

# The Feasibility of Enhancing Red Sea Urchin, *Strongylocentrotus franciscanus*, Stocks in California: An Analysis of the Options

MIA J. TEGNER

## Introduction

The red sea urchin, *Strongylocentrotus franciscanus*, is the largest echinoid in kelp forest communities along the west coast of North America and is fished commercially from British Columbia to Baja California (Sloan, 1986). The California sea urchin fishery began in the early 1970's and grew very rapidly to total landings of more than 20,000 metric tons (t) in 1987 (Kato and Schroeter, 1985; Parker<sup>1</sup>). By 1987, this was the second most valuable fishery in California waters with a landed value of \$13,693,000. There are no unfished stocks left in southern California; only the development of a northern coastal fishery in the mid 1980's allowed the continued increase in landings (Fig. 1).

With the eventual elimination of unfished stocks statewide, and poten-

tially throughout the range of the fishery, the alternatives are a reduced harvest and contraction of the industry, or stock enhancement to maintain populations above what is possible with current fishery practices. The spectacular successes achieved with some finfishes, notably the salmonids, as well as the many recent advances in aquaculture, have led to widespread interest in the second and more economically appealing alternative. Here, I examine potential options for the enhancement of red sea urchin stocks, consider the conditions under which each might be appropriate, and make relative estimates of the costs and effort involved.

The concept of stock enhancement for valuable invertebrate fisheries is not new. Transplantation of abalones, *Haliotis* spp., to better habitats for growth dates to the 19th century (Ino, 1966), and lobster, *Homarus* spp., juveniles were cultured for release on fishing grounds as early as the 1880's (Van Olst et al., 1980). The Japanese in particular have explored a variety of

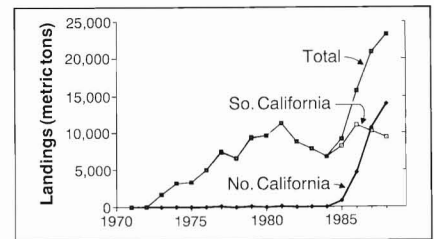


Figure 1.—California landings of red sea urchins, 1971–87 (Calif. Dep. Fish Game. Unpubl. data).

methods to enhance fishable stocks. The success of all attempts to enhance benthic invertebrate stocks by the release of hatchery-reared juveniles will be reviewed, as well as other methods relevant to sea urchins. Because the success of many Japanese approaches is related to the structure of their fishing industry, this and the implications of the American tradition of open-access fisheries for stock enhancement will be discussed.

The success of any enhancement effort will depend upon the answer to a critical question: What stages in the life history of the organism limit the production of fishable stocks? For red sea urchins, the limiting factors could be larval supply, problems associated with settlement, survival of newly settled to mid-sized animals, or adequate

<sup>1</sup>D. Parker, Calif. Dep. Fish Game, 330 Golden Shore #50, Long Beach, California 90802. Unpubl. data, 1989.

**ABSTRACT**—The California fishery for red sea urchins, *Strongylocentrotus franciscanus*, has undergone explosive growth in recent years and is approaching full exploitation. Thus, there is considerable interest in enhancing stocks to maintain a high rate of landings. Fishable stocks of red sea urchins in different areas appear to be limited at three stages in their life history: By the availability of larvae, by the survival of newly settled to mid-sized animals, and by the food available to support growth and reproduction of larger animals. Here I review other efforts, notably

the extensive Japanese work, to enhance fishable stocks of benthic marine invertebrates, and consider the potential options for red sea urchins at different points of limitation. These include collecting or culturing seed for outplanting, physical habitat improvement measures, improving the food supply, and conservation measures to protect existing stocks until alternate methods are proven and in place. The options are compared in terms of biological feasibility, capital and labor requirements, and potential implications for change in the structure of the fishing industry.

Mia J. Tegner is with the Scripps Institution of Oceanography, A-001, University of California, San Diego, La Jolla, CA 92093. Mention of trade names of commercial firms in this paper does not imply endorsement by the National Marine Fisheries Service, NOAA. Views or opinions expressed or implied are those of the author and do not necessarily represent the position of the National Marine Fisheries Service.

food to support growth and/or gonad production. Enhancement efforts which do not address the stage which limits production are not likely to be successful; e.g. seeding of juveniles will do little for a population limited by survival of mid-sized animals or food supply. Furthermore, these factors are likely to vary on local and regional scales, e.g. the survival of mid-sized animals correlates negatively with the abundance of two warm temperate predators, spiny lobsters, *Panulirus interruptus*, and California sheephead, *Semicossyphus pulcher* (Tegner and Dayton, 1981; Tegner and Barry<sup>2</sup>). The northern range limit of these two predators is normally Point Conception, and both are characteristic of bottoms with considerable vertical relief; they will have little impact on red sea urchins north of southern California or in pavement habitats. Finally, enhancement methods will vary considerably in costs, in the length of time required to achieve results, and in how long the results will last.

#### Summary of the Life History of Red Sea Urchins

The biology of *S. franciscanus* has recently been reviewed by Kato and Schroeter (1985). Here I will summarize aspects of the life history relevant to factors potentially limiting the size of fishable stocks.

The timing and length of the spawning season of red sea urchins are highly variable among locations (Kato and Schroeter, 1985). Seasonality may be related to the patterns of food availability (Bernard, 1977); red sea urchins in the Point Loma kelp forest near San Diego, where food is generally abundant, are thought to spawn throughout the year although there is a winter peak. North of southern California, where food may be primarily available from mid spring to mid fall (Ault, 1985), the spawning season is

reported from late spring to early summer or even fall. The length of the planktonic larval phase is temperature dependent. Strathmann (1978) reported a range of 62–131 days for larvae cultured at ambient temperatures (generally 7°–13°C) in Friday Harbor, Wash., and Cameron and Schroeter (1980) found the earliest settlement at 40 days and the peak at 50 days after fertilization for larvae cultured at 12°C. Whatever the temperature, the length of the planktonic phase indicates that the distribution of the larvae is strongly affected by current patterns.

Current patterns, and thus the fate of sea urchin larvae, vary seasonally and with latitude. Parrish et al. (1981) divide the California Current System into four oceanographic regions on the basis of mean geostrophic flow, Ekman transport, and wind stress curl patterns. California falls into two of these regions, the region of maximum upwelling from Cape Blanco to Point Conception which includes the northwestern Channel Islands, and the Southern California Bight. The region of maximum upwelling is characterized by strong offshore surface transport during the spring and summer, whereas the Southern California Bight is an area of minimal upwelling and a closed gyral circulation (Parrish et al., 1981). These oceanographic patterns appear to have major implications for the transport of larvae. The Southern California Bight, the area of minimal upwelling, has the highest known rates of red sea urchin recruitment (to the population) throughout its range (Sloan et al., 1987). Ebert and Russell (1988) report reduced recruitment of intertidal purple sea urchins (*S. purpuratus*) on headlands, predictable sites of upwelling, compared with areas without predictable upwelling within the region of maximum upwelling. Roughgarden et al. (1988) found a negative correlation between a season's recruitment of barnacles, *Balanus glandula*, and the upwelling index at Pacific Grove. Tegner and Barry<sup>2</sup> analyzed red sea urchin recruitment patterns on the Channel Islands of southern California. Recruitment

was highest on the southeastern islands, those most affected by the Southern California Eddy, the closed gyral circulation of Parrish et al. (1981), which appears to aid in the retention of larvae, and was very low on the northwestern islands until the 1982–84 El Niño when upwelling rates were extraordinarily low. While little red sea urchin recruitment data is available from the region of maximum upwelling, it is reasonable to assume that stocks in central and northern California are more likely to be limited by larval supply than those in southern California.

The settlement requirements for red sea urchin larvae are poorly understood. Hinegardner (1969) reported that both red and purple sea urchin larvae settle on an algal and bacterial film. Cameron and Schroeter (1980) observed no substrate specificity among several filmed natural substrates and suggested that sea urchin larvae settle on any surface they encounter once they became competent to undergo metamorphosis. Rowley (1989) found that purple sea urchin larvae settle at significantly higher rates in response to crustose coralline algae and red algal turf than in response to filmed rocks, but was not able to demonstrate density differences among natural substrates for newly settled (<1 mm) red sea urchins. Thus, evidence to date suggests that suitable substrates for settlement are not likely to be limiting as long as excessive sedimentation or pollution are not an issue.

In contrast, the survival rates of newly settled to mid-sized animals do appear to limit the size of fishable stocks in some populations. While red sea urchin larvae do not settle in response to adults (Cameron and Schroeter, 1980), juvenile abundance is often highest underneath the test or spine canopies of conspecific adults (Fig. 2), especially where the substrate affords little cover or in the presence of certain predators (Tegner and Dayton, 1977; Sloan et al., 1987). Breen et al. (1985) have shown experimentally that the spine canopy association is a result of juvenile behavior;

<sup>2</sup>Tegner, M. J., and J. P. Barry. Size structure of red sea urchin (*Strongylocentrotus franciscanus*) populations in southern California; effects of growth, recruitment, predation, and oceanography. Manuscr., 61 p. A-001, Scripps Inst. Oceanogr., La Jolla, CA 92093.

juveniles chose shelter under adults over other protective locations. This association appears to be critical to the recruitment success of this species. Tegner and Dayton (1977) observed both significantly reduced settlement and survival of previously settled juveniles on experimentally fished (all animals >95 mm were removed) reefs in the Point Loma kelp forest near San Diego. The spine canopy association provides juveniles protection from predators such as spiny lobsters (Tegner and Levin, 1983) and the young feed on drift algae snared by the adults (Tegner and Dayton, 1977; Breen et al., 1985). Depending upon the size of the shelter provider and bottom topography, juveniles eventually become too large for the spine canopy association and must move away from adults. This size category (~ 25–30 mm) of red sea urchins is highly vulnerable to predation (Tegner and Levin, 1983) and Tegner and Barry<sup>2</sup> have shown that survival of second year (~ 36–60 mm) animals limits the size of fishable stocks on the southeastern Channel Islands. Red sea urchins appear to attain a partial refuge in size at about 90 mm from spiny lobsters and sheephead, their major predators in southern California (Tegner and Levin, 1983). However, red sea urchins of all sizes are susceptible to predation by sea otters, *Enhydra lutris*, the major predator in central California.

Finally, fishable stocks may be limited by the amount of food available to support growth and/or reproduction. The relationships between food availability, sea urchin behavior and physiology, and kelp forest community structure have been well studied in recent years (Lees, 1970; Pearse et al., 1970; Mattison et al., 1977; Dean et al., 1984; Ebeling et al., 1985; Harrold and Reed, 1985). In a healthy kelp forest, red sea urchins feed on the abundant algal drift produced by *Macrocystis pyrifera* and other laminarians. When food is plentiful, the animals remain in cryptic habitats and move little. When drift algae become limiting, whether from an increase in grazing pressure, or a decrease in drift

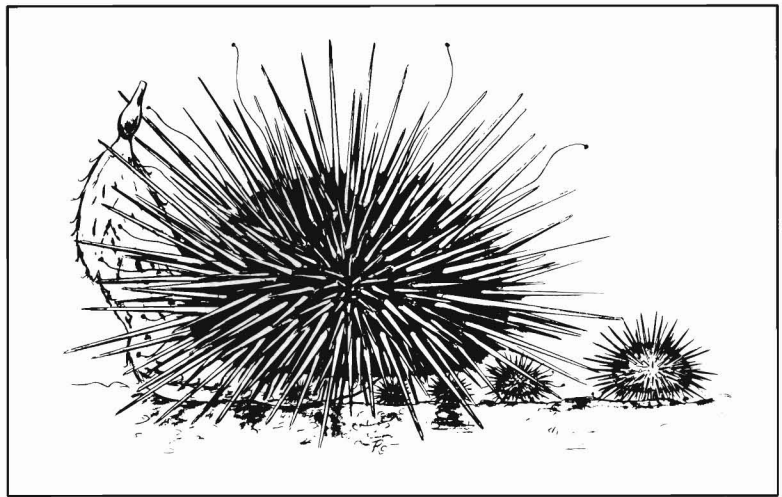


Figure 2.—Juvenile red sea urchins shelter under the spine canopies of conspecific adults and share in the food caught by the larger animal. As the recruits grow, they move toward the periphery of the spine canopy. (From Tegner and Dayton, 1977; copyright 1977 by AAAS.)

availability due to loss of algal standing stocks from such disturbances as storms or El Niños, urchins will leave their protective habitats and forage on attached plants. Moving sea urchins may denude large areas of kelps and, in extreme cases, grazing may eliminate and prevent the recovery of all algae except coralline algae. Sea urchins in barren grounds may persist, but gonad development is poor, and with time, the population may come to consist mainly of small individuals. In addition to their reproductive function, sea urchin gonads function as the main nutrient storage organ (Giese, 1966); as a result, starved sea urchins will resorb their gonads to stay alive (Holland et al., 1967). Starved sea urchins will not grow and they may even shrink in size (Ebert, 1967). Thus, the relative size of the gonad, or gonad index (ratio of gonad to total body volume or weight), is a commonly used estimate of urchin nutritional status (Pearse et al., 1970) which reflects both the quantity and quality of food available (Lees, 1970; Vadas, 1977; Larsen et al., 1980; Harrold and Reed, 1985). Gonad color, a factor in the salability of roe, is also dependent upon the type of food eaten (Mottet,

1976a).

Red sea urchins are highly selective in their choice of algal food and exhibit distinct species preferences. In southern California, Leighton (1966) found that *Macrocystis* was significantly preferred over other algae. Species of intermediate preference included *Gigartina armata (spinosa)*, *Laminaria farlowii*, *Eisenia arborea*, *Pterygophora californica*, and *Egregia laevigata*; least preferred was *Cystoseira osmundacea*. In the San Juan Islands of Washington, Vadas (1977) found *Nereocystis luetkeana* to be most preferred, followed by *Costaria costata* and *Laminaria saccharina*; two species of *Agarum* were actively avoided. Laboratory and field studies have shown that sea urchins eating their most preferred foods grow more rapidly, and have higher food and energy absorption, growth efficiency, and reproductive potential than animals feeding on less preferred foods. On the other hand, growth rates and gonad index of animals switched to a diet of their least preferred food drop significantly, apparently because so little algae is eaten. While sea urchin feeding in nature is a compromise between preference and availabil-

ity, preferential feeding appears to be a strategy designed to maximize growth and reproduction (Vadas, 1977; Larson et al., 1980).

