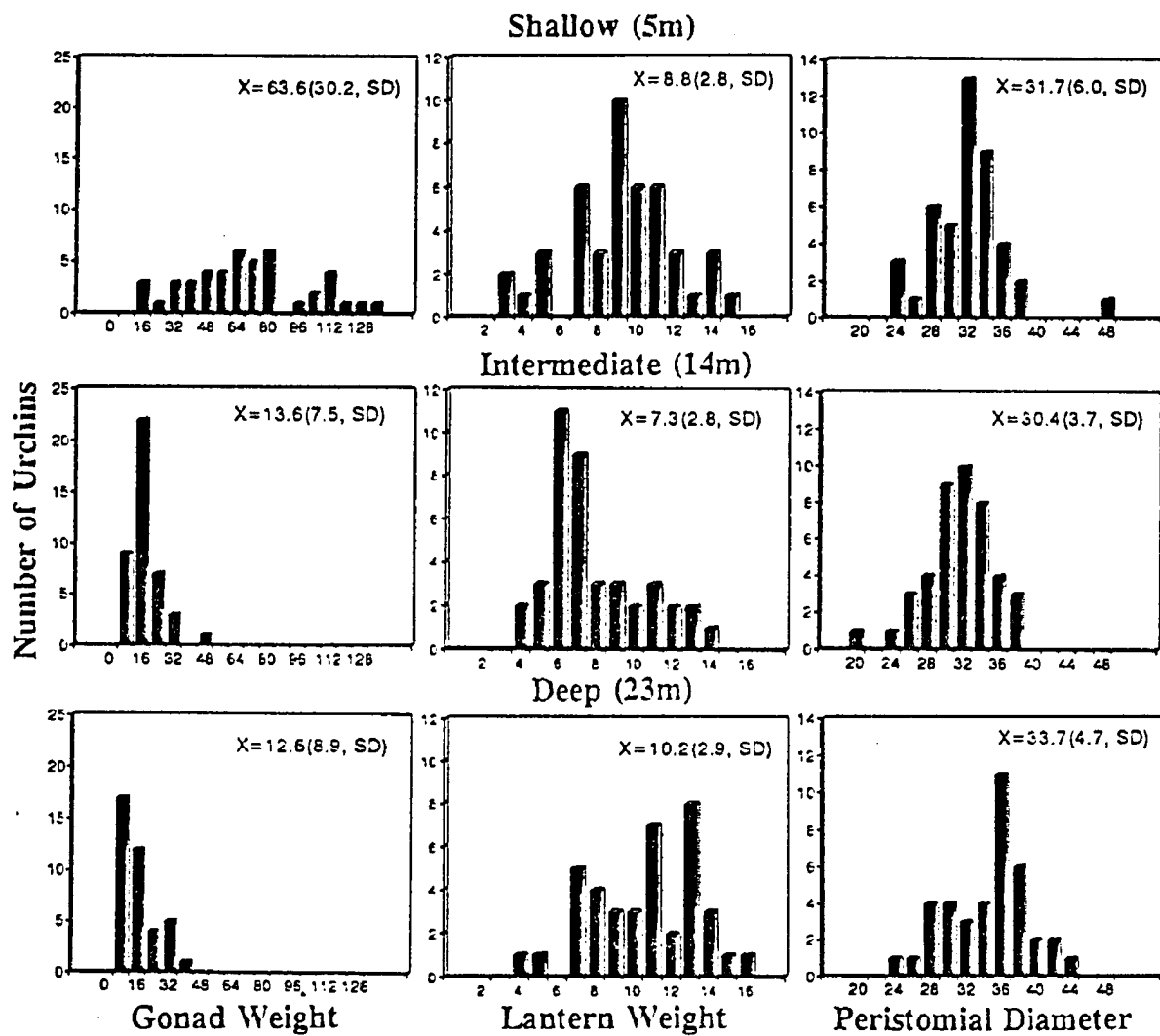


Figure 3.

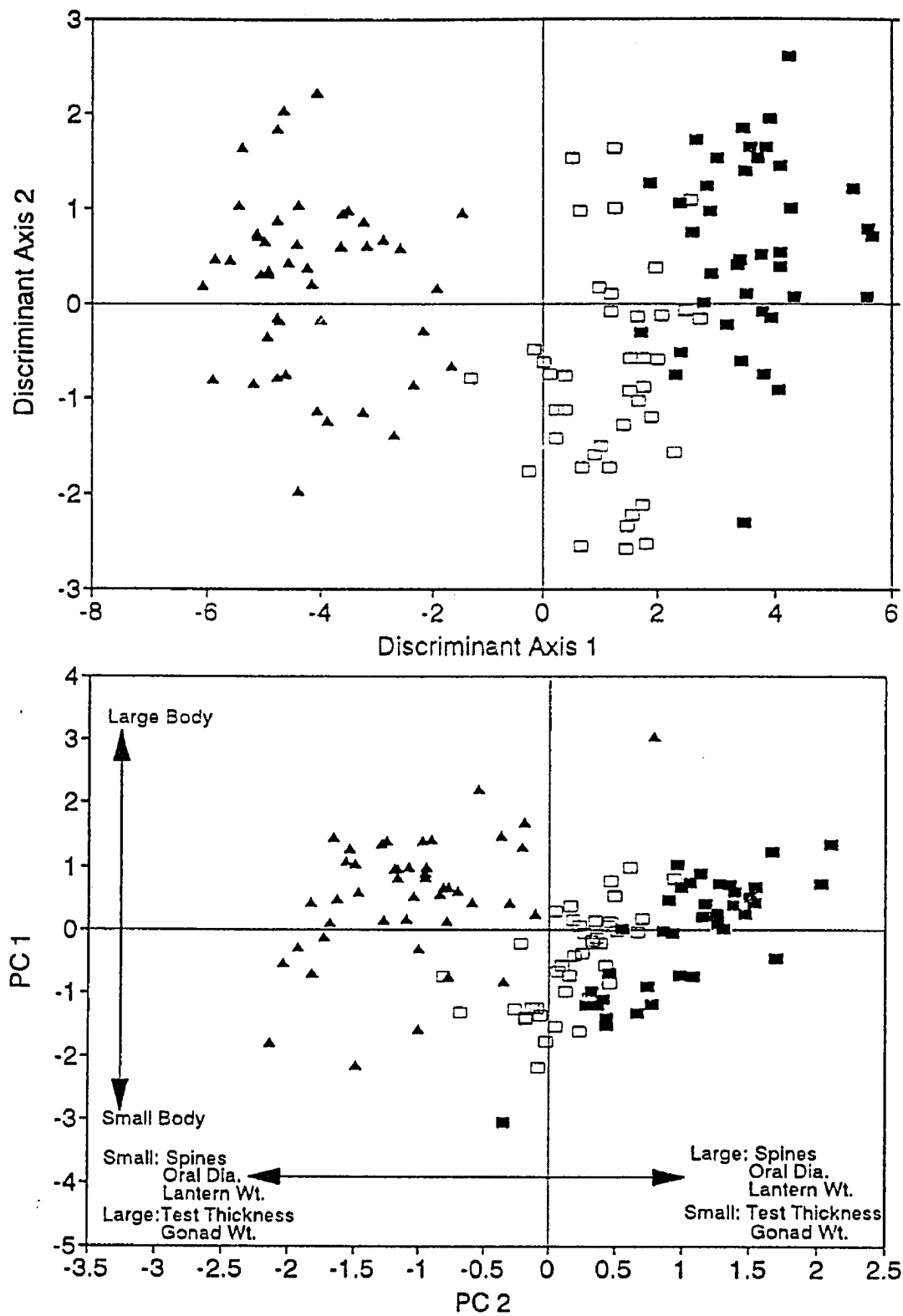


Figure 4.

Running Head.- Jaw emergence and growth in urchins

**Delayed Jaw Emergence and Growth in Cultured Red Sea  
Urchins: Recruitment Implications**

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### Abstract

Red urchins Strongylocentrotus franciscanus, raised in the laboratory lacked (90%) functional Aristotle's lanterns (jaws) and did not grow for 50 days post-settlement, despite having access to microbial films and macroalgae. Larval urchins were fed high densities (60,000-100,000 cells/ml) of Rhodomonas lens, and survival one day prior to settlement was good (32%). Larvae metamorphosed in high numbers (90%) and settlement began 23 days after fertilization. Newly settled red urchins averaged 0.404 mm, ( $\pm 0.038$  mm SD, N=10) in test diameter. By day 80 post settlement, all urchins examined had protruding teeth and functional jaws. Newly settled urchins suffered high mortality during this pre-jaw stage with only 6% surviving to become 1 year olds. Juveniles began eating fleshy red algae immediately after jaw emergence and at 1 year averaged 20.8 mm (SD 9.2 mm) in test diameter. Sibling juveniles reared under identical food, temperature, and light regimes exhibited tremendous phenotypic variability in final test size ranging from 4-44mm. Wild-caught newly settled purple urchins S. purpuratus, also lacked functional jaws (83.33%, N=6) and test diameters ranged from 0.403 to 0.672 mm. More work is needed to determine the relationship between jaw emergence, larval feeding, and factors such as timing of settlement and mortality. We demonstrate jaw emergence affects early growth and could be critical for the recruitment of sea urchins.

## Introduction

Sea urchins are important subtidal herbivores capable of determining the structure of algal assemblages (reviewed by Lawrence 1975, Harrold & Pearse 1987). High densities of sea urchins can decimate algal communities creating "barrens", habitats devoid of fleshy macroalgae (Breen & Mann 1976, Bernstein et al. 1981). Intensive urchin grazing and high population densities have been documented during drift algae shortages following severe storms (Harris et al. 1984, Ebeling et al. 1985, Harrold & Reed 1985), yet much debate remains over the mechanisms responsible for regulating urchin populations. Predation, (Mann & Breen 1972, Estes & Palmisano 1974, Tegner & Levin 1983) disease, (Scheibling 1984) and recruitment (Ebert 1983) have all been proposed as key mechanisms regulating urchin populations.

Research on urchin recruitment traditionally has focused on the abundance of juveniles greater than 5 mm in test diameter (Tegner & Dayton 1977, Ebert 1983, Pearse & Hines 1987; but see Rowley 1989, 1990), while urchins settle at 0.4-0.6 mm. Recent information documents the existence of strong settlement pulses of urchins on both the east (30,000/m<sup>2</sup>) (Harris, personal communication) and west coasts (10,000/m<sup>2</sup>) (Ebert et al. 1994) suggesting larvae periodically survive the plankton and encounter favorable oceanographic conditions for settlement. Despite this, large numbers of juveniles are rare (Ebert 1983, Pearse & Hines



1987) suggesting high mortality occurs post-settlement. Hjort (1914) hypothesized the existence of a "critical period" characterized by massive mortality early in the life history of fish. In fact, many marine invertebrates experience high mortality post-settlement (Keough & Downes 1982, Highsmith 1982, Young & Chia 1982, Connell 1985) including sea urchins (Rowley 1989, 1990). Research has focused on ecological factors as determinants of mortality (e.g. predation) and rather than larval condition. Food limitation and larval starvation has been shown to be important for larval fish recruitment in lakes (Carpenter & Kitchel 1993), but it's importance, if any, for the success of larval echinoderms appears minimal (Olsen & Olsen 1989).

