

AN ABSTRACT OF THE THESIS OF

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Selina Heppell

The red sea urchin, *Strongylocentrotus franciscanus*, is one of the three species of strongylocentroids found on the west coast of North America between Baja California and Kodiak, Alaska. It belongs to the phylum Echinodermata, and it is one of the largest species of sea urchins. Since 1970, red sea urchins have been fished commercially for their highly valued gonads. As a result, the abundance of harvestable size urchins has rapidly declined, and the fishing industry has suffered a dramatic decrease in landings in this relatively short history. Several management strategies have been proposed with the objective to restore the harvestable stock as well as to protect the species. Among these strategies, an upper-size limit has been promoted in addition to existing minimum size limit regulations. This alternative is based on the hypothesis that the recruitment and survival of juvenile urchins is enhanced by the presence of adults, which provide a spine canopy habitat that is utilized by juveniles as refuge against predators. However, the evidence in support of this hypothesis is circumstantial. To understand the ecological relationship between adult and juveniles as well as to identify if different size categories of adult maximize this relationship, I conducted laboratory and modeling investigations that tested the hypotheses that 1) recruitment and survival of juvenile urchins is enhanced by the presence of adult spine canopy, 2) the rate of survival of juveniles is related to the size of the adult and 3) that protection of juveniles by adults can affect population response to harvest. I found that

juveniles look for refuge under adult spine canopies under the risk of predation and have higher survival in the presence of adults. However there is not a significant difference on survival based on the size of the adults. I conclude that the size of the adults is not important, but protection of adults may help restore and preserve a population under harvest conditions. Another potential benefit of implementing an upper size limit was explored since the fecundity of red sea urchins is related to body size. I used size-structured matrix models to further explore the importance of size-specific fecundity and the association between juveniles and adults. I assessed changes in population growth rate under different levels of harvesting that include lower and upper size limits. Under most scenarios, an upper size limit could benefit the recovery of populations of red sea urchins. However, in order to improve management strategies for the red sea urchins, more studies about the life history of red sea urchins should be conducted to reduce model uncertainties.

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Management of the Red Sea Urchin Fishery: a Biological Approach

by

Armando J. Ubeda

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MANAGEMENT OF THE RED SEA URCHIN FISHERY: A BIOLOGICAL APPROACH

1. INTRODUCTION

BIOLOGY AND MANAGEMENT OF RED SEA URCHINS

LIFE HISTORY

The red sea urchin, *Strongylocentrotus franciscanus*, is one of the three species of strongylocentroids belonging to the phylum Echinodermata found on the west coast of North America from Baja California to Kodiak, Alaska. It has a calcareous shell or test covered with a thin epithelium and armed with spines, and they can regrow broken off spines. The urchins move their feet by a system, which creates suction in the end of the foot by pulling water out. It is one of the largest species of sea urchins, growing to a test diameter of about 17 centimeters. It is considered long-lived species, with a maximum life span of at least 100 years (Ebert 1998). Red sea urchins occupy shallow waters, from the mid- or low intertidal zone to depths up to 50 meters; however, some individuals can be found up to 125 meters in depth. Individuals prefer rocky substrates, particularly ledges and crevices, and avoid sand and mud. Sexual maturity is normally reached at about 4 to 5 years, and fecundity is related exponentially to body size (Tegner 1989). *S. franciscanus* are free-spawning invertebrates, and produce a large number of eggs (7.764×10^5 eggs cm^{-3}) (Levitan 1993). Larvae may take 7 to 9 weeks to metamorphose prior to settlement. Rates of juvenile recruitment are typically low due to the low probability of eggs encountering sperm in the plankton. Most eggs are never fertilized (Pennington 1985) and low survival of juveniles in their first weeks of life as benthic organisms (Pfister and Bradbury, 1996) contributes to poor average recruitment.