### Enhancement of Fishable Stocks Limited by Larval Supply

#### Brood Stock Protection

Brood stock protection is one of the oldest fishery management approaches to maintaining adequate larval supply. In the early days of the red sea urchin harvest in California, fishermen focused on relatively few areas, typically those close to ports and international airports. Unfished areas continued to produce larvae. With the expansion of the fishery in the last few years, California can no longer count on unfished stocks to repopulate harvested areas. While red sea urchins become sexually mature between 40 and 50 mm (Bernard and Miller, 1973; Kato and Schroeter, 1985; Tegner and Barry<sup>2</sup>), small animals contribute few gametes for the next generation. A plot of gonad weight as a function of test diameter (Fig. 3) shows that the increase in gonad production is exponential with size; the largest animals contribute a disproportionately large share of gametes to the population. Thus, animals smaller than the legal minimum size of 76 mm are not capable of maintaining larval production at previous rates.

To ensure brood stock protection of their sea urchin populations, the Japanese have taken a threefold approach (Mottet, 1976a). There are minimum size regulations to allow reproduction and to ensure adequate product size. The actual spawning season is closed to fishing, ensuring that reproduction will take place and that sea urchins will not be harvested when the roe quality is poor. Finally, many small sites are designated as "no fishing" areas, an action which also protects recruits. Some sites, known as good recruitment areas from which young sea urchins migrate into fishing areas as adults, are permanently closed. Other sites are fished in 3-year cycles. Harvestable sea urchins are fished out in the first year of the cycle,

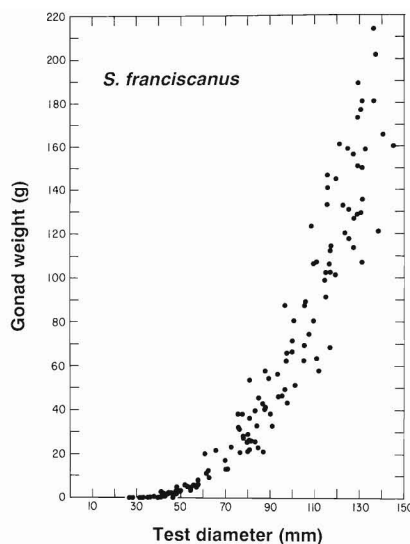


Figure 3.—Gonad weights of 138 *Strongylocentrotus franciscanus* collected from one location in the Point Loma kelp forest in December 1975. (From Tegner and Levin, 1983).

allowing luxuriant algal growth and presumably minimizing competition of juveniles with the adults for food while maximizing growth rates. These animals are taken at the beginning of the next 3-year cycle. Mottet (1976a) reports that the resulting high density of legal-sized sea urchins greatly increases the efficiency of harvesting.

Implications for red sea urchins: Assuming that the existing minimum size limit will not provide adequate larval production, what measures are potentially available under the category of brood stock protection? The State of Washington has both a minimum and a maximum size limit (Sloan, 1986), and Kato and Schroeter (1985) have suggested that this may also be useful in California. Furthermore, the roe of the largest sea urchins (>125 mm) has been reported to be of generally inferior quality<sup>3</sup>. The usefulness of a maximum size limit to provide some degree of brood stock and nursery (see the "Habitat Improve-

<sup>3</sup>R. M. Harbo. Personal commun. cited in Sloan (1986).

ment" section on p. 12) protection depends upon the number and density of sea urchins that have been left behind by the fishery. Significant densities are critical because fertilization efficiency declines rapidly over distances as small as 20 cm between spawners (Pennington, 1985), but where the numbers are adequate, this may be a simple and effective approach.

Because the actual period of spawning is highly variable in both time and space, this may be impractical to legislate but could potentially be controlled at the level of the processor. This approach works in Japan because of the high degree of local control over fisheries (Mottet, 1976a). The State of Washington has also adopted a simple system of rotating fishing closures; sea urchin grounds are divided into three zones, one of which is closed each year to foster repopulation (Kato and Schroeter, 1985). The Japanese approach of closing sea urchin recruitment habitats permanently would not work with *S. franciscanus* because of the spine canopy association; juveniles are abundant in the same habitat as adults (Tegner and Dayton, 1977).

#### Wild Seed Collection

When natural recruitment rates appeared to be the major factor limiting sea urchin population size, the Japanese began experimenting with a variety of collectors on which larvae would settle directly, thus presumably bypassing sources of mortality associated with settlement in their natural habitat. Some of the earliest collectors were apparently slate surfaces covered with tufts of nylon thread (300 denier thread at a density of 30 threads/cm<sup>2</sup>) (Mottet, 1981). Eight months after being placed in the sea, these collectors averaged 1,200 sea urchins of about 2 mm test diameter per m<sup>2</sup>. Long (80 mm) tufts were found to be less susceptible to overgrowth by fouling organisms than short (10 mm) tufts.

Biologists in Hokkaido, one of the three major sea urchin producing areas in Japan (Takagi, 1986), conducted extensive studies on the collection of wild seed of *S. intermedius*, their in-

intermediate culture, and release back into the natural habitat (Department of Mariculture, Hokkaido Central Fisheries Experimental Station, 1984; Kawamura, 1987). Previous efforts in sea urchin propagation in Hokkaido had included policies for resource control, transplantation, and creation of fishing grounds, but it was felt that further increase required large numbers of seed. After observing that sea urchins settled abundantly on scallop culturing facilities, a decade-long research project was initiated to pursue collection of wild seed. Extensive studies related the spawning period to the fall drop in water temperature, determined the distribution of larvae of various stages in time and space, investigated the direction and velocity of currents, and assessed annual variability in larval availability. They found that settlement was from December to January, and that by June, the density of young-of-the-year sea urchins in natural habitats on the coast was consistently below  $15/m^2$  but usually greater than  $100/m^2$  on a collecting apparatus. Furthermore, there was a sharp decrease in abundance (average mortality, 65 percent; range, 43–96 percent;  $n = 5$  years) in the natural habitat from spring to fall which is attributed to predation by crabs and seastars and, when temperatures exceed  $22^{\circ}$ – $23^{\circ}\text{C}$ , to thermal stress.

A large variety of materials and designs for collectors were field tested using different suspension systems and periods of installation in several locations. The most successful collector was constructed from transparent vinyl chloride plates with a corrugated surface called wave plates (Fig. 4). The transparent plates allowed algae to grow on both sides, increasing the surface available for settlement. Three square plates, 30 cm on a side, were suspended vertically in a layered configuration with the corrugations running horizontally. Arrays of this arrangement (Fig. 5) led to the adherence of an annual average of 197 sea urchins per collector (range 42–836;  $n = 9$  years) in January–February at one location in western Hokkaido. The numbers adhering were strongly

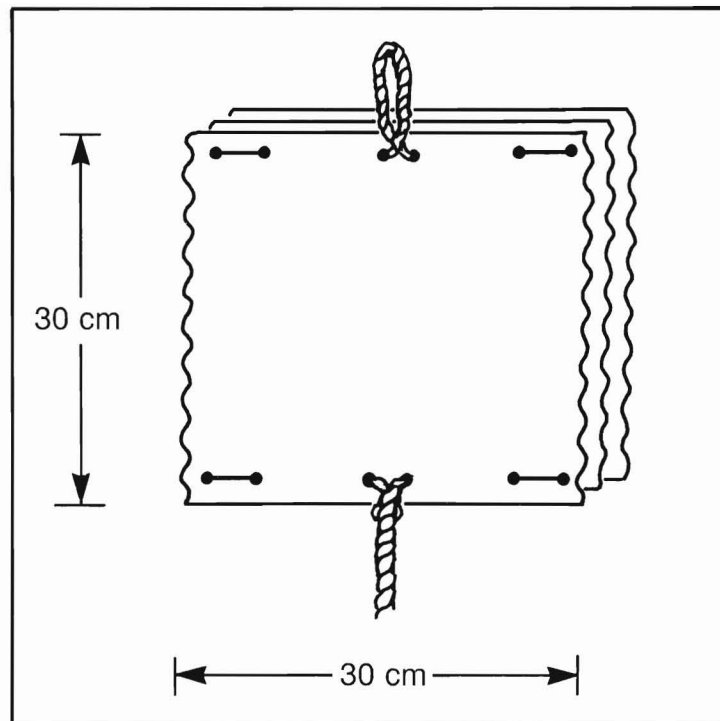


Figure 4.—Diagram of a collector used in Hokkaido for settlement of sea urchin larvae from the plankton. The corrugated (wave) plates are constructed of transparent vinyl chloride. Dimensions are in centimeters. Dep. Maricult., Hokkaido Central Fish. Exper. Sta., 1984)

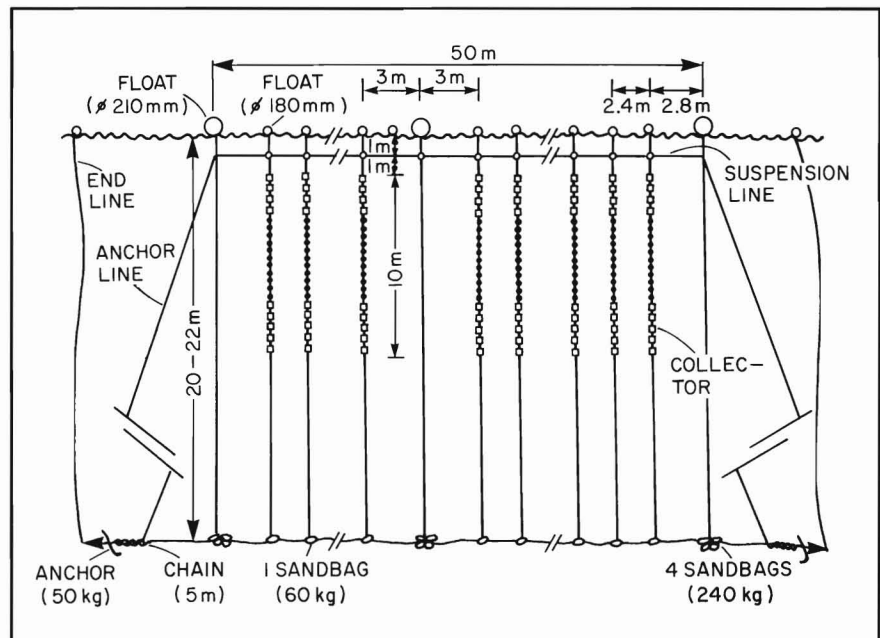


Figure 5.—Diagram of a fixed suspension sea urchin seed collecting facility. (Dep. Maricult., Hokkaido Central Fish. Exper. Sta., 1984).

affected by depth of the installation; 20–30 m bottom depths with the plates suspended at intermediate levels appeared to be optimal. The plates were most successful when installed 3 months before the settling season began.

By April–May of all years studied, the number of adhering sea urchins had decreased from earlier in the year; wave-induced oscillation of the collectors caused animals to drop off once they get to about 3 mm. The high predation rates on small animals during their first spring and summer in the natural habitat, combined with the drop-off problem from culture plates, necessitated going to intermediate culture to ensure good survival rates. Intermediate culture may be carried out in baskets in the sea or in tanks on land. Net baskets (80 × 80 × 40 cm), constructed of 1 or 2.8 mm mesh, were designed to hold 20 seed collectors. In late March, before the drop-off problem becomes serious but after the sea urchins are large enough to be retained by the mesh, the collectors are inserted into the baskets. By the time the seed get to 5 mm, the food adhering to the wave plates is gone, so the collectors are removed and algae is added to the baskets. With 5–6 months of feeding, it is possible to culture sea urchins to release size of about 15 mm by October. A single basket can accommodate 2,000 sea urchins for intermediate culture in the ocean and still allow good growth with survival rates up to 80–90 percent. In onshore culturing facilities, slightly smaller baskets were suspended in seawater-filled tanks with the incoming water sprinkled on top. This arrangement and a 3 mm mesh allowed adequate circulation to maintain water quality. The comparative advantages and disadvantages of offshore and onshore culture are detailed in Table 1. In some areas where algal food is not easily available during the summer, experiments have shown that juvenile sea urchins grow very well on leaves of a terrestrial plant called knotweed, *Polygonum sachaliense*.

The survival rate of seed settled on collectors varies with the size and time

Table 1.—A comparison of onshore vs. offshore intermediate culture of sea urchin seed (Department of Mariculture, Hokkaido Central Fisheries Experimental Station, 1984).

Item	Onshore	Offshore
Preservation of facilities	Easy	Susceptible to wave damage
Management of culture	Can be done intensively with a small staff	Intensive management is difficult
Capital costs	High	Low
Maintenance costs	High	Often low
Stability of the culture environment (e.g., water temperature and quality)	Apt to become unstable, but artificial control is possible	High stability, but artificial control is difficult
Seed health	If control is deficient, apt to become weak	Healthy in many cases

of release into the benthic habitat. If the seed are allowed to fall naturally from the collectors, or kept in intermediate culture until a size of about 5 mm (June), survival rate is less than 10 percent by fall. As with the wild seed, this summer decrease is attributed to predation. Survival was variable but much higher for seed kept in intermediate culture until fall. Averaging the results from three experiments where the seed were released at 15–20 mm test diameter, the survival rate was 60 percent 1 month after release, and in the three experiments, 24–75 percent at 1 year. Thus, this study established the technical basis for natural seed collection, intermediate culture, and release of *S. intermedius*. In the years 1980–82, a total of 4,068, 700 seed were collected and processed through intermediate culture, but the impact on fishery landings 2–2.5 years after release was not reported (Department of Mariculture, Hokkaido Central Fisheries Experimental Station, 1984).

Subsequent studies (Miyamoto et al., 1985) considered the characteristics of juvenile sea urchins obtained from collectors to minimize mortality during handling and after return to the natural environment. Small ( $3.2 \pm 0.5$  mm) but not larger ( $>7$  mm) animals grew on microflora. Experiments with predators showed that the smaller the sea urchin, the higher the predation rate. Sea urchins  $>10$  mm were not consumed by the local seastar, and few of the tested crabs consumed sea

urchins  $\geq 13$  mm. Finally, the tolerance to air exposure was determined to be temperature dependent, and brief (30–60 minute) exposures to low salinity seawater impaired the vitality of the seed as measured by the time required for animals to turn over.