Hjort's hypothesis stresses the importance of first feeding (after yolk sac depletion) and associated early growth in juveniles; larval condition may influence these factors in the newly settled (benthic) juvenile urchins. Since mortality is commonly size-specific (Highsmith 1982, Sebens 1983, Houde 1987) individuals with fast growth at settlement can reduce the time they remain vulnerable compared with slower growing individuals. Thus, early growth can affect survivorship and is important for successful recruitment.

Understanding sea urchin recruitment is especially important in light of expanding sea urchin fisheries around the world (Sloan 1984). In 1989, urchins became the state of

California's most valuable fishery grossing over 40 million dollars (Kalvass 1991). Recent declines in urchin landings have prompted interest in enhancing the fishery (Tegner 1989). Classical enhancement strategies include brood stock protection, habitat improvement, and outplanting cultured juveniles to supplement wild populations. Few facilities have been successful at culturing and outplanting urchin juveniles, although juvenile urchin production in Japan is on-going (Saito 1992; Seki personal communication). Aquaculture interests center around improving survival and growth rates to enhance production.

With both basic and applied interests in early echinoderm biology, we examine survivorship, exogenous feeding, and early growth in newly settled (<0.5 mm) red sea urchins, Strongylocentrotus franciscanus. Specifically, we quantify jaw emergence and early growth of juveniles under controlled laboratory conditions from the time of settlement to 1 year. In addition, we examine the degree of jaw emergence in a small sample of wild newly settled purple urchins S. purpuratus collected off Bodega Head, California. We discuss our findings in relation to the "critical period" concept and propose several hypotheses as potential mechanisms explaining the delay in jaw emergence and growth which we find in the laboratory.

#### Methods

Adult red urchins were collected from the Bodega Marine Reserve, Bodega Bay, California (38°19'03" N, 123°04'12" W). In August 1993, red urchins were spawned by injecting 5-10 ml of 0.5 M KCl into the peristomial membrane. Females were inverted over glass beakers and eggs were spawned into 5 $\mu$ m U.V. filtered sea water and rinsed 3 times. "Dry" sperm was collected into chilled dry bowls from the gonopores of spawning males. Eggs were fertilized and stocked into 1.5 liter glass jars stirred with paddles rotating 30-50 rpm. On day 3 post-fertilization, healthy larvae were counted and stocked at densities of 7 larvae per ml into three replicate glass jars with paddles. Larvae were maintained in static cultures with daily water changes using 5 $\mu$ m filtered, U.V. sterilized sea water at ambient temperature 15.0  $\pm$  2.1 °C. Larvae were fed microalgae daily with 150 ml Rhodomonas lens, cultures at densities ranging from 60,000-100,000 cells/ml. Algae cultures were maintained at 23°C under grow lights, with f/4 nutrients, and aeration (Guillard 1975). Algae cultures attained maximum densities of 1.25 x10<sup>6</sup> cells/ml around day 10 and were used until day 13.

At settlement, juveniles were measured and assessed for jaw protrusion using an Olympus BH-2 microscope at 100 X and an ocular micrometer with a scale of 11.1  $\mu$ m per increment. Jaw development was assessed by examining the peristomial membrane on the oral surface for teeth protrusion. At settlement, juveniles were transferred within culturing jars

(without touching urchins) and submerged in a 150 l outdoor aquaria with flow through sea water at ambient temperatures and photoperiod. Subsamples of ten juvenile urchins were examined for jaw development and growth at weekly, and then monthly intervals.

Settling substrates were deployed from August to October 1990 and June to August 1991 in the Bodega Marine Reserve, Bodega Bay, California. Four scrub brush collectors (see Ebert et al. 1994) were suspended 1m above the substrate from a subtidal cable along a depth gradient and retrieved 1-4 weeks after deployment (N=70 sets of 4 brushes). Brushes were then soaked in 5 liters of fresh cold water (10°C) with 250 ml of saturated MgCl<sub>2</sub> for 5-10 minutes until animals were anesthetized (Harris personal communication). Brush bristles were combed vigorously and newly settled urchins were collected on 500 µm seive, rinsed and sorted or stored in 70% Etoh.

### Results

In the laboratory, 63% (SD3%) of the larvae stocked initially survived until day 16 post-settlement and 32% (SD11%) survived until day 22 one day prior to first settlement resulting in approximately, 3,300 larvae surviving per jar (N=3 jars). Larval settlement began on day 23 and continued for three weeks until 85-95% had settled. Larvae settled within glass culturing jars which had

naturally occurring microbial films.

At settlement, 0-10% of urchins had functional jaws perforating the peristomial membrane. After several weeks some juveniles had developed visible jaws below the surface of the membrane that had not yet emerged. Juvenile urchins at settlement averaged 0.404mm ( $\pm 0.038$ mm SD, N=10) in test diameter. Jaw emergence occurred in 90% of the juvenile urchins sampled at day 64 post-settlement. At this time juvenile growth had just begun and juveniles averaged 0.916mm ( $\pm 0.15$ mm SD, N=10) test diameter (Figure 1). Growth rates remained close to zero ( $< 7 \mu\text{m/day}$ ) for the first two months post-settlement then quickly peaked around day 64 to remain at or around 70-80  $\mu\text{m/day}$  (2.1 mm/mos.) until the end of the first year (Figure 2). At 1 year post-settlement 535 juveniles were alive yielding 6% survival from settlement. Juveniles at 1 year averaged 20.8 mm ( $\pm 9.2$  mm SD, N=10) in test diameter.

Six newly settled urchins were found in the scrub brush collector samples. They ranged in size from 0.403-0.672mm in test diameter and were presumably 1-4 weeks old. These juveniles lacked dorsal pedicellaria indicating they were S. purpuratus (Rowley 1989, Ebert et al. 1994). Of these, 5 lacked functional jaws, and 1 had protruding teeth. Of the five without functional jaws, 1 had jaws visible beneath the surface of the peristomial membrane.

## Discussion

### Delayed Jaw Development and Growth

The majority of cultured red sea urchins had intact peristomial membranes (with no jaws) for the first 80 days post-settlement indicating these individuals were not feeding exogenously. Similarly, five out of six (83%) juvenile *S. purpuratus* (<1mm) from the field lacked emergent jaws. The literature suggests many marine invertebrates feed soon after metamorphosis, however little direct observations of feeding in this stage are published. For example, deposit feeding sand dollars (Telford et al. 1985) have fully formed and apparently functional guts at 7 days post-settlement, although feeding was not observed (Chia & Burke 1978). Newly settled urchins (genus *Strongylocentrotus*) in culture are typically fed diatom films *Nitzschia* (Hinegardner & Tuzzi 1981, Leahy 1986) a technique adapted from abalone aquaculture (Tong & Moss 1989). Wild juvenile urchins are also thought to feed on diatoms or the epithelial cell layer of coralline algae soon after settlement (Rowley 1990, Harrold et al. 1991). Similarly, newly settled sea stars *Acanthaster planci*, feed prior to 7 days but this involves stomach eversion over diatom films (Yamaguchi 1974). Abalone feed using radula ingesting bacteria and diatoms on crustose coralline algae substrates soon after settlement (Garland et al. 1985, Tong & Moss 1989). While sea stars and abalone feed early their feeding mode is unrelated to juvenile

urchins and may not be comparable.

The delay in jaw emergence and growth we observed in cultured red urchins could be explained by several alternative hypotheses. Delayed jaw emergence could be (1) the result of substantial somatic reorganization occurring during metamorphosis from the planktotrophic larval stage to the juvenile stage which requires development of Aristotle's lantern, the digestive tract, and anus (Pearse & Cameron 1991); (2) the product of nutrient deficiency (single microalgae food source) or water quality problems in culture; (3) a consequence of a shortened larval stage (23-40 days) due to food enrichment in culture. If wild juveniles also lack jaws a few weeks after settlement this result would support Hypothesis 1. Our limited data from field caught juveniles suggests wild juveniles may also have delayed jaw emergence however larger samples of wild caught newly settled Strongylocentrotus suggest many wild juvenile may have jaws within 2 weeks of settlement (S. Schroeter personal communication) indicating more work must be done.

Enhanced food rations have been shown to accelerate settlement time in many invertebrate larvae cultured in the laboratory including echinoderms (Pauley et al. 1985). We outline two alternative predictions regarding the consequences of accelerated larval settlement for the new juvenile. First, delayed settlers could be more mature since they have more time in the plankton to develop; this would

suggest a trade-off between time spent as a planktotrophic feeder versus benthic feeder implying time to maturity is generally fixed. Alternatively, early settlers could develop from well fed larvae with plenty of nutrient reserves. Lipid droplets formed within the larval stomach, could be retained by the juvenile after metamorphosis and these reserves could infer an early advantage in jaw development and growth. Well fed larval sand dollars had enhanced growth as newly settled juveniles compared with juveniles developing from unfed larvae (Highsmith & Emlet 1986). However, our well fed larvae (assuming no nutrient deficiency) had delayed jaw emergence and growth which tends to support the former scenario. We have no data to comment on Hypothesis 2.

Our results also indicate a lag in the onset of growth coincident with this pre-jaw period. Delayed growth, post-metamorphosis has been observed in other cultured urchins S. droebachiensis, (Raymond & Scheibling 1987) and S. purpuratus, (Rowley 1989). Rowley (1990) found little increase in test diameter (0.3-0.4 mm/mo.) for Strongylocentrotus spp. during the first 50 days post-settlement compared with double that rate (0.9mm/mo.) 50 days later. Rowley (1990) did record a feeding halo in the diatom film in the first 50 days implying early exogenous feeding. Rowley (1990) attributed the growth burst he observed to a switch in diet from diatom film to macroalgae at a specific juvenile size (either test diameter or mass).



We suggest that a growth burst could also occur after jaw development and the onset of exogenous feeding (Fig. 2). Newly settled juveniles prior to jaw emergence could be absorbing dissolved amino acids from seawater, as has been shown for larval urchins (Manahan et al. 1983). We concur with Rowley (1990) that delayed growth in newly settled urchins imply growth estimates from juveniles (10 mm) and adults (Ebert 1968, Tegner & Dayton 1981, Ebert 1983, Himmelman et al. 1983, Ebert & Russell 1992, Rogers-Bennett et al. in press) overemphasize early growth and underestimate urchin age at the time of first harvest (90mm) which could lead to over-fishing.

