Edible Sea Urchins: Biology and Ecology
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Chapter 19

The Ecology of *Strongylocentrotus franciscanus* and *Strongylocentrotus purpuratus*

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1. INTRODUCTION

Red sea urchins, *Strongylocentrotus franciscanus* (Plate 3C), and purple sea urchins, S. *purpuratus,* are arguably the most-studied and well-known echinoid species in the world. Red and purple sea urchins are dominant members of nearshore rocky reef communities along the North American west coast and are capable of structuring subtidal algal communities and influencing community diversity. While we have long appreciated the role sea urchin herbivory exerts on the surrounding algal community and the creation of sea urchin "barrens," we are only starting to appreciate the positive species associations between sea urchins and the invertebrates and fishes that reside in and around their spine canopy. Red and purple sea urchins are also the basis for important fisheries, with purple sea urchins making up a minor component of the fishery. Purple sea urchins are collected extensively for scientific research, including fertilization biology, embryology, genome analysis and fertilization bioassays that are used to assess the toxicity of marine pollutants, silt, pulp-mill effluent and ultraviolet radiation. More work is needed in assessing how removals from large-scale fishery and scientific collecting affect the role sea urchins play in marine ecosystems. As we understand more we will be able to incorporate this knowledge into wise management practices designed to both provide sustainable fisheries and maintain healthy marine ecosystems.

Increased demand for red sea urchins has led to an expansion of the fisheries from their initial exploitation (Sloan 1985) to fully and overexploited fisheries (Keesing and Hall 1998; Andrew et al. 2002; Botsford et al. 2004). Using traditional measures of overfishing, such as spawning stock biomass below 20% of virgin biomass, overfishing has occurred in parts of the West Coast. West Coast fisheries for red sea urchins have been affected not only by decreases in stocks but also by management policies, El Niño events, shifts in effort, a weakening of the Japanese export market and major competition from fisheries in Canada, Russia, South Korea, and Chile (Andrew et al. 2002). In 2004, the United States sold sea urchin as fresh roe and live fresh product internationally valued at $44.7

and $6.9 million, respectively. The top three importers of fresh roe product from the United States were Japan, Hong Kong, and Taiwan with Japan importing just under 2 million or 80% of the market.

Red sea urchins are important for fisheries in part due to their large body size. Large red sea urchins measure 198 mm in test diameter from British Columbia (Bureau 1996). They are larger than the purple sea urchin, which reaches 100 mm (Morris et al. 1980), but smaller than the giant heart sea urchin *Spherosoma giganteum* from the deep sea measuring 380 mm. The spines of the species differ in length, reaching 50–55 mm in the red sea urchin and less than 20 mm in the purple sea urchin (Tegner and Levin 1983). Spine length, like many other morphological features, is plastic and sea urchins in areas of high-wave action have shorter spines (Rogers-Bennett et al. 1995). The relative size of Aristotle's lantern is larger for sea urchins residing in food-poor habitats (Ebert 1980). Podial coverage however, appears to be conserved and is nearly proportional to test area in 21 species of echinoids (Strathmann and von Dassow 2001) and does not differ for red sea urchins in wave-exposed sites (Rogers-Bennett, unpubl. data). Purple sea urchins are able to withstand greater wave action than red sea urchins and are found in more exposed intertidal habitats.

Red and purple sea urchins reside on rocky substrates with a broad geographic and depth distribution. Red sea urchins range from the tip of Baja California, Mexico north to Kodiak, Alaska (Ebert et al. 1999). Purple sea urchins have a more reduced range from Isla Cedros in Baja California, Mexico north to Cook Inlet, Alaska (Tegner 2001) but span a greater distribution of depths. Red sea urchins are distributed in subtidal habitats to a depth of 90 m while purple sea urchins are common in intertidal and subtidal habitats to 160 m (Morris et al. 1980).

Red sea urchins (Plate 3C) range in color from a light pink to a dark brick red or black, while purple sea urchins are purple in color. Juveniles may be difficult to distinguish by color as they can both be light purple or even white to greenish. The developing echinoplutei of both species are planktotrophic requiring nutritional input (other than the yolk) for metamorphosis. Larval red sea urchins can be distinguished from purple sea urchins because they have a single dorsal pedicellarium which is absent in larval purple sea urchins, as well as other unique skeletal traits (Strathmann 1979).

Recent advances in the study of red and purple sea urchins have increased our awareness of the multifaceted role they play in nearshore subtidal communities as ecosystem engineers. As we learn more about the spatial distribution of sea urchin stocks we see that their populations are divided into metapopulations or microstocks. This spatial structure has important ramifications for population dynamics and exploitation. One surprising recent discovery is that larval purple sea urchins can clone themselves (Eaves and Palmer 2003). This requires that we re-examine estimates of larval-dispersal distances for this species and possibly others. There is a growing awareness of the role oceanographic processes play in the productivity of sea urchin populations. Ocean conditions affect not only the availability of drift-algal food resources required for gonad development (essential for both sea urchin reproduction and the fishery) but also transport processes influencing larval settlement and successful recruitment. Settlement patterns of sea urchins have been studied in California for more than a decade and these patterns are now being linked to what we know about interannual variation in oceanography. Our goal will be to use what we learn about spatial patterns in sea urchin productivity to help us better manage sea urchin fisheries.

2. SEA URCHIN GRAZING AND KELP FOREST ECOSYSTEMS

Sea urchins have long been acknowledged as major structuring forces within subtidal kelp forest communities (Paine and Vadas 1969; Lawrence 1975; Harrold and Pearse 1987; Tegner and Dayton 2000). In some regions, there appear to be two dominate alternate community states (Simenstad et al. 1978): kelp beds with high species diversity and echinoid dominated rocky grounds with low species diversity. Grazing by sea urchins is infamous for altering algal communities from lush, specious kelp forests to "barrens" characterized by crustose coralline algae and the absence of upright fleshy algae (Leighton et al. 1966). When sea urchins overgraze, their foraging behavior changes; they leave cryptic habitats to form dense feeding aggregations or "fronts" which can in turn denude fleshy kelps by eating through the stipes (Dean et al. 1984). In southern California, while there is a range of community types, kelp forests have higher species diversity than sea urchin barrens with more than 90% of the 275 common species more abundant in kelp communities of which 25% are kelp forest obligates (Graham 2004). In some regions overgrazing appears to be related to sea urchin density (Lawrence 1975), with a distinct threshold of sea urchin density ($2\,\mathrm{kg\ m^{-2}}$) above which sea urchins overgraze kelp beds (Breen and Mann 1976). Major recruitment events may increase sea urchin densities to levels where they overgraze kelps, such as the recruitment of 1984 in a central California kelp forest which led to deforestation by sea urchins 2 years later (Watanabe and Harrold 1991). Yet there are also places and times when sea urchins and kelps coexist for decades, as in northern California. Sea urchin overgrazing appears to be less common in South American kelp communities (Dayton 1985).

These two states – kelp beds and sea urchin barrens have led to a popular paradigm of a trophic cascade (*sensu* Carpenter and Kitchell 1988) in which the removal of sea urchin predators leads to sea urchin population explosions and kelp deforestation. This paradigm however, has not been well tested (Sala et al. 1998). There is no debating that human fishing has removed many sea urchin predators (Dayton et al 1998), such as, sea otters (Estes et al. 1998), spiny lobsters (Lafferty 2004) and sea urchin competitors such as southern California's abalone (Dayton et al. 1998; Rogers-Bennett et al. 2002). Deforestation by sea urchins, however, may not be as straight forward as the paradigm suggests. Other processes, such as abiotic factors, are important in dynamics of sea urchin deforestation. For example, shortages of drift algae appears to be an important factor in triggering sea urchins to switch feeding modes from primarily sedentary drift feeders residing in sheltered habitats to active foragers that denude standing algae in southern California kelp forests (Harrold and Reed 1985; Ebling et al. 1985). There may also be negative feedback loops such that, as drift becomes less abundant, sea urchins cause more damage to kelp by grazing pits in the holdfast, a condition termed cavitation (Leighton 1971). This causes structural failure when stressed by waves and leads to further kelp loss (Tegner et al. 1995).

While the mechanisms involved in kelp overgrazing by sea urchins remain an important focus of research and discussion, human activity has profoundly affected this dynamic. Human influences span the gamut from fishing sea urchin predators (Dayton et al. 1998; Jackson et al. 2001), species eradications (Estes et al. 1989; Jackson et al. 2001), climate change coupled with fishing (Harley and Rogers-Bennett 2004), disease intensification (Scheibling et al. 1999; Behrens and Lafferty 2004), species introductions (Levin et al. 2002) and pollution (Pearse et al. 1970). At the same time, it is difficult to distinguish anthropogenic changes from environmental changes. For example, many species removals and declines in marine systems have gone unnoticed as they may be economically unimportant or loosely integrated components of the ecosystem (Dayton et al. 1998). The kelp forests of today are clearly different places than they were 200, 100, or even 50 years ago and the dynamics are probably greatly altered (Dayton et al. 1998). Marine protected areas may be useful places for examining the effects of human fishing on trophic interactions and the dynamics of sea urchins and kelp forests (Rogers-Bennett and Pearse 2001; Behrens and Lafferty 2004).