Implications for red sea urchins: The experience of the Marine Biomass Project (North et al., 1981) suggests that California sea urchins will readily settle on artificial substrates. W. North<sup>4</sup> reports that thousands of red and purple sea urchins settled on a large (32 m diameter) structure designed to test the feasibility of growing *Macrocystis* in the open ocean. The "Test Farm" was deployed about 6 km off Corona del Mar, Calif., in about 550 m of water in September 1978. The arms supporting the kelp plants were at about 20 m depth but other structures of the farm extended to the surface. North reports that sea urchins settled, probably very soon after installation, all over the structure. Some were on I-beams which offered a ledge for support; many others settled on smooth, cylindrical structures. By August 1979, the sea urchins had grown enough to destroy juvenile *Macrocystis* colonizing the central buoy. There were more purple than red sea urchins, but North estimates that the abundance of *S. franciscanus* was probably adequate to warrant collections for stock enhance-

<sup>4</sup>W. North, Kerckhoff Marine Laboratory, 101 Dahlia Street, Corona del Mar, CA 92625. Personal commun., 1989.

ment. It may be possible to minimize the proportion of purple sea urchins settling by manipulating the depth of the collectors.

### Larval Releases

While the seeding of hatchery-reared abalones is practiced on a large scale in Japan (Kafuku and Ikenoue, 1983), experiments in California do not support this as a cost-effective approach to stock enhancement (Tegner and Butler, 1985, 1989). Problems include the high cost of seed cultured for about a year, high predation rates after seeding, and low recovery rates of live animals. Furthermore, hatchery-reared seed behave differently than wild abalones of the same size, apparently increasing their susceptibility to predation (Schiel and Welden, 1987; Tegner and Butler, 1989). In an effort to develop a more natural and less costly seeding technique, experiments tested the release of late stage, competent-to-settle larvae (Tong et al., 1987; Tegner et al.,<sup>5</sup>). Theoretically, this approach is appealing because of the very low production and release costs, and inappropriate behavior patterns should not be an issue. Larvae were released by waders into the shallow subtidal (Tong et al., 1987) or into kelp forests with appropriate rocky habitats by divers (Tegner et al.,<sup>5</sup>). Both studies demonstrated enhancement of existing populations at time periods ranging from 3 to 12 months after larval release, but the results should be considered preliminary until better success rates can be achieved.

### Seeding Hatchery-Reared Juveniles

Seeding is an attractive approach to stock enhancement for several reasons. In contrast with nature, 100 percent fertilization can be achieved and heavy larval losses to predation, starvation, and transport to inappropriate habitats are avoided. Mortality of highly vulnerable, newly settled individuals is also presumably greatly reduced by holding seed in the laboratory

for several months to a year. Furthermore, as seeding in theory reduces the fishing pressure on wild stocks, it may allow managers to avoid more painful restrictions on broodstock harvest.

### Experience with Other Benthic Marine Invertebrates

The earliest efforts to enhance fishable stocks of benthic marine invertebrates by the production and release of cultured juveniles apparently involved homarid lobsters. Van Olst et al. (1980) report that between 1885 and 1920, more than 22 lobster hatcheries were established in New England, the Maritime Provinces of Canada, and Europe. The method involved stripping eggs from gravid females and rearing the larval stages under presumably optimal conditions, i.e. the absence of predation, appropriate food the temperature, and disease treatment. However, it was eventually determined that the eggs were maintained and hatched more efficiently by the females than in culture. Furthermore, because of the problems of tagging lobsters, it was difficult to assess the results of the restocking programs, and the effort was reduced considerably. By 1980, there were only two hatcheries seeking to augment natural stocks by the release of hatchery-reared animals (Van Olst et al., 1980).

Nevertheless, lobsters remain an advantageous animal for culture (high value; tolerance to temperature, salinity, and water quality changes; large size of the larvae; acceptance of inexpensive, dead foods), and recent field studies suggest that survival after release is strongly related to habitat suitability. Howard (1982) proposed that rearing animals beyond metamorphosis followed by placement on substrata (whether natural rock beds or augmented with artificial structures) with an appropriate number and size of interstices would repay the expense of longer time in culture. A new set of studies is currently underway in Great Britain. The internally placed microtags developed for salmonids were adapted for use with juvenile (9–15

mm carapace length) *Homarus gammarus* (Wickins et al., 1986). Tag retention was 85–100 percent as the animals passed through up to 29 molts (90–102 mm carapace length) in captivity. Field releases of tagged individuals were conducted in 1983 and 1984; tag returns from the fishery are expected 5 years later (Walker, 1986). Scuba divers captured five individuals 1 year after release, suggesting that juveniles remain in the area and can survive in the wild. French scientists in Brittany are releasing hybrid American-European juvenile lobsters (which are easily distinguished from natives) in another attempt to determine whether hatchery-reared animals contribute to fishable stocks (Munro, 1982).

Seeding of hatchery-reared juvenile abalones to enhance fishable stocks, practiced on a large scale in Japan, has been reviewed by Grant (1981), Kafuku and Ikenoue (1983), and Uki (1984). After the loss of many abalone beds to overfishing, industrial and domestic pollution, or the loss of algal food, there was much incentive to enhance stocks of this valuable gastropod. Abalone aquaculture has been studied since the early 1960's and techniques for mass culture have been worked out. Advances in conditioning adults, spawning induction, controlling fertilization and larval settlement, and suitable food for the postlarvae have made culture very successful. By 1979, 42 culture centers using standardized techniques produced a total of 11,658,000 seed, almost all for release into the sea. However, despite this large-scale seeding effort, Kafuku and Ikenoue (1983) report that "the number released is too low to determine whether there is any effect on (the total national) catches." These authors document a slow decline in the national harvest from 1970 to 1979.

Published survival rates from abalone seeding experiments in Japan, reviewed by Saito (1984), range from less than 1 to 80 percent. As many studies found decreasing mortality with increasing seed size, fishing cooperatives generally rear the 20–30 mm seed received from the hatcheries

<sup>5</sup>M.J. Tegner, E.E. Ebert, and D.O. Parker, A-001, Scripps Institution of Oceanography, La Jolla, CA 92093. Unpubl. data.

in intermediate culture for an additional year (to a size of 40–60 mm) before release onto the fishing grounds (Uki, 1984). Various habitat improvement structures, such as baskets or cement bins filled with boulders or concrete blocks engraved with slits, are believed to enhance survivorship (see “Habitat Improvement” section, p. 12) and allow for planting at a smaller size. In Hokkaido, both wild-collected and hatchery-reared seed are used for enhancement. Saito (1984) reports recapture rates of 5–10 percent for hatchery seed and 20–25 percent for natural seed. Research continues into rearing methods, including hybridization and artificial diets for faster seed growth, and techniques for intermediate culture and release (Saito, 1984; Uki, 1984).

The enthusiasm for seeding in Japan and a steep decline in abalone landings led to a series of seeding studies by biologists from the University of California and the California Department of Fish and Game (reviewed by Tegner and Butler, 1989). Large-scale experiments were conducted with two species (*Haliotis rufescens* and *H. fulgens*) on both island and mainland sites. In each case, the estimated 1- or 2-year survival rate was 2.8 percent or less, unacceptably low for species that require 10–15 years to enter the commercial fishery. Seed sizes ranged from 10 to 80 mm but there was no evidence that survivorship increased with seed size. Estimations of survival rates were based on censuses of planting sites and their immediate surroundings; they do not take into account possible larger scale migrations because of the problems of sampling rare, cryptic abalones. Shell recoveries suggested that mortality related to the stresses of the seeding process was not the major cause of the poor survival; in one closely monitored experiment, half of the shells recovered exhibited growth up to 40 mm before death (Tegner and Butler, 1985). Laboratory studies found differences in behavior and habitat selection between hatchery-reared abalones and natives of the same size classes. These behavioral

differences may be responsible for the poor survival of outplants; significantly more cultured than native animals were consumed when predators were added to the laboratory studies (Schiel and Welden, 1987; Tegner and Butler, 1989).

Ebert and Ebert (1988) recently designed an abalone seeding module which acts as a temporary shelter, allowing for acclimation to the natural environment before the seed are released. This approach also has the advantage of greatly reducing the effort required to plant seed, although the results of a predator encounter of such a dense concentration of prey could negate this. The long term effects on seed survival are not known.

Seeding studies have also been conducted with a variety of bivalves, notably clams and oysters. Commercial-scale culture techniques have been developed for important species, but economics dictate that juveniles must be outplanted for growth to market size, and adequate survival is a major problem (McHugh, 1981; Castagna, 1983). High mortality has been repeatedly observed within a very short time for seed clams planted without protection from predators, e.g., Craig et al. (1988) report 100 percent mortality within 6 months of *Mercenaria mercenaria* planted in unprotected trays, whereas survival was high in trays protected with gravel and a mesh covering. Techniques to increase clam seed survival include larger seed size, smaller mesh size, baffles to minimize wave disturbance, predator fences, crab traps, and poisoned bait for predators; combinations of various protective devices are more effective than any device alone (Kraeuter and Castagna, 1985a, b). Similar results have been reported for giant clams in the tropics: Small (10–20 mm) seed placed in unprotected trays on reefs rapidly suffer 100 percent mortality from predation, but survival rates were reasonable in sea floor cages (Munro, 1989). Finally, scallops and oysters have been successfully grown in trays, rafts, or nets in the water column, or in protected plots on the bottom (Castagna, 1983).

The queen conch, *Strombus gigas*, has been harvested since prehistoric times in the Caribbean and remains the area’s second most valuable fishery (Berg and Olsen, 1989; Hahn, 1989a). However, the fishery is in serious danger of overharvest and has been placed in the IUCN Invertebrate Red Data Book as a “commercially threatened” species. The seeding of hatchery-reared juveniles was proposed in 1976 as a means to rehabilitate depleted stocks, and the appropriate technology has been developing ever since. While culture of larvae (from wild-collected egg cases) and juvenile growout are feasible, mortality after seeding is very high, sometimes 100 percent. After a series of experiments, Appeldoorn and Ballantine (1983) estimated that only 0.1 percent of seeded 6-month-old juveniles (~ 60 mm) would survive to enter the fishery at an age of 2.5 years. Susceptibility to predation apparently decreases with increasing seed size (Iverson et al., 1986), but seeding with large animals is not economically feasible. Appeldoorn and Ballantine (1983) conclude that seeding of unprotected small conchs does not appear to be a practical way to support a fishery and urge strong fishery management measures to restore the stocks. Once strong management measures are in place, it may be possible to use seeding to build up brood stocks in depleted areas.

The top shell, *Trochus niloticus*, is the most economically important gastropod in the tropical Pacific (Nash, 1988; Hahn, 1989b). The meat is eaten and the shell is exported for the production of mother-of-pearl buttons. Sedentary in habit and found in easily accessible locations, top shell has been overfished virtually everywhere there is a commercial fishery. *Trochus niloticus* is an excellent species for culture because of its year-round spawning which is spontaneous on a lunar cycle, lecithotropic eggs, the short (3–4 day) pelagic period of the larvae, and feeding by juveniles and adults on the algae which grow naturally in outdoor tanks.

The only reported top shell seeding



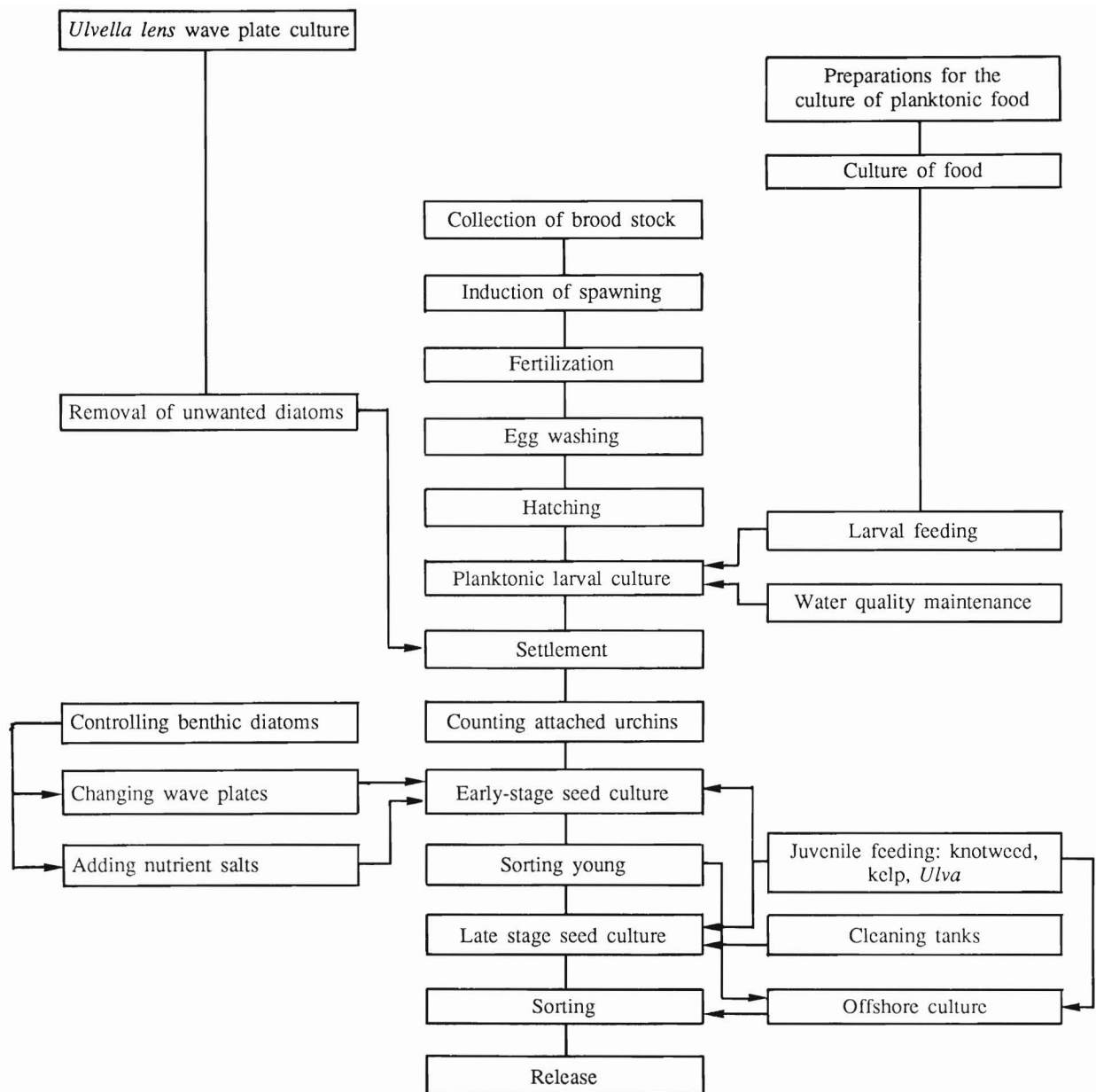


Figure 6.—Steps in the laboratory culture of *Strongylocentrotus intermedius* seed as practiced by the Hokkaido Institute of Mariculture (Saito et al., 1985; Saito, 1987).

experiment was conducted in Palau. In this test, almost total mortality was observed within a couple of days of outplanting; only crushed shell remnants were found<sup>6</sup>. Hahn (1989b) stresses that studies of sources of mor-

<sup>6</sup>G. Heslinga. Personal commun. cited in Nash (1988).

tality, microhabitat use, and movement of juvenile top shell should be carried out before large-scale seeding experiments are conducted. Similarly, Nash (1988) suggests that stock enhancement through seeding of hatchery-reared *Trochus* may only be successful if areas of low juvenile mortality are identified.