#### Mortality and the Critical Period

The pre-jaw stage (post-metamorphosis) was accompanied by high mortality rates in the laboratory (predators absent). Such mortality maybe sufficient to produce a "critical period" in red urchin recruitment. Field observations confirm high post-settlement mortality in urchins. In southern California, Rowley (1989) showed Strongylocentrotus spp. suffered tremendous mortality in kelp forest (90%) and "barren" (75%) habitats in the first 40 days. Much of this mortality could be occurring in the pre-jaw stage. Alternatively, the mortality observed could be the result of accelerated settlement as has been observed with sand dollar juveniles (Highsmith & Emlet 1986) or purely a culturing artifact. Mortality is generally great at

some stage and in our culturing work we had very high survival in the larval stage such that high post-settlement mortality was not unexpected. Larger juvenile urchins (5-30mm test diameter) may better avoid such sources of mortality by seeking out cryptic micro-habitats (Rogers-Bennett 1989) including the spine canopy of adult urchins (Tegner & Dayton 1977, Breen et al. 1985, Rogers-Bennett et al. in press) where they may access drift macroalgae captured by adults.

Our results suggest individuals with functional jaws grow faster than those in the pre-jaw stage. Assuming newly settled urchins are susceptible to size-selective mortality, individuals with faster jaw development would have an advantage over individuals who develop and grow more slowly. More work must be conducted to distinguish between the alternative hypotheses proposed for delayed jaw development and growth as well as associated early mortality. Answering these questions are especially important since slight intra-cohort differences in larval fish and the onset of first feeding and subsequent growth have been associated with higher recruitment events (Houde 1987, Bailey & Houde 1989, Cowen et al. 1993). Our work suggests the timing of jaw emergence may be critical to recruitment success in both aquaculture and natural systems.

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### Literature Cited

- Bailey, K.M., and E.D. Houde 1989. Predation on eggs and larvae of marine fishes and the recruitment problem. *Advan. Mar. Biol.* 25: 1-83
- Bernstein, B.B., Williams, B.E. and K.H. Mann 1981. The role of behavioral responses to predators in modifying urchins' (*Strongylocentrotus droebachiensis*) destructive grazing and seasonal foraging patterns. *Marine Biology* 63: 39-49
- Breen, P.A., and K.H. Mann 1976. Destructive grazing of kelp by sea urchins in eastern Canada. *J. Fish. Res. Bd. Can.* 33: 1278-1283
- Breen, P.A. Carolsfield, W., and K.L. Yamanaka 1985. Social behavior of juvenile red sea urchins (*Strongylocentrotus franciscanus*). *J. exp. mar. Biol. Ecol.* 92: 45-62
- Carpenter, S.R. and J.F. Kitchell 1993. The trophic cascade in lakes. Cambridge Univ. Press, London, England
- Chia, F.-S., and R.D. Burke 1978. Echinoderm metamorphosis: fate of larval structures. In *Settlement and Metamorphosis of Marine Invertebrates*. eds. Chia, F.-S. and M. Rice pp 219- 234 Elsevier, N.Y.
- Connell, J.H. 1985. The consequences of variation in initial settlement vs. post-settlement mortality in rocky intertidal communities. *J. Exp. Mar. Biol. Ecol.* 93: 11-45

- Cowen, J.H., Alpine, A., Cole, B., Wong R., Arthur, J., and M. Ball 1993. Individual-based model of young-of-the-year striped bass population dynamics. II. Factors affecting recruitment in the Potomac river, Maryland. Trans. Amer. Fish. Soc. 122: 439-458
- Ebert, T.A. 1968. Growth rates of the sea urchin Strongylocentrotus purpuratus related to food availability and spine abrasion. Ecology 49: 1062-1074
- Ebert, T.A. 1983. Recruitment in echinoderms. Echinoderm Studies 1: 169-209
- Ebert, T.A., and M.P. Russell 1992. Growth and mortality estimates for red sea urchin Strongylocentrotus franciscanus from San Nicolas, Island, California. Marine Ecology Progress Series 81: 31-41
- Ebert, T.A., Schroeter, S.C., Dixon, J. D., and P. Kalvass 1994. Settlement patterns of red and purple sea urchins (Strongylocentrotus franciscanus and S. purpuratus) in California, USA. Mar. Ecol. Prog. Ser. 111: 41-52
- Ebeling, A.W., Laur, D.R., and R.J. Rowley 1985. Severe storm disturbances and reversal of community structure in a southern California kelp forest. Marine Biology 84: 287-294
- Estes, J.A., and J.F. Palmisano 1974. Sea otters: their role in structuring near-shore communities. Science 185: 1058-1060

- Garland, C.D., Cooke S.L., Grant, J.F., and T.A. McMeekin  
1985. Ingestion of bacteria on the cuticle of crustose  
(non-articulated) coralline algae by post-larval and  
juvenile abalone (Haliotis rubra Leach) from Tasmanian  
waters. J. Exp. mar. biol. Ecol. 91: 137-149
- Guillard, R.R.L. 1975. Culture of phytoplankton for  
feeding marine invertebrates. In eds. Smith, W.L. and  
M.H. Chaneley Culture of Marine Invertebrate Animals.  
Plenum Press, N.Y. p. 26-60
- Harris, L.G., Ebling, A.W., Laur, D.R., and R.J. Rowley  
1984. Community recovery following storm damage: a  
case for facilitation in primary succession. Science  
224: 1336-1338
- Harrold, C., and D.C. Reed 1985. Food availability, sea  
urchin grazing, and kelp forest community structure.  
Ecology 66: 1160-1169
- Harrold, C., and J.S. Pearse 1987. The ecological role of  
echinoderms in kelp forests. Echinoderm Studies 2: 137-  
234
- Harrold, C., Lisin, S., Light, K.H., and S. Tudor 1991.  
Isolating settlement from recruitment of sea urchins.  
J. Exp. Mar. Biol. Ecol. 147: 81-94
- Highsmith, R.C. 1982. Induced settlement and  
metamorphosis of sand dollar (Dendraster excentricus)  
larvae in predator-free sites: adult sand dollar beds.  
Ecology 63: 329-337

- Himmelman, J.H., Cardinal, A., and E. Bourget 1983.  
Community development following removal of urchins,  
Strongylocentrotus droebachiensis, from the rocky  
subtidal zone of the St. Lawrence Estuary, eastern  
Canada. *Oecologia* 59: 27-39
- Hinegardner, R.T., and M.M. Tuzzi 1981. Laboratory culture  
of the sea urchin Lytechinus pictus. In *Marine  
Invertebrates. Laboratory Animal Management.* ed R.T.  
Hinegardner pp 291- 302, National Academy Press,  
Washington, D.C.
- Hjort, J. 1914. Fluctuations in the great fisheries of  
northern Europe viewed in the light of biological  
research. *Rapport du Conseil d'Exploration de Mer* 20:  
1-228
- Houde, E.D. 1987. Fish early life dynamics and recruitment  
variability. *Amer. Fish. Soc. Symp.* 2: 17-29
- Kalvass, P., Taniguchi, I., Buttolph, P., and J. DeMartini  
1991. Relative abundance and composition of red sea  
urchin Strongylocentrotus franciscanus, populations  
along the Mendicino and Sonoma county coasts, 1989.  
California Department of Fish and Game. *Marine  
Resources Admin. Tech. Report No. 91-3.* p. 103
- Keough, M.K. and B.J. Downes 1982. Recruitment of marine  
invertebrates: the role of active larval choices and  
early mortality. *Oecologia* 54: 348-352
- Lawrence, J.D. 1975. On the relationship between marine

plants and sea urchins. *Oceanography and Marine Biology Annual Review* 13: 213-286

Leahy, P.S. 1986. Laboratory culture of *Strongylocentrotus purpuratus* Adults, Embryos, and Larvae. In Schroeder, T.E. *Methods in Cell Biology: Echinoderm Gametes and Embryos*. Academic Press. N.Y. pp. 1-13

Manahan, D.T., Davis, J.P., and G.C. Stephens 1983.

Bacteria-free sea urchin larvae: selective uptake of neutral amino acids from sea water. *Science* 220: 204-206

Mann, K.H., and P.A. Breen 1972. The relationship between lobster abundance, sea urchins, and kelp beds. *J. Fish. Res. Bd. Can.* 29: 603-609

Paulay, G., Boring, L., and R.R. Strathmann 1985. Food limited growth and development of larvae: experiments with natural sea water. *J. Exp. mar. biol. Ecol.* 93: 1-10

Pearse, J.S., and A.H. Hines 1987. Long-term populations dynamics of sea urchins in a central California kelp forest: rare recruitment and rapid decline. *Mar. Ecol. Prog. Ser.* 39: 275-283

Pearse, J.S., and A. Cameron 1991. Echinodermata: Echinoidea. In *Reproduction of Marine Invertebrates Vol VI*. pp 598-623. Boxwood Press Pacific Grove, CA.

Raymond, B.G., and R.E. Scheibling 1987. Recruitment and growth of the sea urchin *Strongylocentrotus*



- droebachiensis (Muller) following mass mortalities off Nova Scotia, Canada. J. Exp. Mar. Biol. Ecol. 108: 31-54
- Rogers-Bennett, L. 1989. Spatial association of juvenile green sea urchins. University of Massachusetts/Boston. Boston, MA.
- Rogers-Bennett, L, Bennett, W.A., Fastenau, H.C., and C.M. Dewees 1994. Spatial variation in red sea urchin reproduction and morphology: implications for harvest refugia. In Press. Ecological Applications
- Rowley, R.J. 1989. Settlement and recruitment of sea urchins (Strongylocentrotus spp.) in a sea-urchin barren ground and a kelp bed: are populations regulated by settlement or post-settlement processes? Mar. Biol. 100: 485-494
- Rowley, R.J. 1990. Newly settled sea urchins in a kelp bed and urchin barren ground: a comparison of growth and mortality. Mar. Ecol. Prog. Sers. 62: 229-240
- Saito, K. 1992. Japan's sea urchin enhancement experience. In sea urchins, abalone and kelp: their biology, enhancement and management. March 19-21, 1992 Bodega Bay, Ca. Report No. T-CSGCP-029.
- Scheibling, R.E. 1984. Echinoids, epizootics and ecological stability in the rocky subtidal off Nova Scotia, Canada. Helgolander wiss. Meeresunters 37: 233-242
- Sebens, K.P. 1983. The larval and juvenile ecology of the

- temperate octocoral Alcyonium siderium Verrill. II. Fecundity, survival, and juvenile growth. J. exp. mar. Biol. Ecol. 72: 263-285
- Sloan, N.A. 1984. Echinoderm fisheries of the world: a review. In (ed.) Keegan, B. F., O'Connor, B. D. S. Echinodermata; Fifth Inter. Echinoderm Conf. Galway, Ireland: Sept. 24-29, 1984.
- Tegner, M.J. 1989. The feasibility of enhancing red sea urchin Strongylocentrotus franciscanus, stocks in California: an analysis of the options. Mar. Fish. Rev. 51: 1-22
- Tegner, M.J., and P.K. Dayton 1977. Sea urchin recruitment patterns and implications of commercial fishing. Science 196: 324-326
- Tegner, M.J. and P.K. Dayton 1981. Population structure, recruitment and mortality of two sea urchins (Strongylocentrotus franciscanus, and S. purpuratus) in a kelp forest. Mar. Ecol. Prog Ser. 5: 255-268
- Tegner, M.J. and L.A. Levin 1983. Spiny lobsters and sea urchins: analysis of a predator-prey interaction. J. exp. mar. Biol. Ecol. 73: 125-150
- Telford, M., Mooi, R., and O. Ellers 1985. A new model of podial deposit feeding in the sand dollar Mellita quinquiesperforata (Leske): The sieve hypothesis challenged. Biol. Bull. 169: 431-448
- Tong, L.J., and G.A. Moss 1989. The New Zealand culture

system for abalone. In eds. Shepard, S.A., Tegner, M.J., Guzman del Proo, S.A. Abalone of the World: Biology, Fisheries, and Culture, Fishing News Books, California.