In the last two decades, kelp deforestation by sea urchins appears to be increasing worldwide (Steneck et al. 2002). Increases in fishing pressures on herbivore predators as well as increases in ocean warming both negatively affect kelp abundances and may act synergistically to increase kelp deforestation events, while, at the same time slowing kelp regeneration. Unfortunately, in regions where kelps are sparse, sea urchin fishing may not be useful in reversing deforestation since sea urchin gonads are of poor quality from barrens and the sea urchins are not fished (K Barsky, pers. comm.). Deforestation appears to strongly affect species diversity (Steneck et al. 2002; Graham 2004). This in turn could impair an ecosystem's ability to rebound from perturbations (Kiessling 2005). We will need a better understanding of the processes involved in deforestation by sea urchins if we are to maintain productive and diverse kelp ecosystems.

3. GROWTH AND SURVIVAL

3.1. Growth

More is known about age and growth in strongylocentrotid sea urchins than perhaps any other genus (Ebert and Russell 1993; Smith et al. 1998; Ebert et al. 1999; Morgan et al. 2000a; Rogers-Bennett et al. 2003). Ebert et al (1999) examined red sea urchin growth in a large-scale tag- recapture program that resulted in 1582 recoveries from Alaska to southern California and found that growth rates were slow. Growth did not peak in red sea urchins until they reached 30–40 mm in test diameter. Growth then tapered off dramatically as the sea urchins became larger. These tagging data demonstrate that growth, though very small, continues even in the very largest animals and suggest that red sea urchins may be a very long lived species.

Researchers have also modeled red and purple sea urchin growth. Growth data for sea urchins often lack information from juveniles since they can be rare and difficult to recapture once tagged. This lack of information from growing juveniles may bias growth-rate estimates in undesirable ways, shortening the estimate of the time it takes for sea urchins to enter the fishery (Yamaguchi 1975; Rogers-Bennett et al. 2003). Since growth continues even as sea urchins grow very large (potentially old), growth models have been used that allow for infinite increase, such as the Tanaka model (Tanaka 1982). Growth model estimates range from 6 to 10 years as the time to reach legal size (89 mm) in the California fishery (Ebert and Russell 1993; Ebert et al. 1999; Morgan et al. 2000a; Rogers-Bennett et al. 2003).

Growth is highly variable between individuals. Full sibling purple sea urchins grown in the laboratory under identical conditions for 1 year ranged in size from 10 to 30 mm (Pearse and Cameron 1991) while red sea urchins ranged in size from 4 to 44 mm (Rogers-Bennett, unpubl. data). Variation in growth of purple sea urchins was also examined at three sites along the geographical extent of their distribution on the west coast of North America. Growth was found to be highly variable with more differences within a site than between sites (Russell 1987). This dramatic individual variation in growth can have important implications for modeling since many models are designed to depict the growth of a single animal rather than the mean of many animals (Sainsbury 1980). Use of these models can result in overestimates of the mean size of a cohort (Sainsbury 1980).

Spatial and temporal variation in growth is also significant for red sea urchins. Examining growth increment data from tagged red sea urchins in combination with growth estimates from size–frequency distributions at two reserve sites suggests growth may vary spatially. Growth model estimates were lower for red sea urchins in the Bodega State Marine Reserve compared to the Caspar Sea Urchin Fishing Closure near Fort Bragg, California which has abundant algal resources (Morgan et al. 2000a). Newly settled sea urchins grew faster in kelp beds than sea urchins barrens (Rowley 1990). Identifying spatial patterns in growth is challenging since patterns can be obscured by large differences in individual growth.

3.2. Survival

Survival estimates for sea urchins have been made using a decaying exponential function with the number of individuals (N_t) of a certain age or cohort as the dependent variable and N_0 as the initial number of individuals

$$N_t = N_0 \mathrm{e}^{-Zx}$$

This function has one parameter Z the mortality coefficient and x is time (say in years). In this function, the annual survival rate is e^{-Z} and annual mortality rate is $1 - \mathrm{e}^{-Z}$ (Ebert 2001). In this simple model, the probability of survival does not change with age. The mortality coefficient, Z can be estimated using a combination of size–frequency data and parameters from a growth function (Ebert 1999). Other studies have also used this method to estimate red sea urchin survival (Ebert 1987; Ebert and Russell 1993; Smith et al. 1998; Ebert et al. 1999).

Survival estimates for red sea urchins, are very high, ranging from $Z\,\mathrm{yr}^{-1}$ of 0.82–0.98 for sites from northern California to Alaska and from 0.67 to 0.91 for southern California sites (Ebert et al. 1999). Likewise, estimates of purple sea urchin survival are also very high ranging from 0.85 to 0.90 for northern sites and from 0.72 to 0.89 for southern sites

(Russell 1987). Both red and purple sea urchins are estimated to have higher survival rates in northern sites compared with southern California. For purple sea urchins the suggestion has been made that the lower survival rates in southern California may be due to higher predation rates and/or higher stress levels associated with warm sea water temperatures (Russell 1987). One caveat for these survival estimates is that assumptions of seasonally stable and stationary size distributions are violated. Irregular recruitment dynamics can change mean size from year to year. Examining the effects of changes in the mean size between one high and one low recruitment year for purple sea urchins did little to change the resulting survivorship curve, which suggests that these results are robust to violations of the assumption (Ebert et al. 1999). The overall conclusion from these data is that sea urchins are very long lived.

3.3. Aging

Growth and survival modeling results lead to a startling conclusion – that 150 mm red sea urchins are 100–200 years old (Ebert et al. 1999). This surprising result of very long life has been validated using an alternative aging method: C^{14} radiocarbon dating. Radiocarbon C^{14} emitted during atmospheric nuclear testing provides a time stamp in the calcium carbonate of animals alive during the 1950s. Ebert and Southon (2003) found that growth estimates from the Tanaka growth curve were validated by quantifying the levels of the C^{14} radiocarbon and calibrating these to the known nuclear testing dates. Their work suggests that the largest red sea urchins found in British Columbia 198 mm in test diameter (Bureau 1996) were more than 200 years old. These estimates far exceed longevity estimates for other sea urchin species (Ebert and Southon 2003). Current work on longevity in red sea urchins suggests that telomerase activity may continue even in the tissues of very large, old individuals (A Bodnar, pers. comm.). These findings, taken together with continuous but slow growth and continuous reproduction in the largest, oldest animals, lead researchers to question the onset of senescence in red sea urchins.

4. REPRODUCTION

Reproduction in red and purple sea urchins follows annual cycles (Giese et al. 1958; Gonor 1973). Food needs to be present for the gonads to develop while most of the year primary oocytes and spermatocytes accumulate, aided by the nutritive phagocytes (see Chapter 2). Prior to spawning, the nutritive phagocytes become reduced as the gametes in both sexes develop and mature. Photoperiod appears to play a large role in the regulation of gametogenesis in purple urchins as well as other species of sea urchins (Pearse et al. 1986). Gametogenesis is triggered when photoperiod is less than 12 h (Pearse et al. 1986). Sea urchins artificially maintained 6 months offset from the natural phase, spawned 6 months behind the natural populations. Furthermore, animals maintained in continuous darkness have reduced gonad growth with enhanced somatic growth (J Pearse, pers. comm.). Reproduction appears to continue throughout the life of red and purple sea urchins. There is no evidence for a decrease in reproductive output or reproductive senescence with increasing age or size as found in other phyla (Rogers-Bennett et al. 2004). In fact, large females produce exponentially more eggs than midsize females (Tegner 1989).

Reproduction in sea urchins in many regions varies spatially primarily in response to food abundance. In northern California, red sea urchins in shallow habitats (5 m) with abundant drift-algae resources have significantly larger gonads (mean = 64 g) more than 4 times greater than red sea urchins at intermediate (mean = 14 g) and deep water habitats (mean = 13 g) (Rogers-Bennett et al. 1995). Gonad index values are positively correlated with drift-algae abundance in the shallow habitats but not in the deep where drift is scarce (Rogers-Bennett et al. 1995). Drift-algae abundance is greatest in the shallow habitats throughout the year and most abundant in the fall (Rogers-Bennett et al. 1995). Red sea urchins in southeast Alaska also have larger gonads in shallow habitats where drift is abundant (Carney 1991). In the inland waters of San Juan Island, Washington, where extreme tidal flows regularly deliver abundant drift-algae resources to deep habitats, red sea urchin gonad indexes are comparable in shallow and deep habitats (K. Britton-Simmons, pers. comm.).