#### Sea Urchin Seeding in Japan

Artificial culture of sea urchins began in Yamaguchi Prefecture in 1968, and Japan produced a total of about 3.5 million cultured seed in 1984. Techniques used to rear *S. intermedius* at the Hokkaido Institute of Mariculture (Fig. 6) have been de-

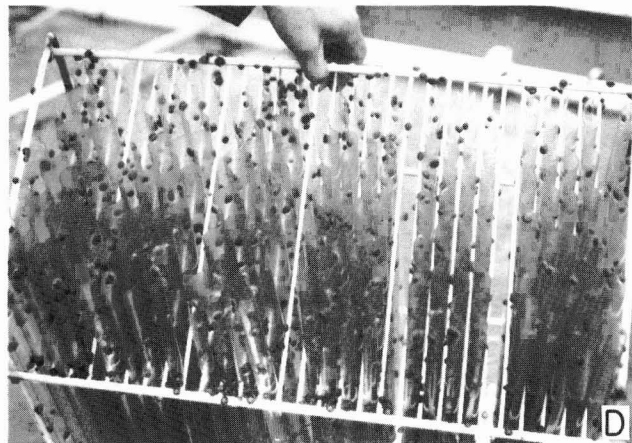
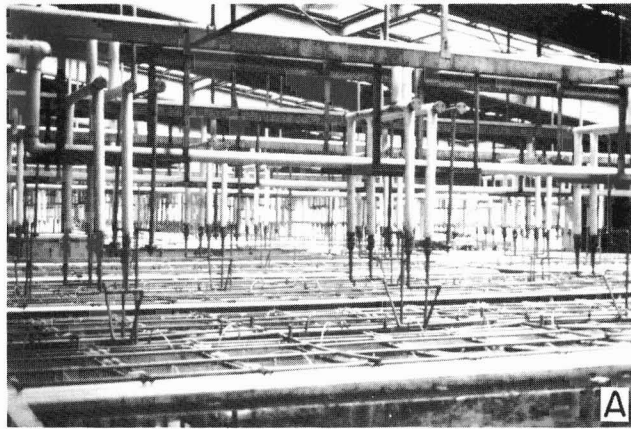


Figure 7.—Hokkaido Institute of Mariculture abalone hatchery in Shikabe to be converted into a sea urchin hatchery. A and B, tanks containing racks of wave plates; C and D, closeups of wave plates covered with juvenile sea urchins. Photographs taken by Christopher Toole, 1987.

tailed (Saito et al., 1985; Saito, 1987). Many of the techniques appear to have been adapted from abalone culture; in fact, the Institute is converting an abalone hatchery at Shikabe, Hokkaido, to a sea urchin hatchery<sup>7</sup>. Toole<sup>7</sup> visited this laboratory in the spring of 1987 and reports that the sea urchin hatchery is slated to produce 5 million 5 mm seed a year.

Briefly, procedures followed in Hokkaido (Fig. 6; Saito et al., 1985; Saito, 1987) allow females to spawn naturally, releasing eggs into a round 10 L tank. Sperm collected from several males is mixed and used for fertilization. The zygotes are washed at least five times at 30-minute intervals

<sup>7</sup>C. Toole, Sea Grant Marine Advisory Program, Eureka, CA 95501. Personal commun., 1988.

and the fertilization rate assessed. The tanks are then left undisturbed until the larvae hatch at about 20 hours after fertilization. Larvae are transferred to 600 L larval culture tanks at 3 days and feeding is begun. The suitable temperature range is 15°–21°C. For larvae cultured at 18°C and fed a diet of *Chaetoceros gracilis*, metamorphosis and settlement begin on the 16th day after transfer to the larval tanks. Wave plates which have been covered with a culture of *Ulvella lens*, a species of disk-shaped Chlorophyta, are installed in 5 m tanks to act as settlement substrates, and the water and swimming larvae are transferred (Fig. 7). Settlement of 70–80 percent of the larvae occurs within 3–4 hours, and the water can be exchanged within 24 hours. Toole<sup>7</sup> reports about 60 percent sur-

vival to metamorphosis. Seed up to a test diameter of 3–4 mm consume benthic diatoms on the wave plates. Once that size is attained, soft seaweed fronds (e.g., *Ulva*) are placed on top of the wave plates for food (Saito et al., 1985; Saito, 1987).

When the cultured seed reach a size of about 5 mm, they are placed into small mesh cages for intermediate culture in tanks on land or suspended in the sea, as is done with seed settled on collectors. Kelp or knotweed is provided as food. It is desirable to adjust sea urchin density and cage mesh size as the seed grow. Release size is 15 mm or larger. With fertilization in September–October and intermediate culture offshore, sea urchins reach release size the following autumn. In shore-based facilities where the water

is heated during the winter, the seed are large enough to be released in 5 months (Saito et al., 1985; Saito, 1987). Fishermen broadcast the seed over the fishing ground from the surface<sup>7</sup>.

Omi (1987) reported the results of seeding experiments using cultured *S. intermedius* in Hokkaido. In each of two tests, 40,000 seed were released into areas measuring 20 × 50 m in water depths of 3 m. Seed were spread uniformly over release sites by divers and from boats. Survival rates were assessed by divers with m<sup>2</sup> sampling frames. Released sea urchins were generally distinguished from natives by test diameter. The survival rate after 622 days for the 1983 release group was 38.7 percent, and 92 percent of these had achieved the minimum legal size of 40 mm. For the 1984 group, the survival rate after 597 days was 22.6 percent, and 91 percent were of fishable size. Other studies showed variation in survival rates between 10 and 40 percent, as well as in growth rates, in different areas. The seed spawning season was the same as that of the parent stock, which varies among different areas of Hokkaido, regardless of where they were planted. Agatsuma and Momma (1988) compared the growth of cultured and native seed. They found that the introduced seed grew faster than the native seed during the first 14 months, but that the cultured seed growth rate decreased thereafter and was lower than that of the native stock after 3 years.

Omi (1987) estimated the economic benefits of sea urchin seeding in a 10,000 m<sup>2</sup> area at a site which supported excellent growth and survival rates. Income was calculated as the number of seed surviving (40 percent) times the catch rate times the gonad weight times the unit price:

$$1,797,120 \text{ Yen} = 16,000 \text{ seed} \times 0.9 \times 7.8 \text{ g/urchin} \times 16 \text{ Yen/g.}$$

Expenditures were calculated as the cost of the seed (produced by the Hokkaido Institute of Mariculture) plus labor costs for the release operations plus transport costs of the seed:

$$1,040,000 \text{ Yen} = 40,000 \text{ urchins} \times 25 \text{ Yen} + 20,000 \text{ Yen} + 20,000 \text{ Yen}$$

Profit was calculated as income minus expenditures divided by the number of fishing seasons:

$$378,560 \text{ Yen} = (1,797,120 \text{ Yen} - 1,040,000 \text{ Yen}) \div 2$$

This estimate suggests a 36 percent return on investment. If the sea urchins are allowed to grow for another year (assuming no further decline in numbers between years 2 and 3), the average gonad weight per sea urchin rises to 12 g, and the profit rises to 574,933 Yen for the same expenditures. Omi (1987) does not appear to have accounted for the capital investment in the hatchery in these calculations.

Studies of *Pseudocentrotus depressus* in Yamaguchi Prefecture indicate that sea urchin seed survival is better on gravel beds (65–76 percent) than on rocky substrates (38 percent), even though food is much more (3–6 times) available on the rocky substrate (Takagi, 1986). Hybrids of *P. depressus* with *Hemicentrotus pulcherrimus* developed larger gonads with better color than *H. pulcherrimus*, the favored species.

#### *Culture of Strongylocentrotus franciscanus in California*

The importance of sea urchins as experimental animals for cell biology has led to extensive studies of their larval development and culture. Hinegardner (1969) developed the basic methodology for culture of west coast species on a laboratory scale, and various refinements have been published (Hinegardner, 1975; Hinegardner and Rocha Tuzzi, 1981; Leahy, 1986). Leahy et al. (1978, 1981) described a laboratory system for long-term maintenance of gravid sea urchins and discovered that ripe animals could be found in the wild throughout the year by collecting from deep-water populations with good food supplies. Because of their importance to cell biologists, much of the focus has been on *S. purpuratus* and the white sea urchin, *Lytechinus pictus*, but with minor

modifications, the same procedures work with *S. franciscanus* (Hinegardner and Rocha Tuzzi, 1981). Thus, culture on a small scale is both feasible and practiced. It may be possible to further reduce the larval period by culture at higher temperature. The key to production on the scale necessary for seeding, however, will be the successful adaptation of mass culture techniques such as those used for abalones and sea urchins in Japan (McCormick and Hahn, 1983; Saito et al., 1985).

McCormick and Hahn (1983) studied abalone aquaculture at prefectural fish farming centers in Japan and estimated what it would cost to establish a Japanese-style abalone hatchery in California capable of producing 20 million juvenile (20 mm) abalones annually. Conversion of a Hokkaido hatchery from abalones to sea urchins clearly indicates that the two groups require similar facilities and treatment; the major differences are that sea urchin larvae are planktonic for a longer period of time and require feeding. Thus, cost estimates for setting up an abalone hatchery are an appropriate base for sea urchins; phytoplankton culturing capabilities and extra tanks for larval rearing would be additional.

McCormick and Hahn (1983) estimated capital costs for land (1 hectare, central California coast), buildings, tanks, culture plates, plate racks, filters, two vehicles, emergency generator, water pumps, plumbing, air pumps, water heater, UV sterilizer, brood stock, and cleaning equipment at \$576,200. Operational costs including wages, utilities, vehicle upkeep, feed, telephone, filter upkeep, and generator upkeep were estimated to be \$205,100 a year. Summing these two with startup salaries and debt service, the funding required to produce the first 1 million abalones would be \$1,155,857 (McCormick and Hahn, 1983). This estimate does not include additional expenses such as financial and legal services, operating permits, taxes, depreciation, or replacement costs. Given the huge increases in the price of coastal land, inflationary increases on goods and salaries since 1983, and the extra costs involved

with culturing sea urchins, the costs of establishing a sea urchin hatchery of similar size in 1989 may be several hundred thousand dollars more.

### Enhancement of Fishable Stocks Limited by Survival of Newly Settled to Intermediate-sized Animals

#### Habitat Improvement

Mottet (1976a, b, 1981) has reviewed the extensive efforts of the Japanese to enhance sea urchin stocks through habitat improvements. The use of rocks to improve the substrate for sea urchins dates to 1912 in Fukui Prefecture and has spread through much of the country. In areas of flat substrate, the addition of rocks may increase the yield of many marine species, especially kelp and sea urchins, by providing algal attachment sites, shelter for the sea urchins, and aid in drift entrapment. This is accomplished either by importing rocks or reef blasting. Generally rocks of 40–50 kg are placed in a layer 1–2 rocks deep with plenty of space between rocks. It was estimated that it takes 50 rocks weighing 40–50 kg each to increase the yield of gonads by 1 kg. At this rate, it took about 3 years for the operation to pay for itself (Mottet, 1976b).

Historically, Japanese habitat improvement projects were funded by fisheries cooperatives and local governments (Mottet, 1981). The national government began providing funding in the 1930's, and the level was greatly intensified in the mid 1970's. With the national government paying for 50–70 percent of the costs of selected projects, habitat improvement efforts became much more complex and capital intensive.

Habitat improvement projects spread to soft substrates (Mottet, 1981). In the simplest procedure, rocks are piled to a height of 0.4–0.6 m to provide habitat for kelp and sea urchins. In areas of high water movement where the rocks would not be stable, they may be piled in enclosures. The most common structure is a "futon" (mattress) cage measuring 4 m long by 1.2 m wide by 0.4–0.6 m

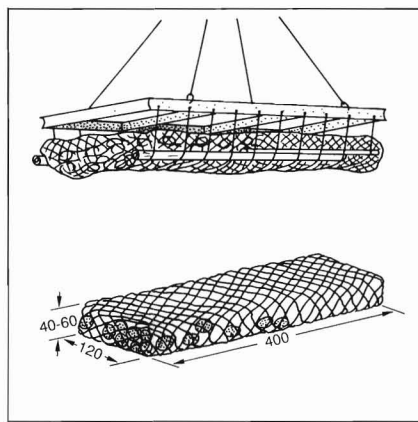


Figure 8.—Futon cages, or mesh bags of rocks of 20–50 cm diameter, are used to create sea urchin habitat in areas of soft sediments. As these cages weigh 2.9–4.4 t, a crane and a sling supported by a steel frame and logs are used to place the cages into position. Dimensions are in centimeters (Mottet, 1981).

high, and made of synthetic fiber net or coated mesh steel (Fig. 8). These are placed by cranes into areas where strong currents ensure circulation through the rocks. Sometimes the cages are set on mats to prevent them from sinking into the sediments. As of 1981, futon cages were the most widely used sea urchin enhancement device, particularly in northern Japan where they were being placed by the thousands in many locations. Mottet (1981) cites one example where 10,000 futon cages were installed in a 27-hectare area in Hokkaido. Other kinds of rock cages, ranging from bamboo baskets to steel or concrete cribs, are also employed.