Yamaguchi, M. 1974. Growth of juvenile Acanthaster planci (L.) in the laboratory. Pacif. Sci. 28: 123-138

Young, C.M., Chia, F.-S. 1982. Factors controlling spatial distribution of the sea cucumber Psolus chitinoides: settling and post-settling behavior. Mar. Biol. 69: 195-205

### Figure Legends

Fig. 1. Test diameter (mm) and the percent of newly settled red sea urchins with functional jaws during the first year following settlement in the laboratory.

Fig. 2. Growth rates ( $\mu\text{m}/\text{day}$ ) of newly settled red sea urchins for the first year following settlement in the laboratory.

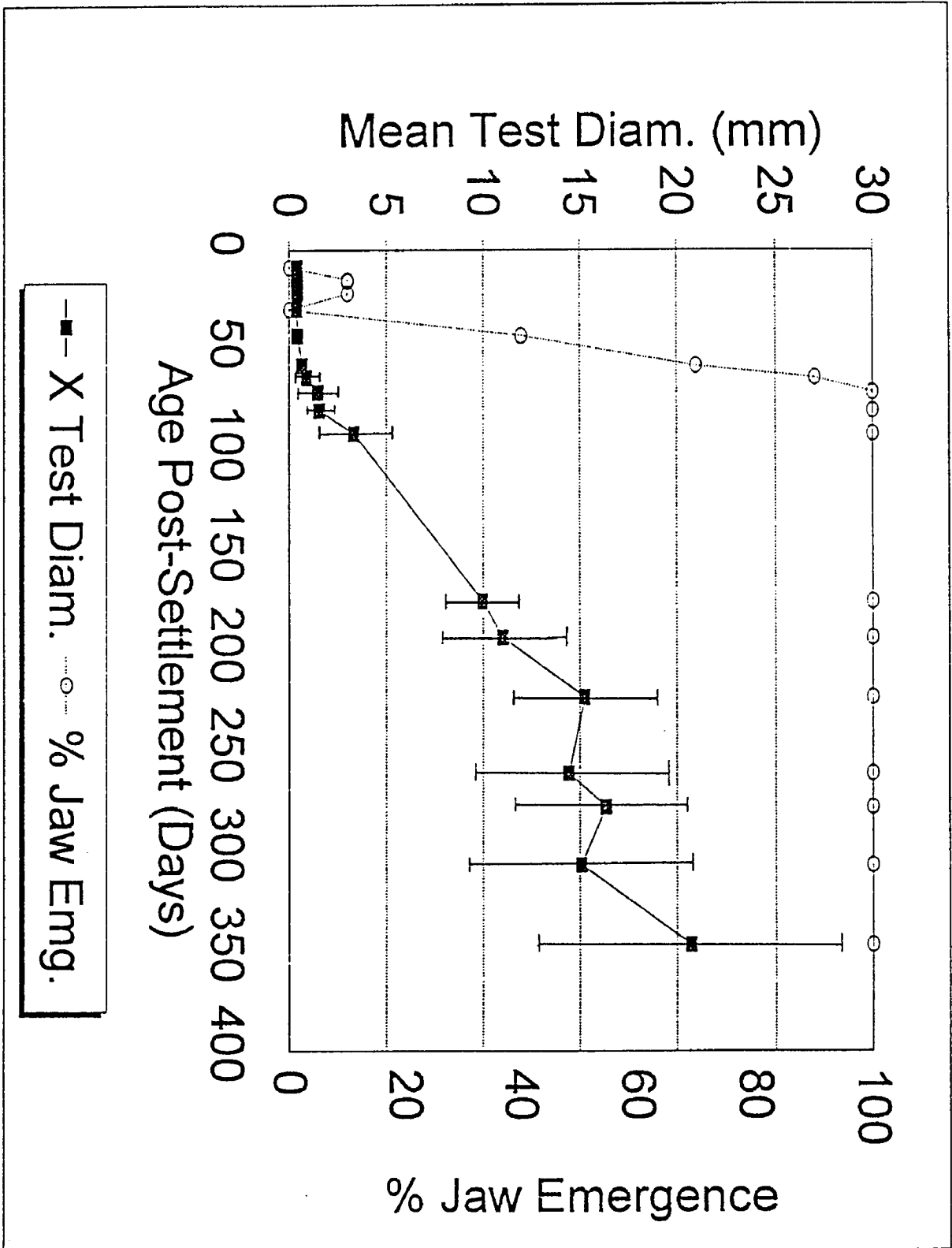


Figure 1.

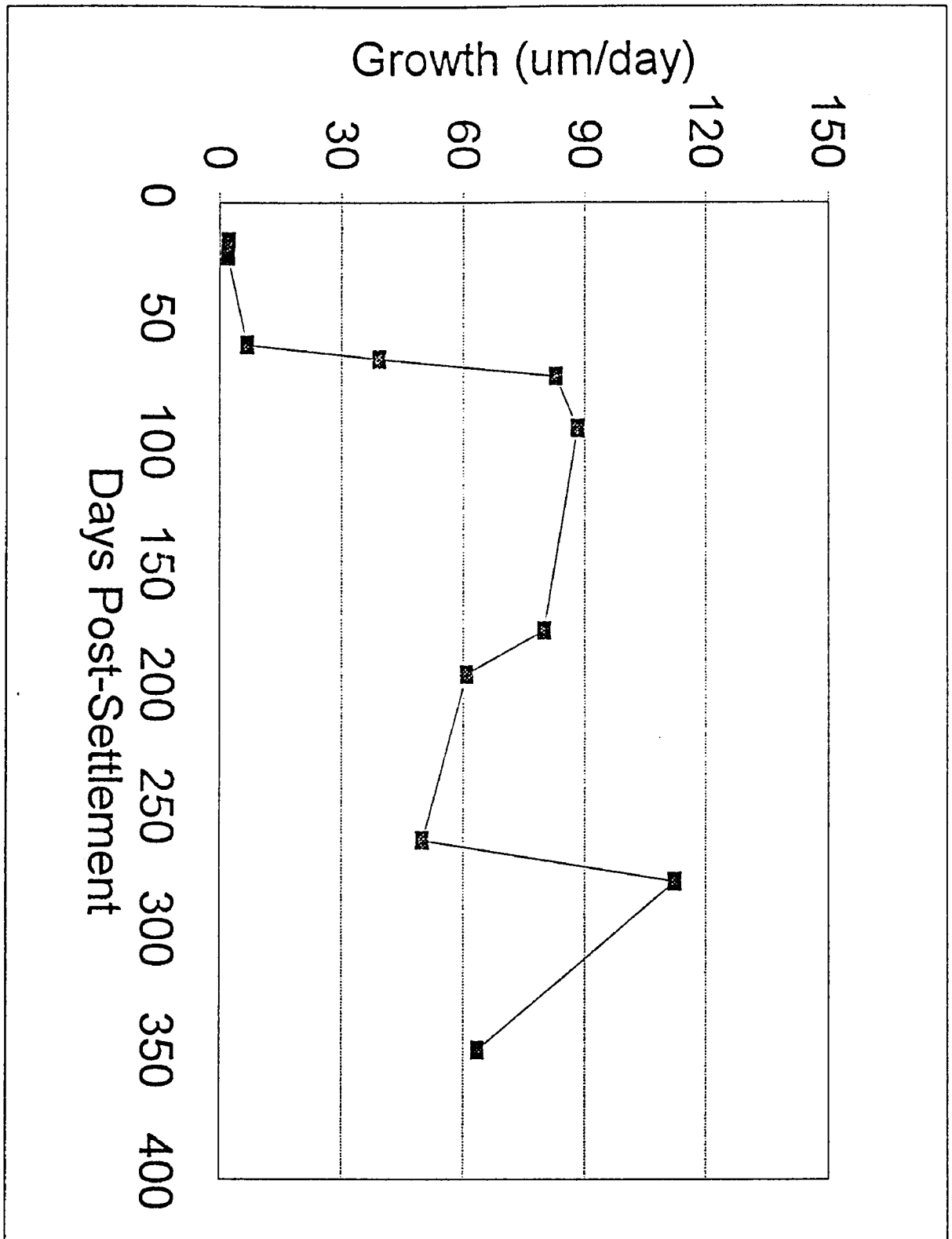


Figure 2.

Running Head.- Red urchin growth model

**Growth of Red Sea Urchins in Northern California:  
an Alternative Model**

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### Abstract

Red sea urchins, Strongylocentrotus franciscanus, were tagged in 1992 and growth rates were obtained after one year from two subtidal sites at Salt Point, northern California. The number of tagged urchins recovered from a shallow site (5m) was more than double (38.5%) the number recovered (15%) from a deep site (15m). Similarly, recapture rates of juveniles cultured in the laboratory then outplanted in the field were double in the shallow (20.8%) compared with the deep site (10.8%). The relationship between final jaw size ( $J_{t+1}$ ) and initial jaw size ( $J_t$ ) was a monotonically increasing function for adult urchins, but data from juveniles show small urchins (small  $J_t$ ) deviate from this function in a regular way. We present a new model to describe urchin growth from settlement to adulthood, the shape of which mimics an airfoil and closely fits the field data at Salt Point ( $r^2 = 0.993$ ;  $F = 31322$ ;  $p < 0.001$ ).

This function is:  $J_{t+1} = J_t + (a + J_t^2)e^{-KJt}$

where  $J_{t+1} = J_t$  is the stasis (no growth) portion of the function and the growth portion  $\Delta J = (a + J_t^2)e^{-KJt}$ . Our function has 3 desirable features (1) it lacks an asymptotic size, (2) it has 2 biologically relevant parameters, and (3) it allows for asymmetry about the function's maximum. Parameter values determined from our data are as follows; size at one year, Y intercept  $a = 4.499$  ( $\pm$  SE 0.207), and growth rate constant  $K = 0.375$  ( $\pm$  SE 0.003). We estimate red



urchins in northern California attain harvestable size (89mm test diameter) in 9.0 years and caution parameter estimates should be generated independently in northern and southern California as juvenile growth appears to vary spatially at this scale.