In populations of red sea urchins, large individuals are considered extremely important due to their high fecundity and because they serve as "canopy" habitat for small juveniles. Once the urchins settle into the benthos, they live for at least their first two years as juveniles in association with adults. This nursery association of adult and

juvenile urchins offers two probable advantages to the smaller animals: a food source and protection from predators (Tegner et al 1977, Breen et al 1985). To compensate for losses due to harvest, populations must exhibit increased growth through recruitment or individual growth or survival rates. Sporadic recruitment and a dependency of small urchin survival on the abundance of large urchins make this species particularly prone to overexploitation (Montano 2001).

HABITAT AND COMMUNITY INTERACTIONS

Red sea urchins are herbivores that profoundly affect the structure of the benthic algal community by restricting macrophytes to a small part of their potential range. Kelp is their preferred food. Urchins typically feed on kelp debris, and they tend to move very little if they are receiving enough food (Vasquez and McPeak 1998). They interact with other community members by providing protection from predators to the juveniles of several species including abalones, gastropods, shrimp, crabs, asteroids, chitons, ophiuroids, other urchins and fish (Tegner and Dayton 1977, Breen et al 1985). Generally their absence or decrease thus has significant consequences for nearshore communities (Pfister and Bradbury, 1996).

FISHERY

Red sea urchins are the most commonly harvested urchin species on the west coast of North America. Red sea urchins are harvested for their roe (gonad), which is extracted for commercial purposes at processing plants for shipment to fresh markets in Japan and France (Montano 2001). Using aluminum rakes, divers extract red sea urchins from the ocean floor. The urchins are delivered from packer vessels to the processing plants where the gonad is extracted and processed. A smaller market for red sea urchins is developing in some countries in North America and some countries in Asia. The yield of roe from whole animal ranges from 5 to 15 percent of total body weight. Red sea urchins are also harvested at local scales for food, social and

ceremonial purposes, where harvesting is mainly opportunistic and associated with extreme low tides. The total yield of recreational harvest of this species is undocumented, but it is considered minimal (Rogers and Convey, 2000).

Commercial harvesting of this species occurs mainly in California, Oregon, Washington and British Columbia. Some harvesting has occurred in Alaska, but the urchin fishery there is considered in the developmental stage. In general, the fishery has dropped significantly since its development in the 1970's, and the primary reasons for this decline are the overexploitation of the species and the lack of information on its biology, which has resulted in inefficient management decisions. A variety of management strategies have been proposed and applied along the Pacific Northwest in order to keep the industry viable and preserve the different populations of red sea urchins (Table 1). Despite these efforts, both the populations of urchins and the fishery are still declining (figure. 1.1).