Mottet (1981) also described a variety of additional techniques which, alone or in combination with other habitat improvement methods, are designed to enhance fishable stocks of grazers. Large concrete "substrate" blocks provide horizontal surfaces for the seaweed attachment and crevice spaces suitable for sea urchins and abalones. As these are often used in areas with strong water motion, they may weigh a ton or more but are no higher than 1 m. Large, concrete

breakwater blocks, designed to dissipate wave action, are good for trapping drift or containing rock piles. If high water movement leads to problems with kelp abrasion on the rock piles or substrate blocks, elevated frames may be installed as supports for stiff, plastic mesh pipe seeded with algae. The fastest way to increase kelp biomass is longline culture of *Laminaria*. Typically such lines are 45–50 m long and buoyed above the bottom; usually a number of lines are employed and spaced 3–8 m apart. A 50 m longline can produce nearly 1.5 t of harvestable kelp in one season, while providing drift food for grazers and seeding nearby reefs. Many large-scale development projects are designed to maximize both kelp and sea urchin production, e.g., sea urchin habitats may be located in such a way that drift entrapment is efficient but sand buffer zones protect benthic kelps from direct grazing.

Finally, one project from Iwate Prefecture suggests perhaps the ultimate in habitat improvement efforts (Mottet, 1981; Noma, 1983). In Japan, many edible seaweeds and grazers do not grow well above the mean spring low tide levels because of dessication in the summer and freezing in winter, but these same species prosper in natural channels which cross rocky benches. In this project, a total of 92 channels (~ 100 m long × 4 m wide × 0.6 m deep) were dug into rocky intertidal platforms at 8 sites along 5 km of coastline. The channels were designed in such a way that waves passing into the entrances are funneled up and over sills which then act as one way valves. Thus wave energy moves the water shoreward until it reaches an excurrent drainage channel slightly deeper than the culture channels, and water circulation is ensured. The design achieved a water flow velocity of 0.15 m/second with waves of 0.2 m height (Noma, 1983). Substrate blocks were added to the culture channels to maximize the surface available for kelp attachment and provide suitable habitat for grazers. Ten of these channels, with a combined length of 1,200 m, were completed in 1975 at a cost

\$326,087. The average annual harvest of kelp, abalones, and sea urchins combined in the initial results was worth \$37,097, suggesting a pay-back period of about 9 years. These observations suggested that the most profitable return would be from the combined culture of kelp and sea urchins. *Laminaria* seeded into the channels in December had grown enough to provide a good source of sea urchin food by May. Sea urchins were collected from areas of inadequate food supply and transplanted into the channels; in a few months of fattening, the gonads increased from less than 7 percent to 25 percent of the total body weight. The relative value of these two commodities and an experiment varying sea urchin numbers were used to determine optimal stocking densities; an intermediate level of sea urchins allowed maximal gonad development of two crops of sea urchins each year with an annual profit of \$5,217 per channel (Mottet, 1981). Noma (1983) compared the productivity of the rocky bench before and after the channels were built; profit in 1980 was 258 percent of the 4-year average before construction.

#### Protection of Juveniles by the Red Sea Urchin Spine Canopy Association

Two papers (Breen et al., 1985; Sloan et al., 1987) have recently explored the biology of the *S. franciscanus* spine canopy association in British Columbia, where the minimum size limit for red sea urchins is 100 mm. Field data showed that the innermost, under-the-test juveniles were significantly smaller than more distal but still under-the-spine-canopy young, and that juveniles not underneath adults, whether clustering nearby or not associated with an adult, were significantly larger than juveniles under the spine canopy. This size-related distribution pattern of young animals suggests that the smaller size limit in California has important implications for the survival of recruits.

To look at the role of different sized adults as shelter providers, individual "associations" were sampled by col-

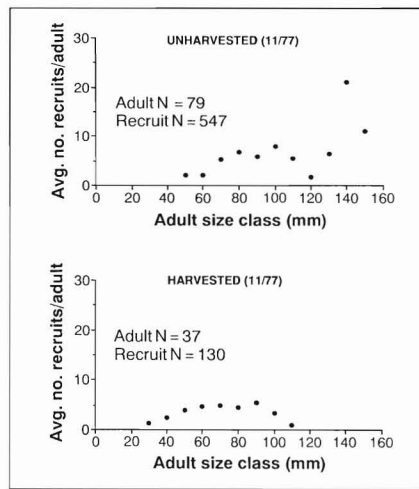


Figure 9.—Average number of recruits per adult versus adult size class in spine canopy associations of *Strongylocentrotus franciscanus* populations on Santa Barbara Island, Nov. 1977.

lecting adults and any associated juveniles and placing each association in a separate bag. Data were collected on Santa Barbara Island, a site of consistently good red sea urchin recruitment<sup>2</sup>, in 1977 and 1978. In 1977 the associations in an area where the size-frequency distribution indicated recent fishing were compared with a nearby site where the abundance of larger animals suggested that the site had not been harvested for some time, if at all. At that time the fishery was generally taking animals larger than 90 mm. At the unharvested site, there was a significant increase in the average number of juveniles sheltered with increasing adult test diameter ( $r^2 = 0.398$ ,  $P = 0.037$ ). There was no such trend at the harvested site where juveniles were found under shelter providers as small as 30 mm, 20 mm smaller than in the unharvested area (Fig. 9).

Despite the sites being only about 200 m apart, the average number of recruits per adult in the harvested area was only about half that in the unharvested area, 3.5 vs. 6.9. The average size of juveniles under adults in the

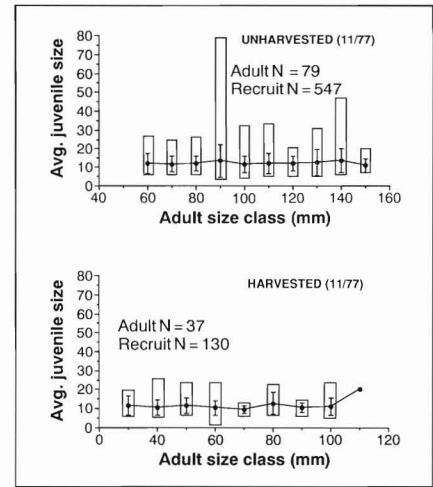


Figure 10.—Average juvenile red sea urchin size vs. adult size class in spine canopy associations of *Strongylocentrotus franciscanus* populations on Santa Barbara Island, Nov. 1977. The error bars represent  $\pm$  one standard deviation and the boxes indicate the range of the data.

unharvested area was 12.20 mm and 10.98 mm in the harvested site; while small, this difference was significant (t test,  $P = 0.005$ ). There was no increase in average size of juveniles with increasing adult size, probably because most of the juveniles resulted from a single settlement episode (Fig. 10). In the unharvested site, 74 percent of the recruits were found under shelter providers 90 mm and larger (Fig. 11). For the harvested population, 29 percent of the juveniles were under animals 90 mm and larger, and 62 percent were under shelter providers 60 mm and larger. Thus, faced with few large sea urchins under which to shelter, juveniles were associating with smaller shelter providers with correspondingly smaller spine canopies and therefore less protection from predators. In addition to there being less space under small spine canopies, red sea urchins smaller than 90 mm have not yet reached the size offering a partial refuge from predation (Tegner and Levin, 1983). This suggests that the associations based on shelter providers less than 90 mm have a lower

probability of survival regardless of fishing.

Samples from the same area of Santa Barbara Island collected in May 1978 contained adults up to 128 mm (data not shown). The average number of juveniles per shelter provider was 5.0 and there was a positive relationship between the size of the adult and the number of recruits sheltered ( $r^2 = 0.867$ ,  $P = 0.0001$ ). Again there was no increase in the average size of juveniles with increasing adult size. Fully 84 percent of the sheltered individuals were under adults of fishable size. Sheephead are attracted to divers and frequently feed on juveniles exposed upon removal of the adults. In a series of adult removal trials on San Clemente Island, some recruits were rapidly eaten while others managed to crawl out of sight to safety. The fate of juvenile sea urchins exposed by fishing depends in part on how much cover, e.g., other shelter-providing urchins, substrate rugosity, or foliose algae, is available (Tegner and Dayton, 1981).

A number of smaller data sets collected in the late 1970's were examined for the relationship between the average number of sheltered recruits and adult size class. Tegner and Barry<sup>2</sup> lumped samples from San Clemente Island and from Santa Rosa and San Miguel Islands to consider the effects of two different population structures on juvenile sheltering. The relationship seems most likely to be positive when the average number of recruits per adult is high. This degree of variability is not surprising given the gregarious behavior of juveniles (Breen et al., 1985) and variability in recruitment rates and habitat structure.

However variable, the relationship seems sufficiently compelling that these observations should be repeated, especially in southern California where predation pressure is higher, to determine the effects of a decade of intense fishing pressure. Ideally, recruitment and spine canopy associations should be assessed in both fished and nearby areas closed to fishing to evaluate the relative effects of brood stock reduction and loss of large spine

canopies. If, as suggested by the results of Tegner and Dayton (1977), survival of recruits is depressed in fished areas, provisions should be made to leave some portion of fishable animals behind to ensure future re-growth of stocks. It is likely that a maximum size limit of 125 mm is not appropriate in southern California; there are simply too few animals that large left. Size-frequency data suggest that this may be a more useful approach in northern California<sup>8</sup>, however. If there are too few animals 125 mm or larger to provide spine canopy shelters, alternatives are to institute a smaller maximum size limit, or to require fishermen to leave some minimum density of animals behind, a much more difficult regulation to enforce.

#### Enhancement of Fishable Stocks Limited by Food Availability

#### Transplantation to Areas of Better Food Supplies

Mottet (1976a, b) reviewed the efforts of Japanese fishing cooperatives to increase gonad development by transplanting sea urchins from areas of high density but poor food supply to areas with rich seaweed populations. Although the animals may be out of the water for 24–26 hours, there is only a 1–2 percent mortality rate associated with transfer. Transplantation is generally done just before the sea urchins begin the period of rapid gonad growth. In Hokkaido, if food conditions are good in the fall, sea urchins can be transplanted then for harvest in the spring. Sea urchins transplanted in the spring are ready for harvest about July. Transplanted animals exhibit gonad weights which are 4–5 times those of nontransplanted controls and similar to the yields of animals originating in the high food areas. A second objective of transplanting is to move sea urchins to high food areas which are also workable during winter periods of bad weather and high sea

<sup>8</sup>P. Kalvass, Calif. Dep. Fish Game, 19160 S. Harbor Drive, Fort Bragg, CA 95437. Personal commun., 1989.

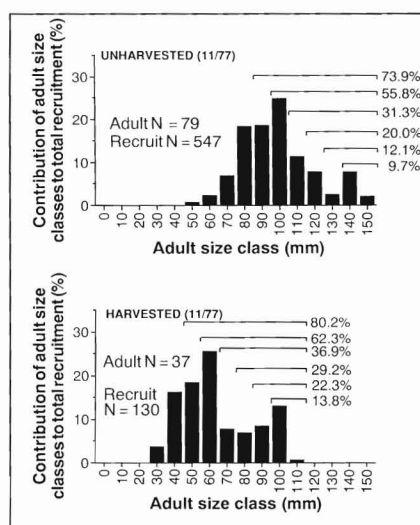


Figure 11.—Contribution in percent of each adult size class to the total sheltering of recruits in spine canopy associations of *Strongylocentrotus franciscanus* populations on Santa Barbara Island, Nov. 1977. The cumulative percent beginning with the largest adults is indicated.

urchin prices. The economic return of this method of enhancing fishable stocks is suggested by the magnitude of the operation; in some localities, up to 20 t of sea urchins had been transplanted by 1969 to improve gonad yield. Takagi (1986) reports cases where the fishery may depend exclusively on annual transplants.

Implications for *S. franciscanus*. While food-limited animals can be found in many areas, large red sea urchins are subject to coelomic collapse if they are out of the water for more than a few minutes. Once air gets into the coelom, survival is uncertain. Kelco<sup>9</sup> has found it possible to minimize transport mortality by hanging sea urchins to be moved below the surface in large mesh bags until it is time to actually move the boat.

#### Reforestation of Areas with Poor Food Supplies

As in California, some rocky bot-

<sup>9</sup>M. Otjens, Kelco, P.O. Box 13216, San Diego, CA 92113. Personal commun., 1989.

tom areas on the northeastern coast of Honshu, the largest island in Japan, are often observed to be nearly devoid of large, foliose plants; encrusting coralline algae cover the bottom<sup>10</sup>. These barren grounds, or isoyake in Japanese, are often characterized by unfishable (small and/or starving) populations of sea urchins and abalones which prevent the regeneration of kelp populations. A 5-year experiment demonstrated that it is possible to re-establish a kelp forest and productive fishery without killing the grazers. The experiment was conducted in a 3-hectare V-shaped bay on Enoshima Island which contained dense populations of urchins (*S. nudus*) and abalones (*H. discus hannai*). To provide food for the grazers, *Laminaria japonica* was cultured on longlines arranged in a grid with 2–3 m spacing and buoyed off the bottom. This proven methodology had already been worked out for the production of edible seaweed. In 1972, longlines totaling 3,825 m produced 33.3 t of kelp, and in 1973, 4,200 m produced 41.5 t. As a result of the increased availability of algal drift, the sea urchin gonads were well developed and the annual increase in abalone body weight was 4 times that of animals in control areas without supplemental feeding. In 1973, over 3.4 t of sea urchins and 3.2 t of abalones were harvested. The reduction in herbivore numbers and the release of spores by the cultured *Laminaria* led to a large natural bloom of algae in the spring of 1974. It was estimated that the standing crop of suitable food for the sea urchins and abalones was more than 100 t, eliminating the need for further longline culture. Kito et al.<sup>10</sup> believed that this amount of seaweed was enough for a gross annual production of 6.6 t of urchins and 3.1 t of abalones.

Implications for California: Kelp culture to improve fishable stocks of red sea urchins is certainly a possibility in California, but several factors

<sup>10</sup>Kito, H., S. Kikuchi, and N. Uki. Seaweed as nutrition for marine life: Technology for artificial marine forests. Pap. pres. at Int. Symp. Coastal Mar. Life, Western Wash. Univ., Oct. 1979, p 55–66.

must be considered. First, the experiment at Enoshima Island described above (and much of the longline mariculture in Japan) was conducted in a relatively protected bay. Most of the California coast is much more exposed. Second, the kelp farming industry, still in its infancy in California, is primarily involved with research and development, suggesting that commercial longline production may be prohibitively expensive. A private company in Goleta has studied *Macrocystis* test farms (Neushul and Harger, 1985), and is currently operating longline farms for a study of marine farm engineering that deals with storm resistance. Neushul<sup>11</sup> estimated that it would cost about \$600 to produce a 50-foot (15.2 m) longline seeded with macroalgae. This estimate does not include the cost of the line, floats, shackles, anchors, or shipping. In Japan, longline cultures are produced by the fishing cooperatives.