5. FERTILIZATION

Red and purple sea urchins have separate sexes and release eggs and sperm into the water column where fertilization takes place. Sperm are activated once they are released and encounter sea water with a short time (10 min) to swim and fertilize an egg before their mitochondria are exhausted (Christen et al. 1986). The acrosomal protein bindin attaches sperm to eggs during fertilization. This requires males and females to spawn somewhat synchronously and to have high enough concentrations of gametes at a range close enough to achieve physical contact and fertilization success. In these sea urchins, spawning by males precedes females (Levitan 2002) and the presence of sperm stimulates females to spawn. Two natural spawning events observed in populations of red and purple sea urchins in British Columbia, Canada, occurred during heavy phytoplankton blooms (Levitan 2002). During these spawning events the sea urchins did not aggregate. Thirty to 44% of the individuals in the area spawned, and during spawning a higher percent of males (88%) spawned than females.

Variations in adult population densities change patterns in gamete release which influence sperm availability as well as sperm competition. In populations where the density of sea urchins is high, sperm are more likely to compete for eggs, whereas eggs may have plenty of sperm. In populations where sea urchin density is low, eggs may be faced with sperm limitation. Reduction of population densities by fishing could have a dramatic effect on fertilization success, perhaps resulting in Allee effects where fertilization decreases precipitously rather than as a smooth linear decline with decreasing density (Allee 1931).

As sea urchin density increases, fertilization success is enhanced, peaking at 1–3 males per square meter (Levitan 2004). Purple sea urchins reside in more densely packed populations than red sea urchins. This results in a greater reproductive success in purple sea urchins (94%) than red sea urchins (64%) at the densities examined (Levitan 2002). At extremely high male densities, fertilization success is again decreased due to polyspermy which can result in abnormal or arrested development (Ernst 1997). Paternity analyses indicate that 98% of the larvae produced in field-spawning experiments with high male densities were sired by more than one male (Levitan 2004).

Red and purple sea urchins differ in egg size, with purple sea urchins having smaller eggs. This makes the eggs more difficult to target for sperm, requiring an order of magnitude more sperm for fertilization, that may even necessitate higher densities of males near females (Levitan et al. 1992). They also differ with respect to their susceptibility to interspecific fertilization and the production of hybrids. Purple sea urchins are less likely to hybridize than red sea urchins. Larval hybrids of both species have higher mortality than nonhybrids. Hybrid crosses with red sea urchin sperm and green sea urchin, *S. droebachiensis* eggs have survived for 3 years; however hybrid crosses with sperm from purple sea urchins, *S. purpuratus,* did not survive past the larval stage (Levitan 2002).

In a model used to examine the dynamics of fertilization success at low stock levels, simulations show differences in recruitment declines based on the spatial distribution of adults and sperm dispersal distributions (Lundquist and Botsford 2004). With random adult distributions and various sperm distributions curves, the simulation model yielded gradually declining sperm distributions as opposed to precipitous declines associated with a set threshold as would occur with an Allee effect. The decline in successful reproduction (zygote production) was more pronounced in high-flow conditions irrespective of adult density. While the shape of the sperm-dispersal curve is unknown, model simulations using broad dispersal curves produced sharp threshold declines (Allee effect) whereas more narrow dispersal curves produced linear declines toward zero (recruitment failure) (Lundquist and Botsford 2004).

6. LARVAE

6.1. Larval Period

Red and purple sea urchins have a feeding lecithotrophic larval stage which must acquire food in order to develop and metamorphose. The larval period ranges from 27 to 131 days, varying with both temperature and food availability. In Washington State, at temperatures ranging from 7 to 13 °C, larvae metamorphosed into benthic juveniles in 62–131 days (Strathmann 1978). Shorter times to settlement (40 days) were found at warmer temperatures (Cameron and Schroeter 1980) and with increased food rations (Paulay et al. 1985). Red sea urchins have been reared through to metamorphosis in 23 days at temperatures of 15 ± 2.1 °C when fed high concentrations (60 000–100 000 cells ml^{-1}) of the unicellular alga, *Rhodomonas lens* (Rogers-Bennett 1994).

Echinoderm larvae are phenotypically plastic with respect to environmental conditions such as food availability and temperature. Larval echinoids in food-limited environments have longer larval arms and reduced stomach diameters compared with larvae in food-rich environments (Boidron-Metairon 1988; Hart and Scheibling1988). Larvae with longer arms have enhanced food-gathering capabilities and thus, ingest more food (Hart and

Strathmann 1994). Moreover, larvae increase the size of their stomachs and shorten their arm lengths prior to their ability to feed suggesting that morphogenesis occurs, rather than simply the extension of a full stomach (Miner 2005). Cold temperatures slow development but do not change the sequence of trait acquisition (Miller and Emlet 1997).

The timing of the presence of echinoderm larvae in the plankton has been examined in southern California. Larvae in the plankton sampled weekly at the Diablo Nuclear Power Plant from December 1996 to June 1998 showed a ratio of 16:1 purple sea urchin larvae to red sea urchin larvae (J Steinbeck, unpubl. data). The timing of the presence of larvae was roughly synchronous between the two species. Purple sea urchins were most abundant in June 1997 with a smaller peak in abundance earlier in April 1997, while red sea urchin larval abundance peaked in March 1997 with another peak in July 1997. This peak in larval abundance in the spring coincided with the start of the strong warm water El Niño event in 1997 (NOAAa).

6.2. Blastulae and Larval Behavior

Early stage larvae may be particularly susceptible to predation due to their small size and limited movement capability (Rumrill 1990). Swimming behavior may help in evading predators and/or be used to migrate vertically in the water column. Blastulae begin to rotate within the fertilization envelop. After hatching, blastulae continue to rotate and begin to swim up in a helical path in the water column. The angle of inclination of the rotation along the animal-vegetal pole differs between species. Red sea urchins have a steep angle whereas purple sea urchins do not (McDonald 2004). Swimming and sinking studies in the laboratory using hatched swimming blastulae and unhatched sinking blastulae suggest sinking speeds frequently exceed swimming rates and that sinking rates increase with decreasing sea water temperature (McDonald 2004). The smaller purple sea urchin blastulae (105 μm diameter) had greater swimming speeds of 0.4 mm s^{-1} than the larger red sea urchin blastulae (170 μm diameter) swimming at 0.2 mm s^{-1} (McDonald 2004). These speeds dropped when temperatures increased 3 °C. The decrease in upward swimming velocity with increased temperature could be a useful physiological survival response for embryos entering an unfavorable portion of the water column which exceeds optimal temperatures.

6.3. Larval Cloning

Our understanding of echinoid larval biology and ecology has recently been radically altered with the discovery of asexual reproduction by larval cloning in purple sea urchins and two other echinoids (Eaves and Palmer 2003). Cloning or larval budding, was first described in sea stars, but not until 1988 (Bosch 1988, Bosch et al. 1989). Was this oversight simply because larvae were cultured in batches and individuals were seldom observed or that our paradigm of “normal” development caused us to ignore or remove larvae that looked different? We now know that cloning occurs in all echinoderm classes with the possible exception of crinoids, which have not been investigated. To make this oversight worse, cloning is quite common, occurring in 10–90% of sea star larvae collected from the field (Bosch 1988) and up to 12% in cultured sea cucumber larvae

(Eaves and Palmer 2003). Clones can be generated from different larval body parts. Larvae reared with high concentrations of food that was high in quality, cloned significantly more then poorly fed sea star larvae (Vickery and McClintock 2000). Investigations into the environmental conditions which promote cloning suggest that cultured purple sea urchins clone more in warm-water, high-salinity conditions (A Eaves, pers. comm.).

Larval cloning challenges the notion of fixed, or "set-aside," larval cells since they can differentiate into juvenile cells once cloning is initiated (Eaves and Palmer 2003). The evolutionary consequences of cloning need to be further investigated to determine if it is an ancestral trait, perhaps retained in other deuterostomes such as acorn worms and sea squirts.

Cloning has important implications for larval dispersal, in the context of both gene flow and larval dispersal distances. Larvae that disperse a given distance in the "normal" developmental time of 2–4 weeks can then bud and travel another 2–4 weeks, spreading that genome further than previously estimated. This can occur because clones can subsequently clone multiple times (Balser 1998). Larval dispersal estimates that do not consider cloning need to be re-examined. It has been suggested that there may be an entirely pelagic bauplan (Eaves and Palmer 2003). Indeed, along the California coast, and particularly in the southern California bight, newly settled sea urchins can be found on settlement substrates year round (Ebert et al. 1994). Is this the result of multiple spawnings throughout the year, clones that continue to reproduce asexually, or both? Dispersal distances have important marine conservation applications, such as in the determination of the size and spacing of Marine Protected Areas (Shanks et al. 2003).