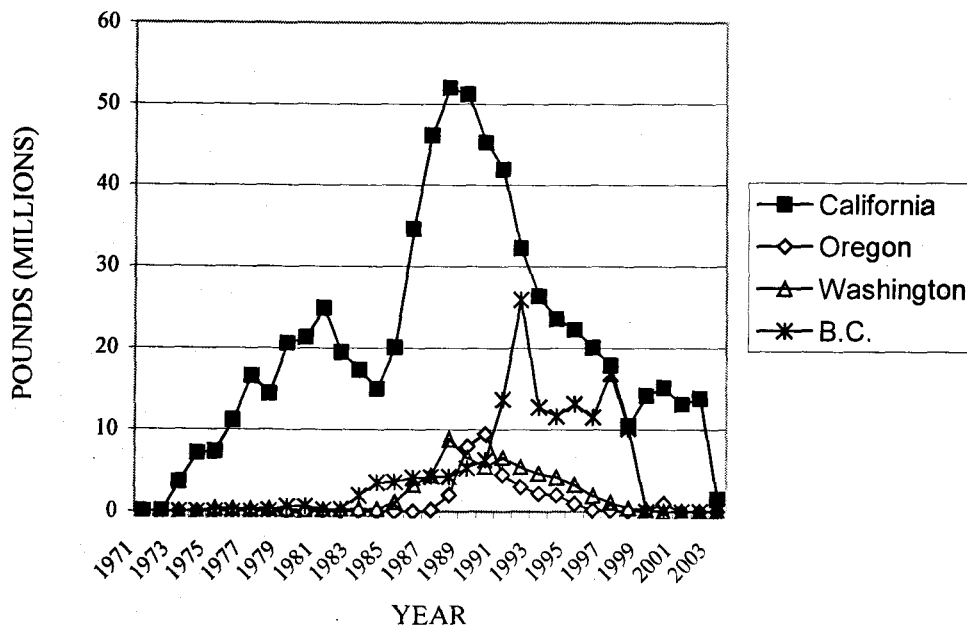


Figure 1.1. Fishery landings of the red sea urchin fishery along the West Coast of North America (ODFW 2000, Campbell et al 2001, Carter et al 2002).

The different management strategies and tools (Table 1) used in the Pacific Northwest are discussed here, along with an assessment of their success. Special attention for this review is given to Oregon.

Table 1.1. Comparison of the different management strategies and tools used to regulate red sea urchin fishery in the Pacific Northwest (Y = currently used management tools, R = formerly used, not currently and N = not used).

Management Strategies	British Columbia	Washington	Oregon	California
Harvest quotas	Y	Y	N	Y
Individual Quotas	Y	Y	N	Y
Upper size limit	N	Y	N	N
Minimum size limit	Y	Y	Y	Y
License restrictions	Y	Y	Y	Y
Limited entry	Y	Y	Y	Y
Season length	N	Y	N	Y
Rotational harvest	N	R	N	N
Minimum depth	N	Y	Y	N
Number of divers per boat	N	Y	Y	N
Closure of certain areas	Y	Y	Y	Y

Washington:

The Washington fishery began in 1971, with low landings through the early 1980s. In the late 1980s landings increased dramatically, peaking at over 8,816,000 pounds in 1988. Landings have declined since then, with 852,948 pounds of sea urchins harvested in 2000 (< 10 % of peak landings). The fishery is managed with harvest quotas, size limits (lower and upper), license restrictions, limited entry, and mandatory log books to track actual harvest. A rotational harvest strategy was implemented from 1977 to 1995, in which each harvest district was harvested once every third year. This rotational harvest was discontinued after the U.S. federal court

ruling on shellfishery management in Washington's coastal marine waters allotted one half of all harvestable shellfish to native tribes (the "Rafeedie Decision"). After this court decision, an annual harvest quota was implemented in order to ensure that all the tribes had equal access to their usual and accustomed fishing areas each year (Carter et al 2002).

Present Status:

Sea urchin harvests declined significantly in the early 1990s, resulting in quota and season length reductions because of over-harvesting concerns. Densities and proportion of legal size sea urchins in the population have declined as well. Harvesters are maintaining catch per unit of effort at high levels by exploiting new populations, thereby masking stock declines (Pfister and Bradbury 1996).

California:

The California commercial fishery for red sea urchins started in 1972 (Parker and Kalvass 1992). This fishery started as a part of a National Marine Fisheries Service program to develop fisheries for underutilized species. Landings increased rapidly, reaching approximately 25,000,000 pounds in 1981. Prior to 1985, almost all landings were from southern California, with most harvest from the Channel Islands. Starting in 1985, the northern California fishery expanded rapidly and the total California landings peaked at about 52,000,000 pounds in 1988. In 1987, the Department of Fish and Game and the Sea Urchin Advisory Committee negotiated a management system to maintain a sustainable fishery. The management program, which began in 1988, included a reduction of harvesting permits from 915 to 400, minimum size limits, season restrictions, logbook require fir divers; and closure of some research areas to the commercial fishery (Deweese 1991). In 1994, minimum size limits were 8.25 cm test diameter (td) in southern California and 8.89 cm in td in northern California (CCR 1994).

Present Status:

Since 1988, landings have declined due to over harvesting and management restrictions. Harvest restrictions have expanded but quotas were not reduced and catches have subsequently declined. Sea urchin densities in some harvested areas in northern California are less than one quarter of those in nearby reserve areas. (Kalvass and Hendrix, 1997). In 1993 commercial landings totaled only 24,900,000 pounds, less than half of the 1988 landings. In 2002, commercial landings totaled only 13,792,762 pounds.