#### The Problem of Competition

Widespread areas within southern California are reported to have undergone large increases in the number of purple sea urchins in recent years, and these animals can also cause overgrazing. There are several, nonexclusive, potential explanations for this apparent increase. First, red and purple sea urchins have similar food (Leighton, 1966; Vadas, 1977) and habitat (Schroeter, 1978) preferences. Schroeter (1978) reported that red sea urchins exclude the shorter-spined purple sea urchins from the most desirable habitats by spine fencing. The harvesting of thousands of tons of *S. franciscanus* may thus represent a release from competition for *S. purpuratus*. Furthermore, the large red sea urchin fishery has undoubtedly reduced larval production in this species; there has been no comparable reduction for purple sea urchins so these animals may be recruiting at a higher rate. Finally, the 1982–1984 El Niño led to a large pulse in sea urchin recruitment on the

<sup>11</sup>M. Neushul, Neushul Maricult. Inc., 475 Kellogg Way, Goleta, CA 93117. Personal commun., 1988.

northern Channel Islands, a pulse that was larger for purple than for red sea urchins<sup>2</sup>. Whatever the reason for this reported increase, large populations of *S. purpuratus* appear to be controlling algal food supplies in some areas, notably on the northern Channel Islands<sup>12</sup>, and this situation will inhibit the regeneration of red sea urchin stocks.

Purple sea urchins are similar in size to the species harvested in Japan so there should be no acceptance problem for the export market. However, their smaller size makes harvesting and processing prohibitively expensive<sup>13</sup>. Less expensive harvesting methods such as dredging or air pumps or mechanical processing may make fishing for purple urchins financially feasible. Alternate uses, such as for animal feed or soil supplements, are also under investigation<sup>14</sup>.

#### The Feedlot Approach

Kelco, a San Diego-based kelp harvesting firm, has been experimenting with enclosing and feeding red sea urchins in barren areas of the Point Loma kelp forest as part of their kelp management activities<sup>9</sup>. Their objective is to reduce grazing pressure sufficiently that kelp will grow in formerly productive areas. After trying several different net configurations, their current model consists of nylon cargo net with 3.5 × 4.1 cm mesh. The netting is cut to dimensions of 0.3–0.6 m by the length of the enclosure. Lead core line (0.64 cm diameter) is threaded through the bottom of the net to act as a weight, and 0.95 cm polypropylene line is threaded through the top of the net to provide flotation. The leadline is anchored to the substrate using mushroom-head, nylon cement anchors and

<sup>12</sup>G. Davis, Channel Isl. Natl. Park, 1901 Spinnaker Dr., Ventura, CA 93001; R. McPeak, Kelco, P.O. Box 13216, San Diego, CA 92113; B. Steele (commercial sea urchin fisherman), P.O. Box 91609, Santa Barbara, CA 93190. Personal commun., 1988–89.

<sup>13</sup>D. Rudie, Catalina Offshore Products, 4537 Mt. Henry Pl., San Diego, CA 92117. Personal commun., 1989.

<sup>14</sup>A. Chadwick (commercial sea urchin tender), Box 3033, California Valley, CA 93453. Personal commun., 1989.

nylon cable ties. Materials cost for this enclosure is estimated at about \$0.50 per linear foot (30.5 cm). Observations suggest that the sea urchins are reluctant to cross the net which is kept in motion by surge; the few escapes were by animals that managed to get under the net.

Kelco has tried several pens ranging in circumference up to 130 m, as well as linear barrier fences to prevent sea urchins from entering areas where kelp was recruiting. About 2,000 red sea urchins per pen were transplanted with a very low mortality rate. The sea urchins were fed chopped *Macrocystis* taken from the surface canopy about once a week, and gonad development was rapid. Two months after these barren ground animals were penned, 100 kg of sea urchins were harvested and found to have good quality roe. Kelco foresees using this technique to reduce grazing pressure during the optimal spring season for kelp recruitment and to control sea urchin fronts<sup>9</sup>.

This technique appears to be low cost and have considerable promise for short-term enhancement of fishable red sea urchin stocks where sea urchin populations are limited by food availability. While it is not yet clear how long these nets will last, Kelco's data suggest that each net could produce several "crops" per year. Furthermore, the environmental results could be long term; where sea urchin densities are reduced, kelp is likely to recruit and end the problem of food limitation.

L. Romina<sup>15</sup> reports that Japanese brokers are encouraging Mexican sea urchin fishermen to establish pens for feeding red sea urchins to increase their gonad yield, in a manner analogous to the feedlot approach widely used for cattle. This method, now apparently practiced in Japan, involves terrestrial forage such as alfalfa. We do know that the Japanese have experimented with knotweed and other easily obtained terrestrial plants in intermediate culture of seed during periods when algae are not readily available.

<sup>15</sup>L. Romina, Inst. Nac. Pesca, Ensenada, Baja Calif., Mex. Personal commun., 1989.

Knotweed leaves supported faster growth than kelp for sea urchins up to 15 mm; for larger animals, the two feeds produced similar results (Department of Mariculture, Hokkaido Central Fisheries Experimental Station, 1984).

Nitrogen is a critical element in the survival and growth of all organisms due to its central role in metabolism, cell structure, and genetic coding. Plants experience shortages of inorganic nitrogen; herbivores encounter shortages of organic nitrogen, often in the presence of abundant calories (Mattson, 1980). Russell-Hunter (1970) calculated that all animals (except ruminants) have adult nutritional requirements for protein amounting to about 16.5 percent dry weight of their diet. This corresponds to a diet with a C/N ratio below 17:1. The C/N ratio of *Macrocystis* varies seasonally following ambient nitrate concentration (which is inversely related to temperature and negligible above 16°C (Jackson, 1977)), and may vary from less than 10:1 to greater than 40:1 (Wheeler and North, 1981).

While the role of nitrogen limitation of kelp forest herbivores is poorly understood, there are indications that nitrogen strongly affects both growth and reproduction. Ogino and Kato (1964) found a strong positive correlation between growth of abalones and the amount of protein in artificial diets. Shifts of feeding preference toward more protein-rich foods have been observed; sea urchins selected bryozoan-encrusted kelp (Bonsdorff and Vahl, 1982) or artificial food made with animal protein (McClintock et al., 1982). Evidence for the effect of nitrogen limitation on reproduction comes from the work of Leahy et al. (1981) who compared oogenesis in shallow (4–6 m) water populations of *S. purpuratus* with that of animals collected from a deep (15–21 m) water, subthermocline habitat where temperatures are more favorable for nitrate availability. The shallow population produced few gametes from August through November, when nitrate concentrations tend to be low (Wheeler and North, 1981), whereas the deep-

water population was equally fertile all year round. D. Rudie<sup>13</sup> reports that red sea urchin roe yields were higher during the 1988–89 period of colder than normal temperatures. While more research is needed, these observations suggest that increasing the nitrogen content of the food, whether by collecting kelp from below thermocline depths, fertilizing warm water kelps, or using terrestrial plants with a high nitrogen content, would increase growth and gonad development rates.

### Structure of the Japanese Fishing Industry and Implications for Enhancement of Red Sea Urchin Stocks in California

Marine fishes in the United States are traditionally common property resources. An individual fisherman has little incentive to conserve or enhance the resource because of the likelihood that someone else will reap the benefits of his actions. In contrast, local control of the fishing grounds was established in Japan during the Tokugawa feudal period (1603–1867) (Mottet, 1980; Sato, 1987). These rights were codified, democratized, and redistributed to assure greater control by the working fishermen during the 20th century. A fishery right (near-shore fisheries are managed by the fishery rights system) is the exclusive right to conduct certain types of fishing operations in a specific area under permit from the prefectural governor. A 1948 law required fishermen to form cooperatives to receive priority in obtaining fixed net (which allows fishing by placing fishing equipment in a designated area) and common (which allows joint use of a designated area for fishery purposes) fishery rights and allowed cooperatives to engage in a variety of activities ancillary to fishing. Now the common fishery right is only granted to fishermen's associations composed of fishermen possessing certain qualifications; there are some 3,000 fisheries cooperatives in Japan eligible for common fishing rights (Sato, 1987). Many fishery regulations are instituted at the prefectural level, but fisheries cooperatives often further restrict access, e.g., limiting



the number of days and the number of hours per day that a certain fishery is open, gear restrictions, etc., to conserve their stocks (Mottet, 1976a; Takagi, 1986).

While the law does not give fisheries cooperatives priority for demarcated (aquaculture) rights, many governors allow the local cooperatives to administer these rights as well to permit all of the necessary compromises between culture areas and other fishing rights to be made without government involvement. The cooperatives which receive these rights then treat them as income and divide the profits among members. If native stocks and aquacultural sites are fully exploited, new memberships in a cooperative may be all but impossible to obtain. Cooperatives frequently sponsor projects to increase productivity of the fishing grounds for the benefit of all members. These projects commonly include bottom improvements, artificial reef construction, or predator control. Some cooperatives are also very involved in the operation of hatcheries and/or seeding projects (Mottet, 1980).

In addition to control over the fishing grounds, a variety of other institutional factors favor and support enhancement activities. The Japanese have the highest annual per capita fish consumption of any major nation, and they consume one-seventh of the world output of fisheries products (Mottet, 1980). With the increase in fuel prices of recent years, the nearly full exploitation of the world stocks of table-grade species, increasing competition from other countries in high sea fisheries, restrictions or loss of access associated with extended fisheries jurisdictions, and the loss to pollution of some domestic coastal fishing areas, Japan has been forced to improve the productivity of her remaining coastal waters to maintain supplies of valuable species. Insecurity over sources of supply have led to a political consensus which makes it possible for fisheries to receive a disproportionate amount of government aid. For example, the 7-year Coastal Fishery Development Project funded in 1976

provided new government subsidies of \$1 billion to increase coastal production. This effort was directed at areas of the continental shelf less than 50 m in depth and included diverse activities such as improving spawning and nursery areas, release of seed and fry, construction of artificial reefs and habitats, wave reducing facilities, bottom improvements, and predator control. As Mottet (1981) summarizes:

“Even with these intense research efforts, the results from the preliminary studies always appear grossly inadequate for justifying the projects. The fact that the projects are still funded probably rests less on biological and economic data than on the political situation which has resulted from the worldwide introduction of 200-mile fishing zones. It seems that Japan is determined to increase its own coastal fisheries production, no matter what the cost, so it will be less susceptible to manipulation by foreign governments.”

Other important aspects of the fishing/culture infrastructure include government subsidies through low-interest loans and culture insurance (Mottet, 1980). The fishing cooperatives take care of many business aspects such as marketing, purchasing, financing, and insurance, leaving the fisherman or culturist more time to devote to his primary activity. Finally, Japan has an extensive network of research, education, and extension services. There are fisheries high schools and college programs. Research is supported by every level of government as well as by the cooperatives themselves, and much is heavily subsidized by the national government.

In California, it is possible to obtain some degree of control over nearshore water bottoms. The Fish and Game Commission leases state-owned tidelands for aquaculture. The primary lessees to date have cultured bivalves, but in recent years leases have been given for abalones, a group ecologically similar to sea urchins. The California Fish and Game Code provides that all lawfully cultivated organisms

that are described in the application for the lease and produced in the area are owned by the lessee. The lessee has the exclusive right to cultivate and harvest the aquatic organisms in the lease site. Thus, a lease would make it reasonable for a fisherman to invest the time and resources to plant collector-caught or cultured seed, to grow kelp, or to feed hungry animals. Exclusive rights would also provide incentive for a fisherman to follow conservative fishing practices such as leaving behind some minimum density of adult red sea urchins to provide spine canopy protection for recruits.

A major problem with water bottom leases in California may be enforcement; there are simply too few Fish and Game Department wardens to police leases. If fishermen (and processors) were to further follow the Japanese model and to enter into agreement over rights to the local fishing grounds, it may be possible to ensure the dividends of each individual's efforts. As leases are subject to public comment, additional potential obstacles to this approach are other sea urchin fishermen who may feel that their rights are being infringed upon, or other users of kelp forest resources such as recreational fishermen or kelp harvesters. Such considerations underscore the importance of an information campaign and involvement of all concerned with the resource before leases are applied for<sup>16</sup>.

Fish and Game Commission water bottom leases do not, however, allow for modification of the bottom<sup>16</sup>. Such habitat improvement approaches as the addition of rock piles or habitat structures would have to go through the same approval process as required for artificial reefs—approval or permits from the U.S. Army Corps of Engineers, California Coastal Commission, State Lands Commission, Department of Fish and Game, and the local Regional Water Quality Control Board. Any potential conflicts with existing sport or commercial fisheries

<sup>16</sup>R. Collins, Calif. Dep. Fish Game, 1416 Ninth Street, Sacramento, CA 95814. Personal commun., 1989.

must be resolved. The importance the Japanese place on locally produced seafood is not apparent in California where esthetic and recreational uses of the nearshore environment often take precedence over mariculture. While artificial reef construction is common and establishes precedent for some types of habitat improvement, major modification of a multiuse resource such as cutting channels in rocky intertidal benches is likely to meet with serious opposition from the Coastal Commission and others.

### Discussion

Thus, there are several biological options for enhancing fishable stocks of *Strongylocentrotus franciscanus* which vary widely in cost, the amount of labor required, duration of the results, and effects on current landings. While all these approaches offer some biological potential for success, none has been adequately field tested in California. These options raise questions about who will pay for enhancement, who will do the work and reap the benefits, and whether any of the approaches will be cost effective now or in the future when wild stocks are likely to be smaller.