7. SETTLEMENT AND RECRUITMENT

Sea urchin (0.5–5.0 mm diameter) settlement has been examined in California on artificial substrates. Ebert et al. (1994) found that settlement is highly seasonal, occurring predominantly from February to July. Settlement is higher and more regular in southern California, within the retention zone of the Bight, compared with northern California, a region with maximum upwelling and strong offshore advection (Ebert et al. 1994). Other studies have found that settlement in northern California and Oregon is favored in years when conditions in June and July are warm with increased salinity and low alongshore windstress (Miller and Emlet 1997; Morgan et al. 2000b; Wing et al. 2003). Settlement of sea urchins on collectors throughout California appears to be highest following warm-water events which may not only reduce offshore transport of larvae but also provide for enhanced larval food and growth (S. Schroeter, pers. comm.). Ebert et al. (1994) also found that purple sea urchins settled in higher numbers and with more geographic coherence than red sea urchins. Furthermore, settlement does not appear to be hindered by the presence of dense kelp forests (Schroeter et al. 1996).

Recruitment dynamics can be inferred from size–frequency distributions so that the absence of juveniles indicates a lack of recruitment success over the past 5–7 years. Examination of tidepools from central California to Oregon revealed few juvenile (5–50 mm) purple sea urchin recruits at sites near headlands and capes (Ebert and Russell 1988). Similarly, in northern California, an examination of the size–frequency distribution revealed more small sea urchins in areas away from headlands that had onshore and poleward movement of water during relaxation events (Morgan et al. 2000b). The mechanism proposed for these patterns is that larvae are advected away from the coast during upwelling and strong offshore jets associated with headlands (Ebert and Russell 1988; Wing et al. 1995). These conclusions are based on the assumption that differences in recruitment, as observed in the size–frequency distribution, arise from differences in settlement, as opposed to post-settlement processes (cf. Connell 1985), over large spatial scales. Post-settlement processes, however, are important for sea urchins at intermediate spatial scales such as on a single reef (Rowley 1989). This highlights the need to distinguish larval settlement (0.5–5.0 mm) from juvenile recruitment (5.0–50 mm).

On smaller spatial scales (1–10 m), juvenile red and purple sea urchins have unique spatial distributions. In some areas, juvenile sea urchins shelter under the spine canopy of adult conspecifics (Low 1975; Tegner and Dayton 1977; Breen et al. 1985; Rogers-Bennett et al. 1995). Adult red sea urchins are more frequently found sheltering juveniles than are adult purple sea urchins, whose spines are shorter. The spatial association of red sea urchins with adults is not due to preferential larval settlement near adults (Cameron and Schroeter 1980). Juvenile red and green sea urchins do actively move toward adult conspecifics contributing to this unique distribution (Rogers-Bennett 1989). Another post-settlement process, differential mortality, is likely responsible for the abundance of juveniles with adults in barrens habitats as compared with kelp forests (Rowley 1989). In laboratory studies, juvenile red and green sea urchins did not prefer feeding adults (Breen et al. 1985) nor did they gain a feeding advantage under the spine canopy of adults. In fact, their growth was significantly reduced compared with juveniles alone (Nishizaki and Ackerman 2004). In preference trials, the number of juveniles moving toward and sheltering under adults increased with increasing water flow and with the presence of potential predators (Nishizaki and Ackerman 2001). Juvenile red sea urchins in northern California were 12 times more likely to shelter under adults in shallow wave-exposed habitats where adults were in rock "scars" compared with deeper-water habitats where adults did not reside in rock "scars" (Rogers-Bennett 1994). Juveniles reacted by sheltering under adults when adults released a secondary chemical cue signaling the presence of predators, while large sea urchins did not react to this cue (Nishizaki and Ackerman 2005).

Recruitment patterns have been observed to differ between southern and northern California. Sea urchin recruitment of juveniles (5–50 mm) was examined in artificial modules made of cinder blocks (surface area 2.6 m^2) at Van Damme State Park in northern California and at three of the Channel Islands in southern California. In 2001–2004, recruitment of juvenile red sea urchins in the modules was 20 times greater in the south, while recruitment of purple sea urchins was nearly 300 times greater in the south (Rogers-Bennett and Kushner, unpubl.). Adult red and purple sea urchins densities on the surrounding natural reef were an order of magnitude lower at the site in northern California than in southern California (Rogers-Bennett and Kushner, unpubl.). Ebert et al. (1999) suggested that the fishery in the north may be driven by unusually successful year classes which persist in the population for many years. These discrepancies in rates of natural recruitment between southern and northern California may have important implications for levels of sustainable fishing between the two regions, suggesting northern California may not be able to sustain as much fishing pressure.

8. POPULATION REGULATION

Regulation of sea urchin populations remains an important research topic in echinoderm studies. Sea urchins populations can boom and bust and we still have more to learn in terms of the mechanisms responsible for these large swings in population density. Certainly the consequences of large populations can be profound and community-wide (see Section 2). A number of biotic factors, such as, competition, predation and disease play key roles in regulating sea urchin populations. Abiotic factors affect sea urchin populations at various stages throughout their life history. For example, fertilization success can be influenced by small-scale hydrodynamics and substrate topography (see Section 5). Larval transport is forced by physical transport processes moving patches of water close to and away from suitable settlement sites (see Section 7). Water flow continues to play a major role in the juvenile stage influencing distribution (Nishizaki and Ackerman 2001) as well as growth and survival. Winter storms can not only dislodge and kill juveniles and adults (Ebling et al. 1985) but also rip out standing kelp beds, thereby negatively affecting drift food supply (Tegner and Dayton 1991).

8.1. Competition

While intraspecific competition occurs in both red and purple sea urchins for limited resources such as food and habitat, there are very few studies examining this process. Within sea urchin barrens there are high densities of sea urchins in close proximity to one another and scarce food resources lead to optimal conditions for competition. There is indirect evidence of intraspecific competition in purple sea urchins: size–frequency distributions show that 90% of the sea urchins in high-density sites (outside reserves) are mid-size and small (< 50 mm) while inside reserves where densities are low, purple sea urchins are much larger (30–70 mm) (D Kushner, KFMP data). There is also evidence for intercohort competition since juvenile red sea urchins (8 mm) in the presence of adults and food have significantly lower growth rates than juveniles without adult conspecifics (Nishizaki and Ackerman 2004). There is no evidence for intraspecific competition between larvae because they are so scarce (Strathmann 1996).

Interspecific competition occurs between red and purple sea urchins in southern California (Ebert 1977; Schroeter 1978). Schroeter (1978) found that red sea urchin are competitive dominants over purple sea urchins because they are able to use their long spines to actively fence with purple sea urchins and exclude them from optimal habitats. Conversely, in Alaska, there is interspecific facilitation between red sea urchins and other congeners. Red sea urchins snag drift kelp with their long spines and provide defense against predatory sun stars *Pycnopodia helianthoides* (Duggins 1981). Little is known about interactions between red and purple sea urchins and the black sea urchin *Centrostephanus coronatus* in southern California.

Abalones are potential competitors with sea urchins (Leighton 1968; Tegner and Levin 1982). Abalones and sea urchins share similar resources: they consume primarily drift algae and live on rocky substrates. Sea urchins are more resistant to starvation than abalones and can even utilize dissolved nutrients living in areas near sewer outfalls (Pearse et al. 1970). In northern California, north of the sea otters' range, there are four species of abalone in the genus *Haliotis*. However, densities are very low for all but the red abalone (*H. rufescens*) (Raimondi et al. 2002; Rogers-Bennett et al. 2002). Red abalone can be very abundant in portions of the subtidal zone in northern California, even at fished sites such as Van Damme State Park (density = 7600 individuals per hectare) (California Department of Fish and Game 2005). At this density adult red abalone and red sea urchins compete for available rocky reef space and for food.(Karpov et al. 2001) During warm-water El Niño events, when drift algae is scarce, hungry red sea urchins move from deeper water (20 m) to shallow water (10 m) to feed (Rogers-Bennett, pers. observ.). When drift food is limiting and competition is intensified, hungry red abalone climb kelp stipes to feed on the blades (Rogers-Bennett, pers. observ.). Red abalone and red sea urchins segregate at the scale of a 60 m^2 transect in the subtidal kelp beds (Karpov et al. 2001). Adult red sea urchin and adult red abalone abundance was negatively correlated on transects at sites in northern California, while purple sea urchin abundance was not correlated with red abalone abundance (Karpov et al. 2001). In sharp contrast, juvenile abalone distribution is facilitated by the presence of the red sea urchin spine canopy. They are more abundant inside reserves with adult red sea urchins than in fished areas with out sea urchins (see Section 11) (Rogers-Bennett and Pearse 2001). In central California where sea otters are present, abalones and sea urchins may compete for deep-crevice habitat which is severely limited (Lowry and Pearse 1973; Hines and Pearse 1982).