### Introduction

The Brody-Bertalanffy growth equation (von Bertalanffy 1938, Brody 1945, Ricker 1975) is used widely to model growth. This model has two parameters  $L_{\infty}$ , and  $K$ , with age at size 0 ( $t_0$ ). These parameters have been interpreted as asymptotic size ( $L_{\infty}$ ), and growth rate constant ( $K$ ). Fabens (1965) least squared method can be used to estimate the model's parameters and requires only paired size data separated by a known time interval (tag-recapture data). To tie the growth curve to a time axis it is necessary to know the age and size of at least one individual such as ( $t_0$ ) size at birth, hatching, or settlement. The simplicity of the Brody-Bertalanffy growth curve and its well defined parameters make it an attractive model. A related growth function, the Richard's function (Richard 1959), has been used to model urchin growth (Ebert 1980, Ebert 1982, Russell 1987, Ebert & Russell, 1992). However, growth data from small red urchins (<5.0 mm) does not fit predictions generated by these models making them unsuitable (Ebert & Russell, 1993).

Growth models are important not only for understanding basic population dynamics but are also used to guide fishery managers. Red sea urchins, Strongylocentrotus franciscanus, are the state of California's most valuable fishery, and recent declines in landings in northern California have prompted more research focusing on fishery management issues

(Tegner 1989). Accurate estimates of growth in juvenile urchins and the time required to achieve legal size are essential for the development of fishery management policies (Tegner 1989, Ebert & Russell, 1993). There has been some debate over the growth rates of juveniles in the first few years post-settlement because in part, individual variation in growth can be high (Pearse & Cameron, 1991, Rogers-Bennett et al. manuscript) and because growth in small urchins is difficult to measure in the field, where mortality is high.

Here we present an alternative model to describe urchin growth over the entire range of post-settlement sizes for red urchins in northern California. This model has two well defined parameters ( $a$  and  $K$ ), and an asymptotic approach to zero (infinite growth). Our model incorporates a short period of exponential growth which begins shortly after settlement (Raymond & Scheibling, 1987, Rowley 1990, Rogers-Bennett et al. 1994), then goes through a growth maximum as juveniles reach a size of 20mm (jaw size 5mm), and finally a very slow growth period for adults. We use field data obtained from a tag-recapture study using juveniles and adults as well as growth data from newly settled juveniles in the laboratory to generate parameters in the new growth model. We use our model to estimate the time required for urchins to grow (recruit) into the fishery (90 mm test diameter) in northern California and discuss how the

inclusion of juvenile growth data impacts these estimates. Finally, we compare our model to the Tanaka (1982) function which has one additional parameter and shares the features of 1) infinite growth, and 2) an early exponential phase, followed by declining growth. Currently this model is the preferred model for red urchin growth (Ebert & Russell, 1993).

## Methods

### Study Site

Growth rates were determined for red sea urchins, Strongylocentrotus franciscanus, at two subtidal sites in the Salt Point Closure (38°33'6" N, 123°19'45" W), in northern California USA. This area encompasses a three mile expansion of the Salt Point Gerstle Cove Reserve which has been set aside as an urchin harvest refuge. We tagged red urchins in one shallow site (5m) south of the southern border of the Gerstle Cove Reserve, 1m from a rocky outcropping at the edge of the shore. Urchins were also tagged at a deep site (15m) on the leeward side of a large wash-rock more than 1000m offshore of Gerstle Cove. Both sites were relatively isolated, surrounded by sand, and in the vicinity of seasonally dense Nereocystis beds.

### Tagging

Urchins were tagged internally with tetracycline injections in situ, using 0.5-1.2 ml of 1g

tetracycline/100ml of seawater (Ebert 1982). Three hundred red urchins were measured and tagged at each site on Aug. 19, 1992. Urchins were harvested 13 months later on Sept. 18, 1993 from each site (N=374 shallow; N=352 deep). Estimates of urchin density were made within a (12 m radius) circle at each site. Drift algae collections were made along a 2x10m transect ( $20\text{m}^2$ ) at each depth.

We also tagged and outplanted 1 year-old juvenile urchins ( $X=17.6\text{mm}$  test diameter) cultured at the Bodega Marine Laboratory into the shallow and deep sites. Juveniles were tagged by immersion in a calcein solution of 125mg/liter seawater with p.H. adjusted to 7.78 for 24 hours (Wilson et al. 1987). After tagging, juveniles were transported to the field and approximately 100-120 were outplanted at each depth on Aug. 31, 1992 and harvested one year later on Sept. 18, 1994 with the adults. In August 1993 additional juvenile urchins were cultured and their size at settlement, growth, and jaw size after one year in the laboratory was recorded.

At the time of tagging and harvest, urchin test diameters were measured with vernier calipers to the nearest  $\pm 0.2\text{mm}$ . At harvest, gut contents were also analyzed from subsamples of 20 urchins from each depth. Gut contents were fixed in alcohol, sorted on a petri dish, and the most abundant items recorded from five  $10\text{mm}^2$  grids (Harrold & Reed, 1985). We used a conservative definition of optimal

food, defining them as fleshy red or brown algae, and defining suboptimal food as green algae, upright and encrusting coralline algae, detritus (animal, plant and inorganic), plant (Phyllospadix), mud and sand.

#### Growth

Growth was estimated from the change in urchin jaw length ( $\Delta J$ ) after one year in the field (Ebert & Russell, 1993). Growth estimates made from jaws are more accurate than those using tags on test ossicles, because ossicles move toward the oral surface during growth (Duetler 1926), and require matching plates at tagging with ambitus plates at the time of collection (Ebert 1977). We also examined the relationship between jaw length and test diameter for urchins at each site and for a large sample of juveniles cultured in the laboratory. Urchin jaws were obtained by dissecting Aristotle's lantern and dissolving excess tissue in 10% sodium hypochlorite. The length of the cleaned jaw was measured for each urchin with vernier calipers to the nearest 0.1mm.

Tagged urchins were identified by their fluorescent jaws under an ultraviolet epi-illuminator (Lite-Mite) on a dissecting scope. Growth increments from tagged jaws were determined using the Argon/Crypton Laser Scanning Confocal Microscope (BioRad MRC-600) with a BHS fluorescence filter (blue wave length) and COMOS software package. Growth was measured from the edge of the glowing fluorescent band

(indicating size at tagging) to the end of the esophageal jaw edge. In addition, we recorded the width of the glowing band plus growth from a second glowing arc at the labial tip of the jaw (if any). Urchin growth was estimated from the increase in jaw length from the size at tagging (initial jaw size  $J_t$ ) to size after one year (final jaw size  $J_{t+1}$ ). Initial jaw size ( $J_t$ ) = final jaw size ( $J_{t+1}$ ) minus the sum of the esophageal and labial growth.

#### Growth Models

Since growth typically slows as organisms get larger (older) this process can be modelled using a simple first order decay equation. This is essentially a von Bertalanffy equation (von Bertalanffy 1957). We use tag-recapture data to find the amount of growth ( $\Delta J$ ) over a time interval from  $t$  to  $t+1$  (1 year), but we do not know  $t$  or  $t+1$  relative to  $t_0$  = start of growth (age is unknown). To explain growth ( $\Delta J$ ) we can add a linear decreasing function to a linear increasing function. This function would be the intersection of two linear functions and is essentially a Walford plot (Walford 1946) however juveniles show a regular deviation from these simple models rendering them unsuitable.

We present a more comprehensive model to explain growth over the entire range of sizes (jaw sizes  $J_t=0.1$  to 25 mm) and we use this growth model to estimate the time required for urchins to grow into the fishery. Our model has three features; (1) a short period of geometric increase as growth

starts soon after settlement  $J_t = 0.1\text{mm}$ , (2) a period of maximum growth for urchins near  $J_t = 5.0\text{ mm}$  (test diameter 10 mm), (3) and an airfoil cross section. Radial distribution functions for exponential decay,  $y = x^2e^{-x}$ , provide all these features and are commonly used in quantum chemistry in the study of spherically symmetric potential fields (Atkins 1994). Growth in this model is analogous to measuring the increase in weight of an orange peel. When the orange is small it is growing rapidly but the increase is small, as it gets larger it goes through a growth maximum. Finally, when the orange is large the increase is small. Adding a radial distribution function to the stasis curve a new function is obtained

$$J_{t+1} = J_t + (a + J_t^2)e^{-KJt} \quad \text{eq. 1}$$

in which  $a$  and  $K$  are empirically derived (fitted) parameters. We define  $a$  as the jaw size at one year, the  $Y$  intercept, and  $K$  as the growth rate constant. This function contains a stasis portion  $J_{t+1} = J_t$  and a growth portion such that  $\Delta J$  can be defined as

$$\Delta J = (a + J_t^2)e^{-KJt} \quad \text{eq. 2}$$

At small values of  $J_t$ , the  $J_t^2$  part dominates, and the curve approximates a parabola  $y = x^2$ . After this, the second term goes through an approximately linear region, then passes through a growth rate maximum. Ultimately there is an asymptotic approach to zero and since this approach can become infinitely small, it allows for continuous (infinite)



growth however, at some point growth will be too small to measure over the time period specified.

We input this function into the software TABLE CURVE (Jandel Corp., 1992) to fit the non-linear curve. TABLE CURVE uses the Levenburg-Marquardt procedure for finding the global minimum of the  $X^2$  squared sum of deviations. This procedure requires matrix inversions with each iteration, and to do this TABLE CURVE Curve uses the Gauss-Jordan method (Jandel Corp., 1992). Our function (eq. 1) is added as a "user defined function" in the form:

$$F1=X$$

$$Y=X+(X^2+\#A)*EXP(-\#B*X)$$

We generate predicted  $J_{t+1}$  values and plot them with the observed  $J_{t+1}$  values (jaw size after one year).

We compare our function with the Tanaka (1982) function which also has an asymptotic approach to zero, but requires an additional ill-defined parameter, and forces a symmetrical bell shaped curve about the growth maximum. This function has been used to model juvenile and adult red urchin growth (Ebert & Russell, 1993). The difference equation form of the Tanaka function is:

$$J_{t+1} = 1/\sqrt{f} \ln|2G+2 \sqrt{G^2+fa}| +d \quad \text{eq. 3}$$

Where  $G = E/4-fa/E+f$  and,  $E = \exp(\sqrt{f} (J_t-d))$ .

We input the Tanaka function (eq. 3) as a "user defined function" in the form:

$$F1=EXP(SQRT(\#A)*(X-\#B))$$

$$F2 + (F1/4) - (\#A * \#C / F1) + \#A$$

$$Y = (1/\text{SQRT}(\#A)) * \text{LN}(\text{ABS}(2 * F2 + 2 * (\text{SQRT}(F2^2 + \#A * \#C)))) + \#B$$

and generate predicted  $J_{t+1}$  values and plot them with the observed  $J_{t+1}$  values (jaw size after one year).