Enhancement of stocks limited by food availability appears to represent both the highest biological probability of success and the shortest time interval before efforts pay off. The capital investment for nets or pens is likely to be relatively low compared to other approaches to enhancement, but operation will be labor intensive. This approach is basically short term in its effects, although areas where grazing pressure is reduced sufficiently are likely to regenerate kelp populations and improve the conditions for the next generation of sea urchins—assuming that larval supply and/or immigration of the desired species are adequate. Unless purple sea urchin densities are reduced, however, some habitats are unlikely to regenerate. This approach is also clearly affected by the supply of food-limited sea urchins, which may vary considerably among areas. Animals from barren grounds (such as several square kilo-

**Table 2.—Comparison of *Strongylocentrotus intermedius* seed collection in the sea and culture in land-based facilities in Hokkaido. Both methods require intermediate culture with feeding to obtain seed of a suitable size for release in natural habitats (Kawamura, 1987).**

Subject	Seed collected in the sea	Seed cultured in land-based facilities
Collecting technique	Planktonic larvae attach to collectors hung in the sea. The system is simple and requires little training.	Larvae are cultured from fertilized eggs. The process is complex and requires specialized training.
Collecting facilities	Collector construction, suspension, and protection from waves are relatively simple.	Complex facilities are required for supplying water, culturing larval food and young sea urchins.
Operations	Minimal labor is required for placing long-lines and retrieving the collectors.	Labor intensive on a daily basis.
Obtaining consistent numbers of seed	Great variation.	As techniques are perfected, the supply may stabilize.
Vitality of seed	Natural selection occurs. Gene pool is large.	Natural selection does not occur. Gene pool is small.
Region	Limited to areas of good larval availability.	Possible in any ice-free area.

meters south of the present day Point Loma kelp forest in San Diego) or those living seaward of the kelp zone in central and northern California (e.g., Pearse and Hines, 1979) are obvious candidates. It may also be possible to increase the period of time during which sea urchins from seemingly non food-limited habitats are of fishable quality by increasing the quantity or nitrogen content of their food. This approach is clearly not capable of supporting all California sea urchin fishermen, but it may prove productive for several individuals to establish water-bottom leases and feeding regimes in each area.

It should be noted that the California Department of Fish and Game requires a permit to transplant animals. There is also a question of the legality of penning sea urchins which are a common property resource (in contrast with seeded sea urchins which have been produced by the owner)<sup>16</sup>.

Increasing the supply of juvenile sea urchins, whether by collection of seed from settlement plates, release of cultured late-stage larvae, or culture of seed in hatcheries, would seem to be the most efficient way of enhancing fishable stocks in areas where populations are limited by larval supply—if any of these approaches can be shown to work in California. Seeding of hatchery-reared juveniles has been

seen as an attractive solution for many species, but as Hahn (1989a) observes, "There is little, if any, evidence that hatchery production has ever had any measurable effect on natural fishery populations of any marine invertebrate." Conversion of an abalone hatchery to sea urchin culture and the data reported by Omi (1987) suggest that managers in Hokkaido are encouraged about the prospects for sea urchin seeding, but until more results are provided, they must be regarded as preliminary. Hatcheries are capital intensive and operational costs are high (McCormick and Hahn, 1983). Collection of settling larvae from the plankton followed by intermediate culture in the sea is much less capital intensive but is subject to the vagaries of current patterns and larval supply (Table 2). Presumably these are the reasons that led to the sea urchin hatchery in Hokkaido.

Tegner and Barry<sup>2</sup> have identified the southeastern Channel Islands, Santa Barbara, and especially San Clemente Islands, as sites of steady and high *S. franciscanus* recruitment due to the influence of the Southern California Eddy. However, these same islands are also areas where survival of mid-sized red sea urchins is poor due to intense predation pressure. Thus, it may be beneficial to establish arrays of collectors on these islands for trans-

plantation to other sites. Northwest Harbor, a semi-protected site on San Clemente Island, may be ideal for placement of seed collectors.

Whatever their source, seed survival rates are likely to be very area-specific and will have to be determined empirically in California. Miyamoto et al. (1985) found that predation was minimal on seed larger than 15 mm in Hokkaido. In contrast, seastars in southern California commonly consume sea urchins up to 50 mm (Tegner and Dayton, 1981). Spiny lobsters feed heavily on sea urchins to 60 mm and will consume animals as large as 90 mm in aquaria (Tegner and Levin, 1983). There are apparently no invertebrate-feeding fishes such as wrasses in Hokkaido. Sheephead are major sea urchin predators and the seniorita, *Oxyjulis californica*, another common wrasse, has been observed picking juvenile sea urchins out of coralline algae and having small sea urchins in its gut contents (Tegner and Dayton, 1977, 1981). The effects of lobster and sheephead predation are apparent in the population structure of red sea urchins on the southeastern Channel Islands<sup>2</sup>.

Thus, the Japanese method of broadcasting seed from the surface is clearly inappropriate for southern California, and protective habitats such as adult spine canopies and rock piles will be critical for seeding to be successful. Given the apparent lack of a reasonable size threshold beyond which there is a significant reduction in predation, it may well be more cost-effective to seed a large number of relatively small seed. Seeding may well be more applicable to northern California where predation pressure appears to be lower. When evaluating the Japanese results, it is also important to consider that they harvest sea urchins as small as 40 mm which may be only 2 years old (Omi, 1987). The minimum legal size in California is 76 mm, about 3 years of age<sup>2</sup>. Thus, red sea urchins in California are exposed to predation for a year longer than sea urchins in Hokkaido before they enter the fishery.

Predation during field growout re-

mains one of the major hurdles to successful culture of mollusks (Jory et al., 1984), and no doubt crustaceans and echinoids as well. Jory et al. (1984) reviewed how predators can decimate unprotected mollusk seed and the many different devices which will provide protection—often at considerable cost. They suggest the importance of planting seed at a size of decreased vulnerability and adequately dispersed to minimize predation. As there may be considerable seasonal variability in predation pressure, studies should determine the optimal time of planting as well.

Physical habitat improvements, such as the addition of rock piles to pavement habitats or even soft sediments, represent considerable initial outlay, but there are no operational costs and the results are long lasting. This approach may be especially important for populations of red sea urchins limited by the survival of mid-sized animals. The enthusiasm for physical habitat improvement shown by the Japanese suggests its effectiveness, but their cost calculations appear to include substantial government subsidies. The major obstacle to this approach in the United States may be opposition by other users of the same environment such as net fishermen<sup>16</sup>.

Broodstock and nursery protection require no capital outlay but they do entail a cost; some landings must be sacrificed now for the sake of future harvests. Where it is not possible to accomplish this with a maximum size limit, there is also the risk that the animals left by one fisherman will be harvested by someone else. The results of leaving a minimum density of adults behind are likely to be modest, but they may prevent the loss of some fishing grounds, especially on the southeastern Channel Islands where predation pressure is high<sup>2</sup>. Rotating area closures should also be tested. Despite their high fecundities and recruitment rates, sea urchin fisheries can be over-exploited. Taki (1986) described a case where a fishery for *S. intermedius* exceeded recruitment leading to stock deterioration, and sea urchin fisheries in France (Southward

and Southward, 1985) and Barbados (Scheibling and Mladenov, 1987) have collapsed. It seems prudent to adopt a conservative approach now to prevent further deterioration of existing stocks until alternate methods of enhancement are tested and put in place.

In these days of budget deficits and limited government means, the cost of any approach to enhancement must be considered in concert with its biological and economic effectiveness. A sea urchin hatchery is a very expensive proposition, especially since it is not clear that seed survival will be adequate in California ecosystems. The sea urchin industry has levied a tax on landings to fund research and development of enhancement methods, but a several-fold increase in funds would be required to finance a hatchery. A logical first step would be to obtain seed from collectors in the ocean, increase their size in intermediate culture, and then conduct experiments to assess survival rates in benthic habitats. While research may be required to adapt Japanese methods of seed collection to California conditions, seed obtained in this manner will be relatively inexpensive and still useful for determining whether seed survival is adequate to pursue this approach. Tegner and Barry<sup>2</sup> have identified San Clemente and Santa Barbara Islands as optimal sites for seed collectors; mainland locations such as the Point Loma kelp forest are likely to produce lower but still useful numbers of recruits (Tegner and Dayton, 1981). If seed collection proves to be an efficient method for obtaining juveniles, then there are a number of options regarding who funds the collections, distribution or sale of the seed, and who owns fishing rights after growth to harvestable size—in short, will enhancement require changes in the structure of the fishery?

Capital-intensive approaches to enhancement such as a hatchery or physical habitat improvement projects may require the financial backing of the entire industry. This can be practical if based on landing taxes. Labor-intensive projects such as enhancing food-limited populations are likely to be

difficult to organize on an industry-wide basis but may be ideal for a few individuals if seafloor leases can be obtained. Broodstock and nursery protection needs the support of all fishermen, but the incentive to conserve is likely to be greater where there is local control of the water bottom.

Sea urchins have been an important part of the Japanese diet for hundreds of years and are intensively harvested. National landings averaged 25,000 t for 1978–82, and there was remarkably little variation among the years (Takagi, 1986). In a country where there is little or no distinction between fishing and marine farming, the stability of the sea urchin harvest appears to be based on both traditional fisheries management measures such as effort restrictions, size limits, etc. and various enhancement activities facilitated by the structure of the fishing industry. As the California red sea urchin will soon, if it is not already, be fully exploited and the landings will start to fall, the long-term success of the Japanese is something for Californians to consider.

#### Acknowledgments

I thank R. Collins, W. North, M. Otjens, D. Parker, D. Rudie, B. Steele, C. Toole, and K. Wilson for providing information and P. Parnell for preparing figures. The California Department of Fish and Game provided ship time and helped gather the spine canopy association data. Thanks are also due to Madelon Mottet and the Washington State Department of Fisheries whose translations and reports about Japanese fisheries were critical to this analysis. I am very grateful to S. Kato for his critical review of the manuscript. D. Parker, D. Rudie, and R. Rowley also provided comments on the text. This research was sponsored in part by the California Department of Fish and Game, and in part by the National Science Foundation and NOAA, National Sea Grant College Program, Department of Commerce, under grant number NOAA 04-8-MO1-189, project number R/F-36 through the California State Resources Agency.

#### Literature Cited

- Agatsuma, Y., and H. Momma. 1988. Release of cultured seeds of the sea urchin, *Strongylocentrotus intermedius* (A. Agassiz), in the Pacific coastal waters of southern Hokkaido. I. Growth and reproductive cycle. Bull. Hokkaido Fish. Res. Sta. 31:15–25. [In Jpn., Engl. abstr.]
- Appledoom, R. S., and D. L. Ballantine. 1983. Field release of cultured queen conch in Puerto Rico: Implications for stock restoration. Proc. Gulf Caribb. Fish. Inst. 35:89–98.
- Ault, J. S. 1985. Some quantitative aspects of reproduction and growth of the red abalone, *Haliotis rufescens* Swainson. J. World Maricult. Soc. 16:398–425.
- Berg, C. J., and D. A. Olsen. 1989. Conservation and management of queen conch (*Strombus gigas*) in the Caribbean. In J. F. Caddy (editor), Marine invertebrate fisheries: Their assessment and management, p. 421–442. Intersci., N.Y.
- Bernard, F. R. 1977. Fishery and reproductive cycle of the red sea urchin, *Strongylocentrotus franciscanus*, in British Columbia. J. Fish. Res. Board Can. 34:604–610.
- \_\_\_\_\_. and D. C. Miller. 1973. Preliminary investigation on the red sea urchin resources of British Columbia (*Strongylocentrotus franciscanus*, Agassiz). Fish. Res. Board Can., Tech. Rep. 400, 37 p.
- Bonsdorff, E., and O. Vahl. 1982. Food preference of the sea urchins *Echinus acutus* and *E. esculentus*. Mar. Behav. Physiol. 8:243–248.
- Breen, P. A., W. Carolsfeld, and K. L. Yamataka. 1985. Social behavior of juvenile red sea urchins, *Strongylocentrotus franciscanus* (Agassiz). J. Exp. Mar. Biol. Ecol. 92:45–61.
- Cameron, R. A., and S. C. Schroeter. 1980. Sea urchin recruitment: Effect of substrate selection on juvenile distribution. Mar. Ecol. Prog. Ser. 2: 243–247.
- Castagna, M. 1983. Review of bivalve culture methods. J. World Maricult. Soc. 14:567–575.
- Craig, M. A., T. J. Bright, and S. R. Gittings. 1988. Growth of *Mercenaria mercenaria* and *Mercenaria mercenaria texana* seed clams planted in two Texas bays. Aquaculture 71:193–207.
- Dean, T. A., S. C. Schroeter, and J. Dixon. 1984. Grazing by red and white sea urchins and its effect on the recruitment and survival of giant kelp. Mar. Biol. 78:301–313.
- Department of Mariculture, Hokkaido Central Fisheries Experimental Station. 1984. [On the natural seeds collection, intermediate culture, and release of the sea urchin, *Strongylocentrotus intermedius*]. J. Hokkaido Fish. Exp. Sta. 41:270–315. Can. Transl. Fish. Aquat. Sci. 5200, 48 p., 1985.
- Ebeling, A. W., D. R. Laur, and R. J. Rowley. 1985. Severe storm disturbances and reversal of community structure in a southern California kelp forest. Mar. Biol. 84:287–294.
- Ebert, T. A. 1967. Negative growth and longevity in the purple sea urchin, *S. purpuratus* (Stimpson). Science 157:557–558.
- \_\_\_\_\_. and M. P. Russell. 1988. Latitudinal variation in size structure of the west coast purple urchin: A correlation with headlands. Limnol. Oceanogr. 33:286–294.
- Ebert, T. B., and E. E. Ebert. 1988. An innovative technique for seeding abalone and preliminary results of laboratory and field trials. Calif. Fish Game 74:68–81.
- Giese, A. C. 1966. On the biochemical constitution of some echinoderms. In R. A. Boolootian (editor), Physiology of echinodermata, p. 547–576. Interscience, N.Y.
- Grant, J. F. 1981. Abalone culture in Japan: Development and current commercial practice. Tasmanian Fish. Res. 23:2–17.
- Hahn K. O. 1989a. Culture of queen conch, *Strombus gigas*, in the Caribbean. In K. O. Hahn (editor), Handbook of culture of abalone and other marine gastropods, p. 317–331. CRC Press, Boca Raton, Fla.
- \_\_\_\_\_. 1989b. Culture of the tropical top shell, *Trochus niloticus*. In K. O. Hahn (editor), Handbook of culture of abalone and other marine gastropods, p. 301–315. CRC Press, Boca Raton, Fla.
- Harrold, C., and D. C. Reed. 1985. Food availability, sea urchin grazing, and kelp forest community structure. Ecology 66:1160–1169.
- Hinegardner, R. T. 1969. Growth and development of the laboratory cultured sea urchin. Biol. Bull. 137:465–475.
- \_\_\_\_\_. 1975. Care and handling of sea urchin eggs, embryos, and adults (principally North American species). In G. Czihak (editor), The sea urchin embryo, p. 10–25. Springer-Verlag, Berl.
- \_\_\_\_\_. and M. M. Rocha Tuzzi. 1981. Laboratory culture of the sea urchin *Lytechinus pictus*. In Laboratory animal management, marine invertebrates, p. 291–302. Natl. Acad. Press, Wash., D.C.
- Holland, L. Z., A. C. Giese, and J. H. Phillips. 1967. Studies on the perivisceral coelomic fluid protein concentration during seasonal and nutritional changes in the purple sea urchin. Comp. Biochem. Physiol. 21:361–371.
- Howard, A. E. 1982. Lobster 'seeding'—a promising approach to the problem of increasing natural stocks. In Proc. 13th Annu. Shellfish Conf., p. 14–22. Shellfish Assoc. Great Britain, Lond.
- Ino, T. 1966. [The abalone science and its propagation in Japan]. Propag. Mar. Prod. Ser. 11, p. 2–105. Publ. by Jpn. Fish. Resour. Conserv. Assoc. Fish. Res. Board Can. Transl. Ser. 1078, 209 p.
- Iverson, E. S., D. E. Jory, and S. P. Bannerot. 1986. Predation on queen conchs, *Strombus gigas*, in the Bahamas. Bull. Mar. Sci. 39:61–75.
- Jackson, G. A. 1977. Nutrients and production of the giant kelp, *Macrocystis pyrifera*, off southern California. Limnol. Oceanogr. 22:979–995.
- Jory, D. E., M. R. Carriker, and E. S. Iverson. 1984. Preventing predation in molluscan mariculture: An overview. J. World Maricult. Soc. 15:421–432.
- Kafuku, T., and H. Ikenoue. 1983. Abalones. In T. Kafuku and H. Ikenoue (editors), Modern methods of aquaculture in Japan, p. 172–182. Elsevier Sci. Publ. Co., Amst.
- Kato, S., and S. C. Schroeter. 1985. Biology of the red sea urchin, *Strongylocentrotus franciscanus*, and its fishery in California. Mar. Fish. Rev. 47:1–20.
- Kawamura, K. 1987. Techniques for obtaining sea urchin seed on offshore longlines. In [Summary lectures for 1986 of the Fisheries Culture Research Society: Techniques for collecting sea urchin seed and results of releases]. [Public Corp. Promot. Aquacult. Hokkaido]. Transl. (extended summ.) Madelon Mottet, Jpn. Sci. Liason, 595 Tuck-