In southern California, abalone populations have declined dramatically due to a combination of intense fishing (Rogers-Bennett et al. 2002) followed by disease (Moore et al. 2002). Due to the large-scale removal of abalone biomass, competition between abalones and sea urchins may be greatly reduced. There is some evidence that the dynamics of competition for algal resources may be changing as the red sea urchin fishery in northern California decreases grazing pressure, thereby enhancing kelp beds at one site (Karpov et al. 2001). In southern California, red sea urchin fishing and sea urchin wasting disease may be affecting the competition between red and purple sea urchins (Richards and Kushner 1994).

8.2. Predation

There is a wide range of sea urchin predators. Predation affects both sea urchin population density and the size–frequency distribution. Large sea urchins may reach a refuge in size from predation. Little work has been done to examine the effect of micropredators on sea urchin populations although this appears to be an important source of predation on newly-settled sea urchins (Rowley 1989; McNaught 1999).

Sea otters, *Enhydra lutris,* have the largest predation effect on sea urchins. They were hunted to near extinction, but remnant populations have expanded and today exist in central California, Washington, British Columbia and Alaska (Estes and Duggins 1995). When sea otters move into a habitat, sea urchin and other shellfish populations decline dramatically and individuals are restricted to cryptic microhabitats. The sea otter/sea urchin predation link is well documented (Bertness et al. 2001). Sea otters have been referred to as a “keystone species” (Paine 1966) whose presence is instrumental in shaping the structure of the surrounding nearshore community (Estes and Palmisano 1974; Simenstad et al. 1978). The “keystone” paradigm emerged from studies in Alaska in which habitats with sea otters had lush diverse kelp forests that were visually distinct from barrens habitats which lacked sea otters and were dominated by echinoderms (Estes and Duggins 1995). This is thought of as a three-level trophic cascade with sea otters, invertebrate herbivores (sea urchins), and algae. Another level has been added to this cascade, in which the killer whale, a sea otter predator, indirectly influences sea urchin populations through the trophic cascade (Estes et al. 1998). In central California, the sea otters range now extends from San Francisco south to Santa Barbara (Vogel 2000). Along the pipeline offshore of Santa Barbara sea otters have reduced sea urchin and shellfish populations dramatically (L Rogers-Bennett, pers. obs.).

There is little debate about the widespread effects of sea otters on echinoid populations within their range. However, outside the range of sea otters in California and Baja California, there is a suite of potential community types (e.g. only 10% of more than 200 sites surveyed were sea urchin barrens) (Foster and Schiel 1988). Foster and Schiel's (1988) work suggests (1) there may be a suite of intermediate community states outside the sea otters' range as opposed to two alternative stable states, (2) care must be taken in applying this mutually exclusive states concept to the entire west coast of North America and elsewhere, and (3) a number of other factors have an important role in driving sea urchin-mediated deforestation (see Section 2). More work is needed at sites where sea urchins and kelps routinely coexist.

In southern California, two sea urchin predators are important in regulating sea urchin populations: the spiny lobster, *Panulirus interruptus*, and the sheephead, *Semicossyphus pulcher,* a labrid fish (Tegner and Dayton 1981). Spiny lobsters prefer purple to red sea urchins and juveniles to adults (Tegner and Levin 1983). By comparing sea urchin abundances at sites inside and outside reserves in the northern Channel Islands, where spiny lobsters are protected from fishing, Lafferty (2004) was able to assess the effects of lobsters on sea urchin populations. Inside the reserves, lobster abundance was high and purple sea urchin abundance was low (<100 red and purple sea urchins per square meter) and kelp was abundant (Lafferty 2004). This suggests that lobster predation may be important in regulating sea urchin densities in this region. Sheephead have massive jaws and eat juvenile and adult sea urchins. In a sheephead removal experiment in southern California, in an area devoid of lobsters, sheephead regulated red sea urchin populations and drove sea urchins into cryptic microhabitats (Cowan 1983). At that time it was estimated that sheephead consume more than 8000 sea urchins per hectare per year (Cowan 1983). Making modern estimates of predation rates is difficult since sheephead abundances do not differ significantly inside and outside the reserves in the Channel Islands (Behrens and Lafferty 2004). In the last 3500–4500 years, Indian middens show that the size of sheephead bones decrease with increasing human fishing pressure (Salls 1995). Above the sheephead bone layer in the middens is a lens of purple sea urchin remains (Salls 1995). This finding led to the hypothesis that prehistoric overfishing of sheephead caused a decline in this important predator, which in turn led to extreme sea urchin population increases (Erlandson et al. 1996).

Red and purple sea urchins are also vulnerable to predation by the white sea urchin *Lytechinus anamesus* (= pictus) in southern California. Groups of the small white sea urchin completely consume large red sea urchins. White sea urchins attack both red and purple sea urchins in the field and laboratory, although they prefer to eat kelp (Coyer et al. 1987). Despite this, the abundance of the predatory white sea urchin declined from the mid 1980s in a mixed-species sea urchin barrens at Anacapa Island, in southern California, suggesting other dynamics are operating to regulate sea urchin populations in these barrens (Carroll et al. 2000).

In the north, the sun star (*P. helianthoides*) consumes both red and purple sea urchins <90 mm in test diameter (Duggins 1983; Lafferty and Kushner 2000). Therefore, red sea urchins >90 mm reach a refuge in size from sun star predation while purple sea urchins do not (Duggins 1983).

8.3. Disease

Sea urchin diseases, such as the bald sea urchin disease, affect sea urchin populations around the world (see Chapters 11, 13, and 18). Diseased red and purple sea urchins have been documented in both central and southern California (Richards and Kushner 1994). A red sea urchin mortality event was seen in Santa Cruz in the 1970s, killing an estimated 14 000 sea urchins (Pearse et al. 1977). In the Channel Islands diseased sea urchins exhibit spine loss and dark patches of necrotic tissue (Richards and Kushner 1994). These symptoms are consistent with a *Vibrio* bacterial disease (Gilles and Pearse 1986). However, the causative agent of this disease in the Channel Islands has not been identified. While this disease is fatal, sea urchins do appear to be able to recover as evidenced by the presence of sea urchins with regenerated spines.

The Kelp Forest Monitoring Program has been recording the health and density of sea urchins in the Channel Islands since 1982. In 1992, during a strong El Niño, disease was first recorded in the sea urchin populations (Richards and Kushner 1994) suggesting this disease may have come from elsewhere (Lafferty 2004). Using data from 1992 to 2001, the prevalence of the disease has been shown to have a significant negative effect on population growth in purple sea urchins as measured by r, the logarithm of the relative change in density N, between years t and $t+1$, where (Lafferty 2004)

$$r = \ln\left(\frac{N_{t+1}}{N_t}\right)$$

Disease at these Channel Island sites over the decade did not result in a widespread mass mortality event as has been observed elsewhere for other species (Scheibling 1986; Lessios 1988).

8.4. Physical Factors and Ocean Warming

Wave forces and water motion can have a large direct and indirect affect on sea urchin populations. Red sea urchins may suffer greater mortality due to wave-induced movement of boulders in the subtidal zone (Schroeter 1978). Purple sea urchins appear to be more resistant to disturbance, perhaps due to their smaller size and shorter spines. Purple sea urchins are also more tolerant of the wave forces, heat and desiccation found in intertidal tidepools than red sea urchins. In sheltered subtidal habitats, purple sea urchins can also withstand low oxygen and high-silt concentrations while red sea urchins cannot

(Schroeter 1978). Little work has been done to examine the effects of these physical factors on earlier life history stages although, presumably siltation could affect respiration and survival of newly settled sea urchins.

Wave forces ripping up intact kelp beds can cause food shortages for sea urchins. Sea urchin grazing can further exacerbate this damage leading to total structural failure if kelps are weakened anywhere along the stipe or within the holdfast (Tegner et al. 1995). Even small amounts of herbivore damage when combined with otherwise innocuous current and wave forces can be enough to cause catastrophic failure and total kelp loss (Duggins et al. 2001).

Ocean warming can have multiple indirect affects as warmer water conditions reduce the nitrogen content of the seawater thereby negatively affecting kelp quantity and quality. The appearance of the bald sea urchin disease during the 1992 El Niño and increased incidence of the disease in the warmer easternmost Channel Islands, such as Anacapa and Santa Cruz Islands (Richards and Kushner 1994), suggest a direct link between ocean temperature and this sea urchin disease. In a warm reserve site at Anacapa Island, where no fishing was permitted and lobster abundances were high, sea urchins were at low densities and were not impacted by the disease (Lafferty 2004). This suggests that while sea water temperatures may play a role in the outbreak of the disease, population density, as regulated by predators, also influences the onset of sea urchin epidemics (Lafferty 2004). More work is needed on the interactions between ocean warming and other factors regulating populations, such as, food abundance, disease outbreaks, and predator abundance.