### Results

Urchins tagged at the shallow sites had higher recovery, 116 out of 301 tagged (38.5%) compared with 45 out of 300 (15%) at the deep site ( $X^2=31.310$ ,  $df=1.0$ ,  $P<0.001$ ). Similarly, juvenile urchins outplanted in shallow sites had high recovery, 25 out of 120 (20.8%) compared with 13 out of 120 (10.8%) at the deep site ( $X^2=3.789$ ,  $df=1.0$ ,  $P<0.1$ ). Size frequency distributions of urchins recovered from the shallow site were not significantly different than those recovered at the deep site (K-S mean diff=0.162,  $P=0.673$ ). Despite this, many urchins ( $N=20$ ) with jaw sizes greater than 22mm were recovered at the shallow site while none were found at the deep site.

Urchin density at the shallow site ( $4.2/m^2$ ) was greater than in the deep site ( $0.75/m^2$ ). In addition, drift algae abundance was greater in the shallow ( $2.66/m^2$ ) than the deep site ( $1.39/m^2$ ). However, this provided less algae per urchin in the shallow site compared with the deep ( $0.63g$  and  $1.85g/urchin$  respectively). Gut contents of urchins from the deep habitats had more optimal food (fleshy red and brown algae) than urchins in the high density shallow sites

( $t=2.79$ ,  $df=19$ ,  $P=0.012$ ). Gut fullness was generally uniform, approximately 50ml/urchin.

There is a strong relationship ( $r^2=0.989$ ,  $DF=382$ ) between test diameter (D) and jaw length (J) which can be described by (Fig. 1)

$$J = 0.3545 D^{0.868} \quad \text{eq. 4}$$

Growth rates, as measured by the change in jaw size ( $\Delta J$ ) were not significantly different for urchins in the shallow and the deep sites (ANCOVA  $F=0.246$ ,  $N=199$ ,  $P=0.62$ ) using initial jaw size ( $J_t$ ) as the covariate (independent variable) (Fig. 2). Since there were more large tagged urchins recovered at the shallow site this tended to decrease the mean growth ( $\Delta J$ ) for shallow urchins ( $X=1.155$ ,  $N=141$ ,  $SD=1.738$ ) compared with deep urchins ( $X=1.511$ ,  $N=58$ ,  $SD=1.716$ ). Growth rates ( $\Delta J$ ) were also similar for juveniles between shallow and deep sites (ANCOVA  $F=0.387$ ,  $N=38$ ,  $P=0.538$ ).

#### Growth Models

Shallow and deep data were pooled, because urchin growth was similar at each depth (Fig. 2). Next, we empirically derived the fitted parameters (using TABLE CURVE) for our function (eq 1.) obtaining  $a = 4.499$  ( $\pm SE=0.2068$ ), and  $K = 0.375$  ( $\pm SE=0.0028$ ). With these 2 parameter values we calculated predicted values of  $J_{t+1}$  from our  $J_t$  values using (eq. 1). A regression of predicted values from our model with measured values is highly

significant ( $r^2 = .994$ ,  $F = 31322$ ,  $P < 0.001$ ) (Fig. 3).

Equation 4 suggests urchins with jaw lengths of 17.45mm and larger are typical of legal size urchins  $\geq 89$  mm in northern California. By using our model (eq.1) we started with  $J(t) = 0$  so that at 1 year  $J(t+1) = 4.499$  and we determined the size for year 2 and so on. In this way we determined it would take 9 years for urchins to grow to a jaw size of 17.45mm with a test size of 89.04 mm (Table 1). If we add a 2 month lag in the onset of growth which has been observed in the laboratory (Rogers-Bennett et al. manuscript) we estimate it can take 9.166 years until red urchins grow to harvestable size.

In addition, we empirically derived values for the three fitted parameters in the Tanaka function (eq. 3). Using TABLE CURVE we obtained  $A=0.050$  ( $\pm SE=0.003$ ),  $B=15.567$  ( $\pm SE=0.409$ ), and  $C=0.039$  ( $\pm SE=0.002$ ). A regression of the predicted values with the measured values (Fig. 4) is also highly significant ( $r^2 = .993$ ,  $F = 13,185$ ,  $P < 0.001$ ) but, TABLE CURVE ranks the Tanaka function below our model based on the  $r^2$  value.

### Discussion

While many models appear to adequately explain growth for adult sea urchins they fail to describe growth during the juvenile stage. Ebert and Russell (1993) use the Tanaka function to describe accelerating growth for small urchins,

maximum growth and then a long period of decelerated growth. Our new model maintains some of the attractive features of the Tanaka function such as an asymptotic approach to zero (infinite growth) but has several improvements. Our model has one less parameter and our two parameters  $a$  (size at one year) and  $K$  (growth rate constant) are biologically well defined. In addition, our model allows for asymmetry about the maximum growth rate while the Tanaka function forces a symmetrical curve. This feature results in a premature peaking of the Tanaka growth curve for this data (Fig. 4), slightly overestimating growth for small urchins shortening the estimated time when urchins reach harvestable size.

Growth models have implications for fishery management and managers require models such as these which accurately predict growth in small urchins. Our results concur with others (Rowley 1990) that growth estimates using large juveniles (10 mm) and adults (Ebert 1968, Tegner & Dayton 1981, Ebert 1983, Himmelman et al. 1983, Ebert & Russell 1992) overemphasize early growth and underestimate urchin age at the time of first harvest (90mm). Bias shortening time to harvestable size could have negative impacts on the fishery leading to overharvesting while bias in the opposite direction would lead managers to more conservative fishing policies. Time to harvest estimates made for red sea urchins in southern California range from 3 - 12 years (Tegner 1989, Ebert & Russell, 1993, Ebert et al. 1994). Estimates from

our model are the long end of this continuum despite the fact that juveniles are growing very fast (Table 1). In fact there is good data to suggest that juveniles grow twice as fast in northern California than in southern California (Ebert et al. 1993, Rogers-Bennett et al. manuscript) however age at 100 mm in the north appears to be 14+ years, while estimates made in southern California put age at 100mm at 12 years (Ebert & Russell, 1993). Since growth appears to be spatially variable over large scales (northern to southern California) we caution that growth parameters must be calculated independently in each region.

Our model incorporates an early exponential phase representing growth in the first year. While growth data for newly settled urchins (0.4-20mm) were obtained in the laboratory, a similar pattern in early growth has been observed in closely related species S. purpuratus and S. droebachiensis (Rowley 1990, Raymond & Schiebling, 1987). Growth of juveniles in the field can have a tremendous impact on their survival since many studies indicate mortality can be size specific (Highsmith 1982, Sebens 1983, Houde 1987). Early exponential growth is consistent with this notion that rapid early growth is important for survival. Not surprisingly, growth appears to be related to macroalgae availability such that juveniles with access to kelp exhibit exponential growth whereas juveniles deprived of kelp exhibit linear slower growth (Raymond & Scheibling,

1987).

Newly settled urchins appear to have a lag in the onset of growth (Rowley 1990; Rogers-Bennett et al. manuscript) prior to the exponential phase. While we do not formally incorporate this lag period into the model we can add 2 months (0.166 mos.) to our estimate of time to harvest. The mechanism responsible for this observed lag is unknown. This lag may be due to a switch in diet from diatom films to algae (Rowley, 1990), a developmental delay in the emergence of jaws prior to exogenous feeding, or nutritional condition of the larvae prior to settlement (Rogers-Bennett et al., manuscript). More studies of newly settled urchins are needed to evaluate lags and early growth of juveniles both in the laboratory and in the field since juvenile growth at this stage influences predictions from growth models.

Our results indicate that despite differences in food availability, urchin density, and gut contents, growth rates were similar between depths. This result may have been produced by highly variable growth among individuals that could mask local depth-related effects on growth. Additionally, the time of growth differed slightly for adults and outplanted juveniles (12 days) and for the newly settled juveniles in the laboratory (3 weeks) potentially generating unknown error. In addition, movement was greater in the deep site than in the shallow site which is a pattern consistent with other studies examining depth related

movement in red urchins (Carney 1991, Rogers-Bennett et al. in press) but which may have also confounded depth-related patterns in growth.

There is tremendous individual variation in growth rates of newly settled sea urchins reared under identical, food, temperature, and light regimes reared in the laboratory. Size of full siblings at one year can vary from 10 to 30 mm in purple urchins (Pearse and Cameron unpubl. data) and 4 to 44 mm in red urchins (Rogers-Bennett et al. manuscript). Similarly, fish (Allendorf et al. 1987) and other commercially cultured marine invertebrates exhibit similar phenotypic variation in growth (Beaumont 1994). This problem along with problems associated with linking the tag-recapture data to a time axis can bias growth parameters estimates (Sainsbury 1980). In combination these two problems can bias time to enter fishery estimates generated from model parameters and could be another explanation for the the range in estimates found in the literature.

Individual variability in growth has been incorporated into individual based models which suggest that only the fastest growing (as opposed to the average growers) individuals survive to become adults (Cowen et al. 1993). If this is true, then average and slow growers observed in the laboratory and aquaculture facilities will be rare or absent in the field. Since our parameters are generated from tag-recapture data it may be that only the fastest growers



survived to be recaptured and are therefore the only ones represented in our model. We caution against using laboratory data exclusively to generate model parameters because of the bias this data may introduce.

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### Literature Cited

- Allendorf, F.W., Ryman, N., and F.M. Utter 1987. Genetics and Fishery Management: past, present and future. In Population Genetics and Fishery Management. Washington Sea Grant. Seattle, Washington. pp 1-19.
- Atkins, P.W. 1994. Physical Chemistry. Ed. Freeman, W.H. N.Y. N.Y.
- Beaumont, A.R. 1994. Genetics and aquaculture. In Genetics and Evolution of Marine Organisms. Chapman & Hall, Cambridge University Press, Cambridge, England. pp 467-486
- Bertalanffy, L., von 1938. A quantitative theory of organic growth. Hum. Biol. 10: 181-213
- Brody, S. 1945. Bioenergetics and Growth. Reinhold Publishing Corporation, New York, NY.
- Carney, D. 1991. A comparison of densities, size distribution, gonad and total-gut indices, and the relative movements of red sea urchins Strongylocentrotus franciscanus, in two depth regimes. M.S. Thesis University of California, Santa Cruz, Santa Cruz, California, USA.
- Cowen, J.H., Alpine, A., Cole, B., Wong R., Arthur, J., M. Ball 1993. Individual-based model of young-of-the-year striped bass population dynamics. II. Factors affecting recruitment in the Potomac river, Maryland. Trans. Amer. Fish. Soc. 122: 439-458

- Duetler, F. 1926. Uber das Wachstum des Seeigelskeletts. Zool. Jb. (Abt. Anat. Ontag. Tiere) 48: 119-200
- Ebert, T.A. 1988. Calibration of natural growth lines in ossicles of two sea urchins Strongylocentrotus purpurtaus and Echinometra mathaei, using tetracycline. In Burke, R.D. Mladenov, P.V. Lambert, P., Parsley, R.L. (eds.) Echinoderm Biology. Proceedings of the Sixth International Echinoderm Conference. A.A. Balkema, Rotterdam, p.435-443
- Ebert, T.A. 1982. Longevity, life history, and relative body wall size in sea urchins. Ecol. Monogr. 52: 353-394
- Ebert, T.A. 1980. Estimating parameters in a flexible growth equation, the Richards function. Can. J. Fish. Aquat. Sciences. 37: 687-692
- Ebert, T.A. 1977. An experimental analysis of sea urchin dynamics and community interactions on a rock jetty. J. exp. mar. Biol. Ecol. 27: 1-22
- Ebert, T.A. 1975. Growth and mortality of post-larval echinoids. Am. Zool. 15: 755-775
- Ebert, T.A. and M.P. Russell 1993. Growth and mortality of subtidal red sea urchins Strongylocentrotus franciscanus at San Nicolas Island, California, USA: problems with models. Mar. Biol. 117: 79-89
- Ebert, T.A. and M.P. Russell 1992. Growth and mortality estimates for red sea urchins Strongylocentrotus franciscanus from San Nicolas Island, California. Mar.