- er Ave., No. 39, Friday Harbor, WA 98250.
- Kraeuter, J. N., and M. Castagna. 1985a. The effect of clam size, net size, and poisoned bait treatments on survival of hard clam, *Mercenaria mercenaria*, seed in field plots. *J. World Maricult. Soc.* 16:377-385.
- \_\_\_\_\_, and \_\_\_\_\_. 1985b. The effects of seed size, shell bags, crab traps, and netting on the survival of the northern hard clam, *Mercenaria mercenaria* (Linne). *J. Shellfish Res.* 5:69-72.
- Larson, B. R., R. L. Vadas, and K. Keser. 1980. Feeding and nutritional ecology of the sea urchin *Strongylocentrotus droebachiensis* in Maine, USA. *Mar. Biol.* 59:49-62.
- Leahy, P. S. 1986. Laboratory culture of *Strongylocentrotus purpuratus* adults, embryos, and larvae. *Methods Cell Biol.* 27:1-13.
- \_\_\_\_\_, B. R. Hough-Evans, R. J. Britten, and E. H. Davidson. 1981. Synchrony of oogenesis in laboratory-maintained and wild populations of the purple sea urchin (*Strongylocentrotus purpuratus*). *J. Exp. Zool.* 215:7-22.
- \_\_\_\_\_, T. C. Tutshulte, R. J. Britten, and E. H. Davidson. 1978. A large-scale laboratory maintenance system for gravid purple sea urchins (*Strongylocentrotus purpuratus*). *J. Exp. Zool.* 204:369-380.
- Lees, D. C. 1970. The relationship between movement and available food in the sea urchins *Strongylocentrotus franciscanus* and *Strongylocentrotus purpuratus*. M.S. Thesis, San Diego State Coll., San Diego, Calif., 119 p.
- Leighton, D. L. 1966. Studies of food preference in algivorous invertebrates of southern California kelp beds. *Pac. Sci.* XX:104-113.
- Mattison, J. E., J. E. Trent, A. L. Shanks, T. B. Akin, and J. S. Pearse. 1977. Movement and feeding activity of red sea urchins (*Strongylocentrotus franciscanus*) adjacent to a kelp forest. *Mar. Biol.* 39:25-31.
- Mattson, W. J. 1980. Herbivory in relation to plant nitrogen content. *Ann. Rev. Ecol. Syst.* 11:119-161.
- McCormick, T. B., and K. O. Hahn. 1983. Japanese abalone culture practices and estimated costs of juvenile production in the USA. *J. World Maricult. Soc.* 14:149-161.
- McClintock, J. B., T. S. Klinger, and J. M. Lawrence. 1982. Feeding preferences of echinoids for plant and animal food models. *Bull. Mar. Sci.* 32:365-369.
- McHugh, J. L. 1981. Recent advances in hard clam mariculture. *J. Shellfish Res.* 1:51-55.
- Miyamoto, T., M. Ito, and Y. Mizutori. 1985. Experiments on the qualities for the seeds of the sea urchin (*Strongylocentrotus intermedius*) collected by the hanging plates in nature. Hokuishu Geppo, J. Hokkaido Fish. Exper. Sta. 42:203-221. Transl. (extended summ.) by Madelon Mottet, Jpn. Sci. Liason, 595 Tucker Ave., No. 39, Friday Harbor, WA 98250, Jan. 1989.
- Mottet, M. G. 1976a. The fishery biology of sea urchins in the family Strongylocentrotidae. *Wash. Dep. Fish., Tech. Rep.* 20:1-66.
- \_\_\_\_\_. 1976b. The fishery biology of sea urchins in the family Strongylocentrotidae. *Compl. Rep. to Dep. Commer., Wash. Dep. Fish., p.* 67-176.
- \_\_\_\_\_. 1980. Factors leading to the success of Japanese aquaculture with an emphasis on northern Japan. *Wash. Dep. Fish., Tech. Rep.* 52:1-83.
- \_\_\_\_\_. 1981. Enhancement of the marine environment for fisheries and aquaculture in Japan. *Compl. Rep. to Dep. Commer., Wash. Dep. Fish., 176 p.*
- Munro, A. L. S. 1982. Prospects for enhancing British fishery resources by release of cultured juveniles. *Scott. Fish. Bull.* 47:32-39.
- Munro, J. L. 1989. Fisheries for giant clams (Tridacnidae: Bivalvia) and prospects for stock enhancement. In J. F. Caddy (editor), *Marine invertebrate fisheries: Their assessment and management*, p. 541-558. Wiley Intersci., N.Y.
- Nash, W. J. 1988. Hatchery rearing of *Trochus* as a management tool. *Aust. Fish.* 47:36-39.
- Neushul, M., and B. W. W. Harger. 1985. Studies of biomass yield from a nearshore macroalgal test farm. *J. Solar Energy Eng.* 107:93-96.
- Noma, T. 1983. Enhancement of seaweed and sea urchin by utilization of wave energy. *Tech. Rep. Natl. Res. Inst. Fish. Eng. (Jpn.) (Aquacult. Fish. Port) / Suikokengihu Suisan-doboku.* 4:1-10.
- North, W. J., V. A. Gerard, and J. S. Kuwabara. 1981. Biomass production by freshwater and marine macrophytes. In D. L. Klass (editor), *Biomass as a nonfossil fuel source*, p. 77-98. *Am. Chem. Soc. Symp. Ser.* 144, Wash., D. C.
- Ogino, C., and N. Kato. 1964. Studies on the nutrition of abalone. II. Protein requirements for growth of abalone, *Haliotis discus*. *Bull. Jpn. Soc. Sci. Fish.* 30:523-526.
- Omi, T. 1987. Results of sea urchin releases. In [Summary lectures for 1986 of the Fisheries Culture Research Society: Techniques for collecting sea urchin seed and results of releases]. [Public Corp. Promot. Aquacult. Hokkaido]. Transl. (extended summ.) by Madelon Mottet, Jpn. Sci. Liason, 595 Tucker Ave., No. 39, Friday Harbor, WA 98250.
- Parrish, R., C. Nelson, and A. Bakun. 1981. Transport mechanisms and reproductive success of fishes in the California Current. *Biol. Oceanogr.* 1:175-203.
- Pearse, J. S., M. E. Clark, D. L. Leighton, C. T. Mitchell, and W. J. North. 1970. Marine waste disposal and sea urchin ecology. In W. J. North (editor), *Kelp habitat improvement project, annual report, 1969-1970*. p. 1-93. *Calif. Inst. Technol., Pasadena.*
- \_\_\_\_\_, and A. H. Hines. 1979. Expansion of a central California kelp forest following the mass mortality of sea urchins. *Mar. Biol.* 51:83-91.
- Pennington, J. T. 1985. The ecology of fertilization of echinoid eggs: The consequences of sperm dilution, adult aggregation, and synchronous spawning. *Biol. Bull.* 169:417-430.
- Roughgarden, J., S. Gaines, and H. Possingham. 1988. Recruitment dynamics in complex life cycles. *Science* 241:1460-1466.
- Rowley, R. J. 1989. Settlement and recruitment of sea urchins (*Strongylocentrotus* spp.) in a sea urchin barren ground and a kelp bed: Are processes regulated by settlement or post-settlement processes? *Mar. Biol.* 100:485-494.
- Russell-Hunter, W. D. 1970. Aquatic productivity: An introduction to some basic aspects of biological oceanography and limnology. *Macmillan Co., Lond.*, 306 p.
- Saito, K. 1984. Ocean ranching of abalones and scallops in northern Japan. *Aquaculture* 39:361-373.
- \_\_\_\_\_. 1987. Techniques for the artificial culture of sea urchin seed. In [Summary lec- tures for 1986 of the Fisheries Culture Research Society: Techniques for collecting sea urchin seed and results of releases]. [Public Corp. Promot. Aquacult. Hokkaido]. Transl. (extended summ.) by Madelon Mottet, Jpn. Sci. Liason, 595 Tucker Ave., No. 39, Friday Harbor, WA 98250.
- \_\_\_\_\_, K. Yamashita, K. Tajima, A. Obara, Y. Nishihama, M. Sawasaki, K. Kawamata, and K. Kawamura. 1985. [Manual of artificial seed production of sea urchin, *Strongylocentrotus intermedius*.] Hokkaido Inst. Maricult., 22 p. Transl. (extended summ.) by Madelon Mottet, Jpn. Sci. Liason, 595 Tucker Ave., No. 39, Friday Harbor, WA 98250.
- Sato, O. 1987. The Japanese fisheries system. *Oceanus* 30(1):9-16.
- Scheibling, R. E., and P. V. Mladenov. 1987. The decline of the sea urchin, *Tripneustes ventricosus*, fishery of Barbados: A survey of fishermen and consumers. *Mar. Fish. Rev.* 49:62-69.
- Schiel, D. R., and B. C. Welden. 1987. Responses to predators of cultured and wild red abalone, *Haliotis rufescens*, in laboratory experiments. *Aquaculture* 60:173-188.
- Schroeter, S. C. 1978. Experimental studies of competition as a factor affecting the distribution and abundance of purple sea urchins, *Strongylocentrotus purpuratus* (Stimpson). Ph.D. Dissert., Univ. Calif., Santa Barbara, 184 p.
- Sloan, N. A. 1986. World jellyfish and tunicate fisheries, and the northeast Pacific echinoderm fishery. *Can. Spec. Publ. Fish. Aquat. Sci.* 92:23-33.
- \_\_\_\_\_, C. P. Lauridsen, and R. M. Harbo. 1987. Recruitment characteristics of the commercially harvested red sea urchin *Strongylocentrotus franciscanus* in southern British Columbia. *Fish. Res.* 5:55-69.
- Southward, A., and E. Southward. 1975. Endangered sea urchins. *New Sci.* 10 April 1975:70-72.
- Strathmann, R. 1978. Length of pelagic period in echinoderms with feeding larvae in the northeast Pacific. *J. Exp. Mar. Biol. Ecol.* 34:23-27.
- Takagi, K. 1986. Aspects of the sea urchin fishery in Japan. *Proc. 37th Annu. Gulf Carribb. Fish. Inst., Cancun, Mex., Nov. 1984*, p. 41-51.
- Taki, J. 1986. Population dynamics of *Strongylocentrotus intermedius* in Akkeshi Bay. Hokuishuho [abbrev. title] 28:33-43. *Can. Transl. Fish. Aquat. Sci.* 5229, 21 p., 1986.
- Tegner, M. J., and R. A. Butler. 1985. The survival and mortality of seeded and native red abalones, *Haliotis rufescens*, on the Palos Verdes Peninsula. *Calif. Fish Game* 71:150-163.
- \_\_\_\_\_, and \_\_\_\_\_. 1989. Abalone seeding. In K. O. Hahn (editor), *Handbook of culture of abalone and other marine gastropods*, p. 157-182. *CRC Press, Boca Raton, Fla.*
- \_\_\_\_\_, and P. K. Dayton. 1977. Sea urchin recruitment patterns and implications of commercial fishing. *Science* 196:324-326.
- \_\_\_\_\_, and \_\_\_\_\_. 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.
- \_\_\_\_\_, and L. A. Levin. 1983. Spiny lobsters and sea urchins: Analysis of a predator-prey interaction. *J. Exp. Mar. Biol. Ecol.* 73:125-150.
- Tong, L. J., G. A. Moss, and J. Illingworth.

1987. Enhancement of a natural population of the abalone, *Haliotis iris*, using cultured larvae. *Aquaculture* 62:67-72.
- Uki, N. 1984. Abalone culture in Japan. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 16:83-88.
- Vadas, R. L. 1977. Preferential feeding: An optimization strategy in sea urchins. *Ecol. Monogr.* 47:337-371.
- Van Olst, J. C., J. M. Carlberg, and J. T. Hughes. 1980. Aquaculture. In J. S. Cobb and B. F. Phillips (editors), *The biology and management of lobsters*, Vol. II, p. 333-384. Acad. Press, N.Y.
- Walker, R. S. 1986. The first returns of tagged juvenile lobsters [*Homarus gammarus* (L.)] after release to the wild. *Aquaculture* 52:231-233.
- Wheeler, P. A., and W. J. North. 1981. Nitrogen supply, tissue composition, and frond growth rates for *Macrocystis pyrifera* off the coast of southern California. *Mar. Biol.* 64:59-69.
- Wickins, F., T. W. Beard, and E. Jones. 1986. Microtagging cultured lobsters, *Homarus gammarus* (L.), for stock enhancement trials. *Aquacult. Fish. Manage.* 17:259-265.