Ocean warming trends have been correlated with sea urchin-predator abundances. The Pacific Decadal Oscillation, defined as the leading principal component of North Pacific monthly sea surface temperature variability (north of 20° N for the 1900–1993 period), indicates ocean conditions have been anomalously warmer from 1977 to 1999 as compared with long-term (100 year) averages (Mantua et al. 1997). Since 1976–1977 the commercial fishery for spiny lobsters has increased threefold, from less than 100 t per year to 375 t in 2004 (Sweetnam 2005). While these data are suggestive, implying warmer ocean conditions favor lobster populations, it should also be noted that in 1977 escape ports were first required in lobster traps to decrease retention of undersize lobsters. The usual caveats associated with landings data also apply here. In particular, there is no information on fishing effort. Fishery-independent data also suggest warm water events enhance the recruitment success of spiny lobsters and sheephead in southern California (Cowan 1985).

Ocean warming also influences the intensity of human fishing for sea urchins, in that there is a negative-feedback loop maintaining sea urchin barrens. Warm ocean conditions can lead to poorly fed sea urchins with decreased sea urchin gonad quality, which would result in decreased human fishing effort. Less sea urchin fishing will maintain high sea urchin abundances, thereby potentially facilitating barrens formation and overgrazing. Patterns of kelp harvest are correlated with landings patterns in the sea urchin fishery in South Korea (Andrew et al. 2002). It has been suggested that the strong El Niño event of 1982–1983 was responsible for decreased red sea urchin landings in southern California (Kato and Schroeter 1985) and Baja California, Mexico (Hammann et al. 1995). If the frequency and intensity of El Niño warming events (defined by NOAA as positive Oceanic

Niño Index greater or equal to +0.5 °C for at least five consecutive months) increases, it will be important to determine if this feedback loop is coincident with an increase in the temporal and spatial extent of sea urchin barrens and kelp deforestation.

9. GENETICS

The systematics and phylogenies of sea urchins in the genus *Strongylocentrotus* remain poorly understood despite abundant ecological, fishery and developmental studies on this group. Selection of the purple sea urchin as a target species for genome analysis (Pennisi 2002) may increase attention to this. Molecular phylogenies with mitochondrial DNA sequences reveal that the genus is divided into two distinct clades, with red sea urchins in one and purple sea urchins in the other, that diverged 13–19 million years ago (Lee 2003). However, recent mitochondrial DNA sequencing data suggest that a major revision of the genus *Strongylocentrotus* may be in order (Biermann 1998). The phylogeny resulting from this work supports the inclusion of three additional species into the group *Strongylocentrotus* which were previously thought to be closely related (Biermann et al. 2003).

Red and purple sea urchins are model organisms to study genetic variation in marine invertebrate populations with potentially broadly dispersing planktonic larvae and a benthic adult stage. The genetic structure of purple sea urchins along the coast of California and Baja California was examined using allozyme and mitochondrial DNA. Neighboring purple sea urchins had as diverse allozyme and DNA structure as sea urchins from geographically distant sites (Edmands et al. 1996). Similarly, neighboring red sea urchins in California had as much or more diverse allozyme structure as sea urchins from distant populations (Moberg and Burton 2000). Northern California populations were not distinguishable from southern California populations based on the six polymorphic loci examined (Moberg and Burton 2000) despite the large geographic distance and potential barriers to dispersal. Surprisingly, juveniles (<30 mm diameter) differed from adults collected from the same location, and genetic variation among the juveniles, in both space and time, was greater than would be predicted with a well-mixed larval pool (Moberg and Burton 2000). This suggests that although there is apparently sufficient gene flow to prevent genetic divergence of populations along the California coast, the larval pool is likely not always homogenous across the geographic range despite the long larval period which Strathmann (1978) indicated is 4–20 weeks.

Debenham et al. (2000) examined DNA sequence data from the binding gene in populations across the species' range from Alaska to Baja California. Their work and previous studies suggest the binding locus is an appropriate marker with sufficient polymorphism to detect genetic structure. The bindin marker revealed sea urchins at six locations had at least four alleles suggesting that, at least for this marker, they are highly polymorphic (Debenham et al. 2000). Multiple microsatellites ($N = 14$) were isolated for paternity studies and were highly polymorphic for red sea urchins from British Columbia (McCartney et al. 2004). Eleven polymorphic, di- and trinucleotide microsatellite loci for three sites in British Columbia show heterozygosities of the loci ranged from 0.39 to

0.85, showing that variability is high (Miller et al. 2004). More work needs to be done to compare allelic frequencies among populations.

Sea urchins have been used as a direct test of the "sweepstakes" hypothesis for marine invertebrates, which states that for free-spawning organisms with high fecundity and high larval mortality, it is possible that only a few adults reproduce successfully each year (Hedgecock 1994). Small effective population sizes relative to stock sizes are observed in many marine invertebrate populations including sea urchins (Hedgecock 1994). In this scenario, where chance plays a large role and few adults reproduce, juvenile sea urchins would have less genetic differentiation than the genetically mixed pool of adults. Using mitochondrial DNA, Flowers et al. (2002) determined that there was no evidence for reduced genetic variation in newly settled (1–14 days post-settlement) purple sea urchins and only slight evidence to suggest cohorts were genetically distinct. This leaves the importance of the sweepstakes hypothesis for sea urchins in question.

10. FISHERIES

Red sea urchins are the primary target of sea urchin fisheries on the west coast of North America while purple sea urchins make up less than 1% of the landings (for reviews see Kalvass and Hendrix 1997; Keesing and Hall 1998; Andrew et al. 2002). Japan is the primary market for sea urchin "roe"; the gonads of both males and females. Sea urchin roe is a specialty food eaten year round but is especially popular during New Year celebrations; a tradition which started as early as the 1600s (Andrew et al. 2002). In Japan, domestic production of wild sea urchins peaked in 1969 leading to a demand for imported sea urchin products both frozen and fresh. Sea urchin imports have increased over the last 30 years with imports of fresh products having risen from 7000 metric tons (t) in 1999 to over 13 000 t in 2004, while imports of roe in brine have also increased. There is no suggestion of a decline in future demand (NOAAb).

10.1. West Coast Fisheries

The fishery in southeast Alaska is in open coastal waters with a small portion of the catch from the inland straights. Commercial exploitation began in the mid 1980s but the fishery did not have landings greater than 500 t until the mid 1990s. In 1994, the Alaskan fishery expanded into the Ketchikan area, away from sea otters. The fishery peaked in the 1997–1998 season at 2235 t but since then has declined nearly threefold to 817 t for the 2004–2005 season (M Pritchard, pers. comm.).

In British Columbia, Canada the fishery remained small in the 1980s and then peaked at 13 000 t in 1992. Since 1994, the fishery has remained stable with approximately 5000–6000 t per year taken. The TAC for the 2004–2005 season was 4884 t of which 4359 t were landed worth an estimated CN$7.8 million (J Rogers, pers. comm.). Catch per unit effort has remained fairly stable for the decade at or around 0.575 t per diver hour (J Rogers, pers. comm.).

In Washington State, sea urchin fishing increased in the 1980s to peak at 3658 t in 1988 and has since declined to less than 10% of this amount (Bradbury 2000). By

2000, red sea urchins made up approximately 60% of the catch with green sea urchins *S. droebachienensis* making up the remainder (Carter and VanBlaricom 2002). Fishery-independent surveys of red sea urchin size indicated that only 5% of the population was lower then the minimum legal size (102 mm). This suggests that the population is an accumulation of large, old individuals with poor recruitment success (Carter and Van Blaricom 2002). Fishery-independent surveys also suggest that sea urchin density has declined since the 1980s although catch per unit effort estimates do not reflect a decline because fishers are able to exploit new subpopulations (Pfister and Bradbury 1996). Density estimates using underwater video and dive surveys were used to establish biomass estimates and set total allowable catches for the state, however these were terminated following budget problems in 1997 (Bradbury 2000).

In Oregon, the red sea urchin fishery followed a similar course as that in Washington State, with a rapid rise in landings in the late 1980s to a peak of 4222 t in 1990, and then a dramatic collapse to less than 5% of the peak by the end of the 1990s. The mean size of red sea urchins has declined as has the proportion of large sea urchins in the catch (Richmond et al. 1997). Purple sea urchins make up a small proportion (<10%) of the fishery (Richmond et al. 1997)

California's red sea urchin fishery has dominated the sea urchin producing regions along the west coast of North America. Despite California's dominance it has not been immune to declines in sea urchin landings. The fishery began in 1971 as an experimental fishery in southern California (Kalvass 2000). The fishery quickly rose to 4540 t by 1980 and then experienced a decline precipitated by a strong El Niño event which affected landings for 3 years. In 1985, the fishery expanded into northern California where landings increased to 13620 t in just 3 years. However, northern California has not seen landings higher than 2724 t for the last decade (Kalvass 2000). The majority of landings in the north from 1988 to 1994 came from a small (65 km) section of the rocky coast (Kalvass and Hendrix 1997). In 2004, an estimated 5.36 t were landed statewide worth $7.1 million, of which 4.75 t were landed in southern California (Sweetnam 2005). Even in the southern portion of the state where landings had been fairly stable, landings are now below the long-term (1975–2004) yearly average (7.53 t) (Sweetnam 2005). Sea urchins are not landed in central California from Point Conception to San Francisco Bay where predation by sea otters precludes a fishery.