- Ecol. Prog. Ser. 81: 31-41
- Fabens, A.J. 1965. Properties and fitting the von Bertalanffy growth curve. Growth 29: 265-289
- Gage, J.D. 1991. Skeletal growth zones as age-markers in the sea urchin Psammechinus miliaris. Mar. Biol. 110: 217-228
- Harrold, C., and D.C. Reed 1985. Food availability, sea urchin grazing, and kelp forest community structure. Ecology 66: 1160-1169
- Highsmith, R.C. 1982. Induced settlement and metamorphosis of sand dollar (Dendraster excentricus) larvae in predator-free sites: adult sand dollar beds. Ecology 63: 329-337
- Houde, E.D. 1987. Fish early life dynamics and recruitment variability. Amer. Fish. Soc. Symp. 2: 17-29
- Pearse, J.S. and R.A. Cameron 1991. Echinodermata: Echinoidea. In Giese, A.C., Pearse, J.S. and Pearse, V.E. (eds.) Reproduction of marine invertebrates. Vol. VI. Echinoderms and Lophophorates. Boxwood Press, Pacific Grove, Ca. pp 513-662
- Pearse, J.S., and V.B. Pearse 1975. Growth zones in the echinoid skeleton. Amer. Zool. 15: 731-753
- Raymond, B.G., and R.E. Scheibling 1987. Recruitment and growth of the sea urchin Strongylocentrotus droebachiensis (Muller) following mass mortalities off Nova Scotia, Canada. J. Exp. Mar. Biol. Ecol. 108: 31-

- Richard, F.J. 1959. A flexible growth curve for empirical use. *J. exp. Bot.* 10: 290-300
- Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. *Bull. Fish. Res. Bd. Can.* 191: 1-382
- Rogers-Bennett, L., Bennett, W.A. Fastenau, H.C. and C.M. Dewees. Spatial variation in red sea urchin reproduction and morphology: implications for harvest refugia. In press *Ecological Applications*.
- Rogers-Bennett, L., Hibbard-Robbins, T. and C.M. Dewees. Delayed jaw emergence and growth in cultured red sea urchins: recruitment implications. Manuscript.
- Rowley, R.J. 1990. Newly settled sea urchins in a kelp bed and urchin barren ground: a comparison of growth and mortality. *Mar. Ecol. Prog. Ser.* 62: 229-240
- Sainsbury, K.J. 1980. Effect of individual variability on the von Bertalanffy growth equation. *Can. J. Fish. Aquat. Sci.* 37: 241-247
- Sebens, K.P. 1983. The larval and juvenile ecology of the temperate octocoral Alcyonium siderium Verrill. II. Fecundity, survival, and juvenile growth. *J. exp. mar. Biol. Ecol.* 72: 263-285
- Table Curve Jandel Corp. 1992
- Tanaka, M. 1982. A new growth curve which expresses infinite increase. *Publ. Amakusa Mar. Biol. Lab.* 6: 167-177

Tegner, M.J. 1989. The feasibility of enhancing red sea urchin, Strongylocentrotus franciscanus, stocks in California: an analysis of the options. Fish. Bull. U.S. 51: 1-22

Walford, L.A. 1946. A new graphic method of describing the growth of animals. Biol. Bull. 90: 141-147

Wilson, C.W., Beckman, D.W., Dean, J.D., J. Mark 1987. Calcein as a florescent marker of otoliths of larval and juvenile fish. Trans. Amer. Fish. Soc. 116: 668-670

Table 1. Predicted sizes at ages 0-15 years using our model (eq. 1) and parameters  $a=4.499$ , and  $K=0.357$  fitted with growth data from Salt Point, northern California.

Years	Jaw Length	Test Diameter
0	0	0
1	4.50	18.67
2	9.08	41.93
3	11.97	57.64
4	13.63	66.96
5	14.78	73.50
6	15.65	78.53
7	16.35	82.62
8	16.94	86.06
9	17.45	89.04
10	17.90	91.65
11	18.29	93.99
12	18.65	96.10
13	18.97	98.02
14	19.27	99.79
15	19.54	101.42



### Figure Legends

Figure 1. Relationship between test diameter and jaw length for red urchins in northern California. Open circles represent wild red urchins (N=200) and X's are cultured juvenile urchins grown in the laboratory (N=182).

Figure 2. Growth as measured by change in jaw length of wild red sea urchins (N=199) after 13 months in the Salt Point Urchin Closure, northern California and of juveniles (N=38) cultured in the laboratory and then outplanted in the field for 12.5 months. Open circles are urchins (N=141) from the shallow site (5 m), crosses are urchins (N=58) from the deep (15 m) site, X's represent urchin size (N=3) 1 year post-settlement reared in the laboratory. Diagonal ( $45^\circ$ ) represents no growth (slope =1.0) during the year.

Figure 3. Predicted values of  $J_{t+1}$  from our alternative growth model (eq. 1)

$$J_{t+1} = J_t + (a + J_t^2)e^{-KJ_t}$$

shown with measured values of  $J_{t+1}$  for red urchins in the field at Salt Point and juveniles cultured in the laboratory. This model generates two fitted parameters the growth rate  $K = 0.375$  (SE  $\pm 0.003$ ) and the Y intercept  $a = 4.499$  ( $\pm$ SE=.335) shown with significant regression results ( $r^2 = 0.994$ ;  $F = 31,322$ ;  $P < 0.001$ ).

Figure 4. Predicted values of  $J_{t+1}$  from the Tanaka growth model (eq. 3) shown with measured values of  $J_{t+1}$  for red urchins in the field at Salt Point and juveniles cultured in the laboratory. This model generates three fitted parameters  $A=0.05$  ( $\pm SE=0.003$ ),  $B=15.567$  ( $\pm SE=0.409$ ), and  $C=0.039$  ( $\pm SE=0.002$ ) and are shown with significant regression results ( $r^2 = 0.993$ ;  $F = 13,185$ ;  $P < 0.001$ ).

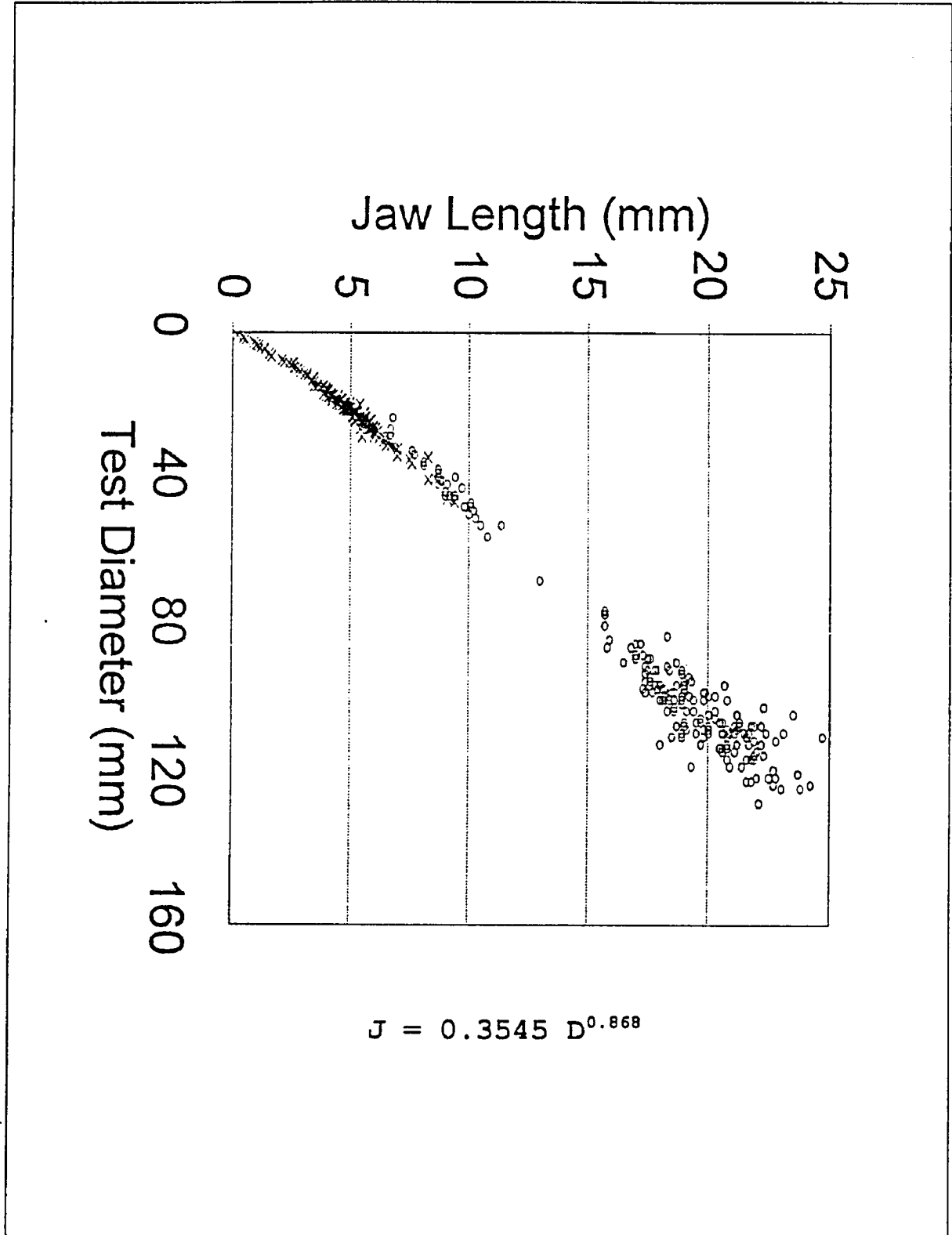


Figure 1.