In the southern portion of the red sea urchins' range, the fishery is located along the Pacific coast in the northern third of the Mexican Baja peninsula. The red sea urchin fishery began in the early 1970s and landings rose to peak in 1986 at 8493 t. Landings fell drastically the next year to only 1590 t due to a strong El Niño event which affected roe quality and led to decreased effort (Andrew et al. 2002). Landings in 1999–2000 have been just under 2200 t. Purple sea urchins make up a small portion of the total catch in Baja California.

10.2. Fishery Experiments

Experimental fishing studies inside a marine reserve examined how red sea urchins recover from various levels of fishing treatments such as existing regulations (lower size limits only), proposed selective fishing (upper and lower size limits), and fishing reserves (no fishing). The population of highly mobile sea urchins at intermediate depths recovered quickly (1 month) from fishing by the migration of adults from neighboring areas. Sedentary sea urchins from shallow sites recovered slowly or not at all depending on experimental fishing treatment (Rogers-Bennett et al. 1998). Existing regulations led to a decline over 10 years in sea urchin density and poor recruitment of juveniles, while fishing treatments that protected adults led to enhanced recruitment (Rogers-Bennett et al. 1998). Similarly in Washington State, recovery from fishing was via migration of neighboring adults as opposed to juvenile recruitment (Carter and Van Blaricom 2002). Recovery rates observed in small-scale fishing experiments should be considered as maximum rates since commercial fisheries operate at larger scales leaving few neighboring adults available for recolonization (Rogers-Bennett et al. 1998; Carter and VanBlaricom 2002).

10.3. Fishery Enhancement

Fishery enhancement experiments, including stocking juvenile red sea urchins, pioneered in Japan (Omi 1987) have been examined on the west coast of the United States (Tegner 1989). Juvenile red sea urchins cultured in aquaculture facilities were released in California. In one study, 5000 juveniles were tagged with calcein and stocked into two northern and two southern sites. While recovery rates after 1 year were spatially variable (1–22%) with no discernable latitudinal patterns, juvenile size did influence recovery. The largest juveniles (12–18 mm) were recovered more than the two smaller size classes of 3–7 mm and 8–12 mm at all sites (Dixon et al. 1992). Clearly, there are tradeoffs between the cost of producing larger juveniles prior to stocking and higher rates of recovery. In a second study in northern California, red sea urchins reared in the laboratory for 1 year to a mean size of 18 mm were tagged with calcein and stocked into shallow (5 m) and intermediate depth (15 m) habitats inside a sea urchin marine reserve. Twice as many juvenile sea urchins (21%) were recovered from the shallow than the intermediate depth habitat (11%) suggesting that spatial patterns related to depth may be important in selecting enhancement sites (Rogers-Bennett 2001).

10.4. Gonad Enhancement

Another fishery enhancement method is that of gonad or roe enhancement. This involves transplantating of wild juveniles or adults from habitats with poor food quantity or quality to optimal habitats in the ocean at sea ranches or land-based aquaculture facilities (Tegner 1989). Small red sea urchins (33 000) in southern California were transplanted from a barren area to a kelp forest with low densities of large adult red sea urchins (Dixon et al. 1999) Growth and survival were good at the transplant site 1 year later with an estimated 58% (±30%) of the sea urchins surviving. The source site continued to have high recruitment even after the removal of >30 000 juveniles. However recruitment was sporadic and transplant outcomes may not be as good during periods of poor natural recruitment (Dixon et al. 1999). Despite the vagaries of natural recruitment, this method, in addition to the movement of underfed adult sea urchins with poor gonad quality to kelp-rich habitats, may be more promising than the labor-intensive methods required to culture larvae for stocking.

11. FISHERY MANAGEMENT

Stock assessment estimates have been made for a number of red sea urchin stocks using fishery-independent data. Surplus production models are used because they are simplistic with few data requirements, but these models have a number of assumptions that must be examined closely. Densities are determined for a given area from fishery-independent dive surveys along transects or video transects. Densities of sea urchins are generally patchy and include areas with zero densities. Confounding estimates of biomass for red sea urchins are a subset of the population that may be counted in the surveys, but are poorly fed and do not yield marketable gonads. How to treat these poor quality sea urchins in estimates of stock biomass remains an open question.

Another method for estimating red sea urchin biomass is based on fishery-dependent data using a Leslie depletion model. A series of catch-per-unit-effort estimates for each year is plotted and then fit with a regression line. Using this model for stocks in northern California, the prefishing (prior to 1988) biomass was estimated at 76 290 t of which 50 800 t was removed by the fishery from 1988 to 1994 with 13 846 t taken in 1988 alone (Kalvass and Hendrix 1997). For 1988 this is equivalent to an instantaneous fishing mortality rate of $F = 0.2$. This fishing rate was not sustainable and resulted in a boom and bust fishery in the north (Kalvass and Hendrix 1997) and landings have not rebounded in the last decade (Sweetnam 2005). Another method for estimating fishing mortality (F) is based on size distributions of individuals greater than 90 mm (to reduce the influence of new recruits) from fished sites and vital rate parameters from unfished sites. Estimates of F ranged from 1.87 to 0.11 across 11 sites in northern California (Morgan et al. 2000a). Estimates of population parameters can aid in developing fishery management strategies that control fishing intensity and sustain fishery yields. Estimates of lifetime egg production (R_o) based on age or size can help guide fishery managers to set target and limit reference points in an effort to fish sustainably despite inherent uncertainty in the population dynamics (Botsford et al. 2004).

Fisheries management traditionally used size limits to allow certain size classes to spawn before they enter the fishery. All fisheries, expect Alaska, have lower size limits. The processors and market prefer midsize red sea urchins over the largest individuals. Since the largest red sea urchins potentially contribute the most toward reproduction this suggests that a maximum legal size could protect spawners while allowing fishing for high quality product (Rogers-Bennett et al. 1995). This, in combination with the density-dependent mechanisms of adults sheltering juveniles (Tegner and Dayton 1977) and enhanced spawning efficiency (Levitan et al. 1992) supports implementation of a maximum legal size to protect the largest individuals which may have enhanced reproductive output (Birkeland and Dayton 2005). Population growth rate in a size-structured population model was most influenced by changes in the growth and mortality of the largest size classes suggesting again that large sea urchins are important to protect (Ebert 1998). Incorporating maximum legal sizes into a population model of red sea urchins in Washington State resulted in more stable fishery yields and red sea urchin populations (Lai and Bradbury 1998).

Management of sea urchin fisheries on the west coast of North America has focused on single species with few attempts to incorporate multi-species management strategies despite the variety of potential benefits (Pikitch et al. 2004). There is no plan to manage red sea urchins as part of the nearshore communities in which they live. Multi-species resource assessments are only now being initiated in some regions. Despite our knowledge of fishery interactions between sea urchins and abalone (Rogers-Bennett and Pearse 2001) and sea urchins and lobster (Lafferty 2004) we still do not use this information in management. Furthermore, species interactions involving red sea urchins may differ significantly throughout the species' range. Similarly, oceanographic influences on productivity are not measured or incorporated into sea urchin fishery management. In the end, we do not fully understand the effects of large-scale removals of sea urchin by the fishery and what ramifications they may have on the broader nearshore subtidal community (Tegner and Dayton 2000). To assist in understanding the drivers of sea urchin population dynamics we need to look closely at the complex role sea urchins play as members of marine communities throughout the range.

12. CONSERVATION

Conservation of sea urchin populations, at first, may sound unnecessary to some since in the 1960s and 1970s kelp bed management in southern California included the eradication of sea urchins using quick-lime (calcium oxide), hammers, and dredges (Wilson and North 1983). Yet today, we see that sea urchins also have positive interspecific interactions within kelp communities. While sea urchins sometimes viewed as pests in kelp forests when they are starved, more frequently (90%) they are an integral, vital component of nearshore ecosystems (Foster and Schiel 1988). As we strive to understand more about destructive grazing by sea urchins, we see this is a complex phenomenon involving multispecies interactions, recruitment dynamics, and large-scale oceanographic processes. Ocean climate change operating on several temporal scales further compounds the complexities of this herbivore-algal coevolutionary relationship (Steneck et al. 2002).