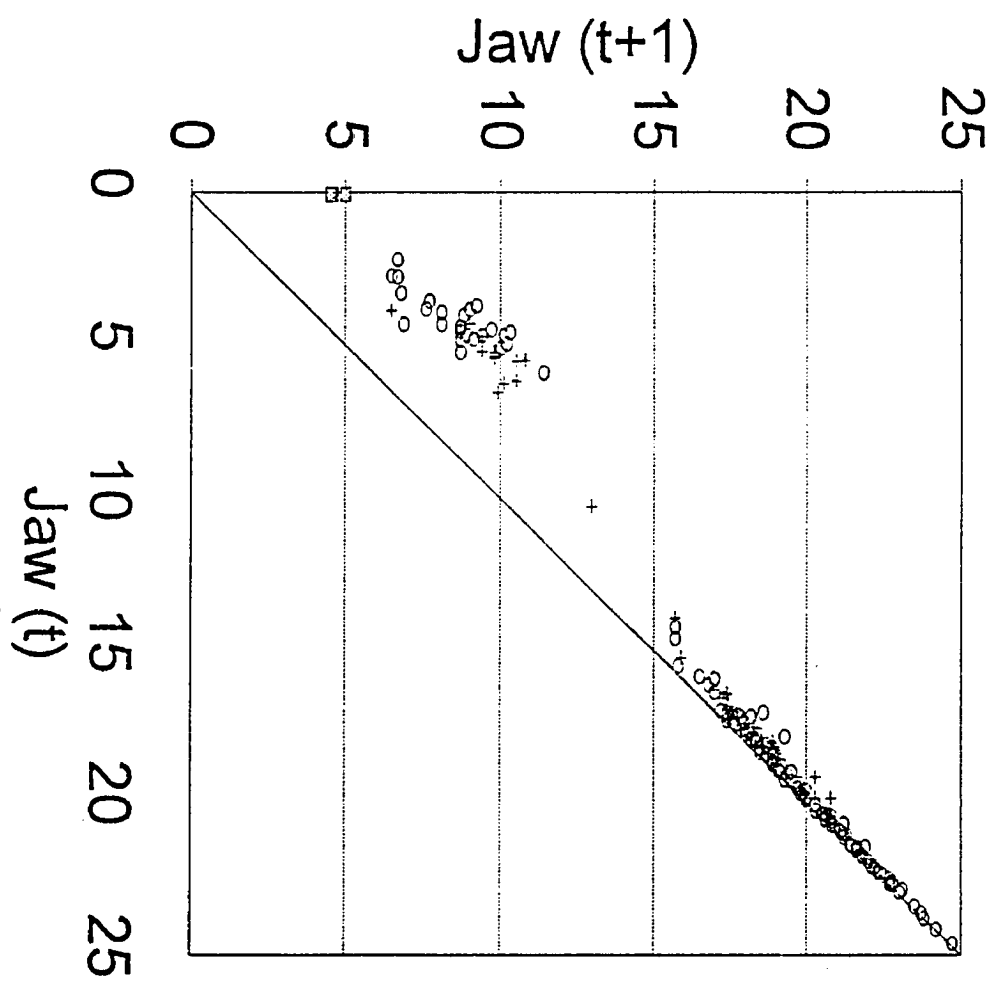


Figure 2.

Salt Point

Rank 1 Eqn 8001  $y = \text{nov14a.udf}()$

$r^2 = 0.993655226$  DF Adj  $r^2 = 0.993591459$  FitStdErr = 0.387352376 Fstat = 31322.0029

$a = 0.37535382$

$b = 4.4999518$

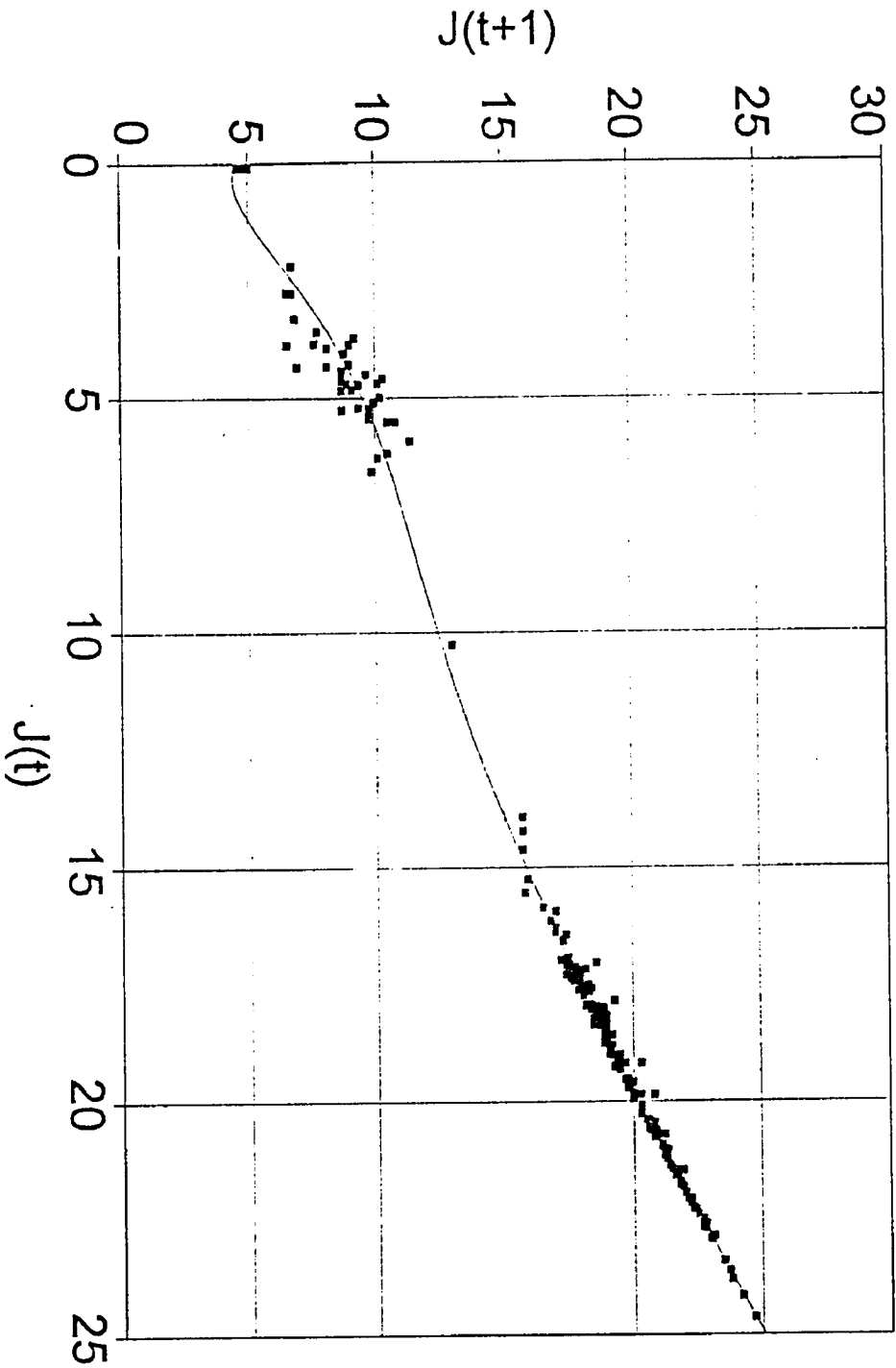


Figure 3.

Salt Point

Rank 2 Eqn 8009 y=nov22.udf()

$r^2=0.992510208$  DF Adj  $r^2=0.992396726$  FitStdErr=0.421911609 Fstat=13185.2476

a=0.05018306 b=15.567538

c=0.038659324

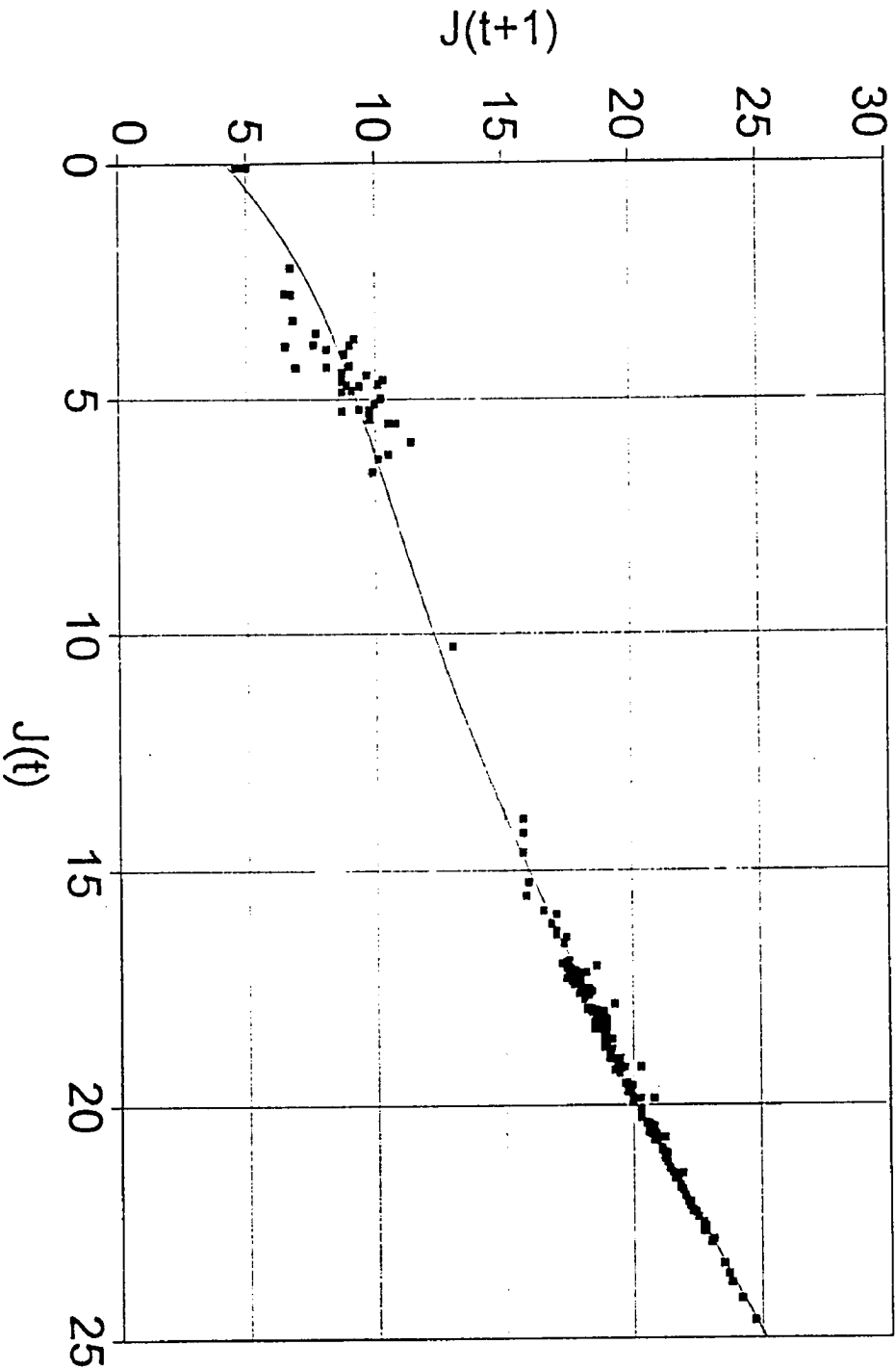


Figure 4.