Sea urchins are also economically important as valuable targets for expanding fisheries worldwide (Andrew et al. 2002). If we consider that sea urchins, like other valuable fisheries, can be overfished then we will be more inclined to examine sustainable fishing strategies. In fact, there are a number of life history features which make red sea urchins particularly susceptible to fishing and these include (1) extreme long life (Ebert and Southon 2003), (2) high densities in close proximity are required for fertilization success (Levitan et al. 1992), (3) successful recruitment of juveniles is temporally and spatially patchy (Pearse and Hines 1987), (4) legal size adults shelter juveniles (Tegner and Dayton 1977), and (5) populations are structured as metapopulations (Rogers-Bennett et al. 1995). These unique life history features highlight the need for vigilance in maintaining sustainable sea urchin fisheries.

12.1. Metapopulation Dynamics

Sea urchins exist in spatially discrete sets of populations. These combined population patches make up a metapopulation (Levins 1969). Patches may be unique with respect to growth, reproduction, and survival rates, while some are sources of reproduction others are sinks (Pulliam 1988). These spatially segregated subpopulations are well known in both the ecology literature and by fishers exploiting different reefs. Fishing "hot spots" can be temporally stable features lasting decades or may blink on and off depending on environmental factors such as oceanographic circulation patterns (Ebling and Hixon 1991). Dispersal between patches, the source of juveniles, and the fishing intensity per patch are all important to our understanding of sea urchin metapopulation dynamics, however they are difficult to quantify. Shallow habitats in northern California (Rogers-Bennett et al. 1995) and southeast Alaska (Carney 1991) have the qualities of source habitats with large fecund animals, an abundance of drift food resources, and high densities of juveniles. These shallow areas are also more susceptible to fishing pressure and respond differently than intermediate and deep habitats (Rogers-Bennett et al. 1998). Spatially explicit metapopulation models with fishing reserves and high exchange rates maximized economic gains and yield when sink areas were fished while source areas were protected in reserves, however, this did not always maximize spawning stock biomass (Tuck and Possingham 2000).

More work is needed on small-scale (reef) variability in life history information relevant to population dynamics. One such study using fishery-independent data has examined spatial variability in productivity at three unfished sites in northern California. Growth was similar at the three sites but estimates of natural mortality varied with some estimates difficult to interpret due to zero and negative values (Morgan et al. 2000a). Fishery-dependent data such as catch-per-unit-effort estimates will be a poor predictor of population trends in metapopulations since fishers can move to exploit new subpopulations (Keesing and Baker 1998). Spatial heterogeneity of fished populations can have important consequences for the dynamics of the fishery and this heterogeneity has been thought about and incorporated into fishery models for some time (Hilborn and Walters 1987).

12.2. Sea Urchins as Ecosystem Engineers

Sea urchin grazing directly and indirectly modulates the availability of algal resources for other species within the community thereby meeting the definition of an ecosystem engineer (Jones et al. 1994; Rogers-Bennett and Pearse 2001). Along with their ability to structure surrounding algal communities through direct herbivory (see Section 2), sea urchins can create cavities within kelp holdfasts and make cryptic microhabitats. In the process they significantly weaken kelps increasing their chances of loss during storms (Tegner et al. 1995). Sea urchins also excrete ammonia which can be important at microscales when nitrogen is limited. In temperate rocky reefs, red and purple sea urchins are effective rock borers scouring out rock pits. Red sea urchins residing in rock pits have restricted movement (Rogers-Bennett 1994) as do purple sea urchins (B Grupe, pers. comm.). In addition, purple sea urchins inside pits are significantly smaller, have larger lantern/body weight indexes, and longer jaw lengths compared to urchins outside of pits, suggesting they are food limited in pits (B Grupe, pers. comm.). Comparatively little work has been done on rock pit formation and bioerosion by purple sea urchins in temperate rocky reefs as compared to sea urchin mediated bioerosion in coral reef systems (Carreiro-Silva and McClanahan 2001; Griffin et al. 2003). More work is needed that examines the role purple sea urchins play in creating large beds of scoured rock pits in the intertidal. Furthermore, more work is needed on the effects of fishing sea urchin ecosystem engineers and the consequences of this on biodiversity and ecosystem functions (Rogers-Bennett and Pearse 2001; Coleman and Williams 2002).

Sea urchins and their extensive spines are themselves structuring components of subtidal communities that modulate the availability of sheltered microhabitat. The spine canopy of red sea urchins and purple sea urchins is structurally complex making an ideal microhabitat for a wide variety of small invertebrates and fishes. Juvenile conspecifics are known to reside under the spine canopy (see Section 7). Likewise, juvenile red and flat abalones are frequently found under the spine canopy of red sea urchins in areas where sea urchins are protected from fishing (Rogers-Bennett and Pearse 2001). Juveniles may be protected from predation and wave action under the spine canopy of sea urchins (Tegner and Dayton 1977), although experiments reveal they do not have enhanced access to food resources (Nishizaki and Ackerman, 2004). While the flow of algal resources as mediated by sea urchins has been examined, less is known about the potential benefits that associated organisms may receive under the spine canopy. Adult sea urchins, by sheltering juvenile sea urchins and abalones under their spines, may be acting as "essential fish habitat" as defined in the Magnuson-Stevens Fishery Conservation and Management Act (Rogers-Bennett and Pearse 2001). This sheltering relationship is not restricted to red sea urchins and has been found in a variety of sea urchin species elsewhere in the world making a strong case for ecosystem management (Mayfield and Branch 2000; Hartney and Grorud 2002).

12.3. Ecosystem Management

Federal agencies in both the United States and Canada have encouraged development of ecosystem-based management (Fluharty 2000; Pikitch et al. 2004), but it has not be implemented for red sea urchins on the West Coast of North America. While there is good biological rationale for such an approach, implementation is confounded by competing fishery interests within ecosystems, determinations of the spatial bounds for ecosystems, and even definitions of goals such as "ecosystem health" or "ecosystem integrity" (Simberloff 1998). Despite these challenges, nearshore kelp beds on rocky substrates are ideal candidates for pilot programs exploring ecosystem management for several reasons (1) they support a diverse assemblage of relatively benthic fished species including invertebrates and fishes, (2) the habitat type and community is well defined by the substrate, (3) they are close to shore facilitating assessment, and (4) wise management will be more important as human populations along the coast expand increasing fishing pressures. Sea urchins within these systems are also prime candidates for ecosystem management as they modulate the flow of resources through the community, interact with other valuable fisheries, and are key species that drive community structure.

Marine protected areas (MPAs) can be used as a tool for ecosystem based management. MPAs have a wide array of uses and designations ranging from no access to multiple uses. No-take MPAs that prohibit fishing have been recommended as one tool for managing sea urchin fisheries with a vast array of goals including natural recruitment areas, buffers in case of population catastrophes, reducing volatility in fishery catch, enhancement of fishery yields, and ecosystem restoration (Botsford et al. 1997; Murray et al. 1999). Algorithms that optimize biodiversity, ecological processes, and socioeconomic factors have been used as tools for the development of plans for MPA networks (Sala et al. 2002; Airame et al. 2004). No-take MPAs might have a wide range of scenarios for sea urchins including population explosions that denude algal forests, robust populations that enhance multiple species, small cryptic populations within the sea otters range or even areas devoid of sea urchins due to disease. This range of outcomes is due in part to trophic cascades (Sala et al. 1998) reflected as conflicts between shellfish fisheries and protected species such as sea otters (Gerber et al. 1999) which are challenges to implementing ecosystem-based management. When restored upper trophic levels have dramatic effects on target fisheries, as is the case for sea otters and sea urchins, it may be necessary to have two types of MPAs – one focused on ecosystem restoration and the other on sustaining shellfish fisheries (Fanshawe et al. 2003). In Japan and South Korea ecosystem management includes both the fishing of target species as well as active habitat enhancement designed to increase productivity of sea urchin fisheries and other fisheries (Andrew et al. 2002).

The productivity of nearshore rocky ecosystems that support sea urchins, however, is very different than it was even 100 years ago as animal populations have declined primarily due to anthropogenic factors (Dayton et al. 1998). Baselines have shifted (Pauly 1995) and expectations of what is abundant or even normal have been greatly reduced. Sea otters are absent from some regions, spiny lobsters, sheephead and other sea urchin predators have dramatically altered abundances. Fishing predators can radically change sea urchin size–frequency distributions, converting them from bimodal to unimodel, and affecting their population dynamics (Tegner and Levin 1983; Behrens and Lafferty 2004). Novel fisheries like the live-fish fishery have emerged since 1993 and targets primarily rockfish 200 t in 10 years (Sweetnam 2005). Emerging nearshore fisheries such as the commercial fishery in southern California for Kellet's Whelk *Kelletia kelettia* have also grown from 8 t in 1997 to 32 t in 6 years (CDFG data). Despite the onset of these new fisheries we still do not have a clear understanding of what effect removing metric tons of a species will have on species interactions and ecosystem functioning. Along with the realization that fishing changes community interactions we have grown more aware of and are starting to quantify the effects of ocean climate on productivity (Tegner and Dayton 1991; Mantua et al. 1997). Ecosystem management will only be feasible with more knowledge of the biological and physical processes involved in population regulation.

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