British Columbia:

The British Columbia commercial fishery began in the 1970s. Annual landings increased very rapidly in the early 1980s for the south coast of B.C. and the late 1980s for the north coast. The fishery reached its peak in 1992, with 24,000,000 pounds landed. After 1992, landings were reduced and stabilized by quotas. The fishery is considered "data-limited" and, while stock assessments are undertaken in many areas, the fishery continues to be managed under a precautionary regime that includes limited entry licensing, a minimum size limit, harvest quotas, area licensing, and an individual quota (IQ) program (Campbell et al 1999).

Present status:

Most of the potential beds in B.C. are harvested, although there are a few beds that are closed due to overfishing or depletion by sea otters. Some areas have been closed to the fishery for research purposes, including areas with low densities of urchins and areas where urchins have limited food sources and poor gonad quality. Although quotas have decreased in recent years, this is attributed primarily to a refinement of assessment techniques (for urchin density and bed estimation), rather than to significant declines in stock biomass. Sea otters populations are growing more abundant in B.C. and they might in the future become a major influence on red sea

urchin populations. At the present, there is no management to restrict sea otter populations as the species is considered threatened (Campbell et al 2001).

Oregon:

The sea urchin fishery in Oregon started almost ten years later than elsewhere (mid 1980s), but soon developed into a significant industry. Rapid development of this fishery was aided by a number of factors, including particularly strong markets and favorable exchange rates in Japan. In addition, with well-developed fisheries in California, Washington and British Columbia, Oregon's red urchin stocks were readily developed into an efficient and productive industry in just a few years. Prior to that development, Oregon fishermen knew little about the urchin industry or the factors that had to be addressed to determine whether urchin harvesting and marketing was a reasonable enterprise along the Oregon coast (Washburn 1984).

During 1983-84, Washburn (1984) conducted a study to determine the economic viability of harvesting the red sea urchin along the Oregon coast. The main goals of this study were (1) to survey for populations and densities of the species to determine if harvesting could be established, (2) to monitor seasonal variation in the quality of the gonads, and (3) to harvest a sub sample of red urchins to process and ship to Japan to evaluate the feasibility of the enterprise. As part of his project evaluation, Washburn stated that an urchin industry could succeed, but that close attention had to be given to management to avoid diminishing available populations of red sea urchins. As to the positive potential of an urchin fishery, Washburn reported the existence of hundreds of relatively small (45 to 92 m) beds over an 80-kilometer area in Southern Oregon, an abundant kelp supply, and the availability of labor and boats. All these factors, plus a declining California urchin fishery, that could increase the price for urchin gonads in the Japanese market, could facilitate expansion of the urchin fishery to Oregon.

The fishery officially began in 1986, and was one of the first fisheries to be managed by a restricted participation system prior to significant development. In 1987, a limited entry program was created by the Oregon Legislature with the goal to “provide a sea urchin commercial fishery with optimum profits to those engaged in the fishery and to prevent a concentration of fishing effort that would deplete the resource” (Oregon Revised Statutes 508.760). Once their goal was set, the Oregon Fish and Wildlife Commission established by rule a limited participation system “which may include, but it is not limited to, initial eligibility, annual qualifications, and terms and conditions for transferring participation rights” (Oregon Department Fish and Wildlife – ODFW 2000).

During the first three years of the fishery, many in the urchin industry worked to improve overall economic return from the resource by acknowledging the need to control total harvest. The industry recommended that Orford Reef was closed for five to six months in the summer; the establishment of 1,500 lb daily trip limits per diver, and the freezing the number of permits. At the same time, the ODFW participated in a series of public meetings with the fishing industry to review all state limited entry programs. Some changes to the regulations were made to adjust recommended levels of participation, improve program administration, and to make limited entry programs as consistent as possible (ODFW 2000).

The maximum harvest of the fishery occurred in 1990 with 62 harvesters landing 9,300,000 pounds of sea urchins. Since then, catch and effort have declined. In 1994, ODFW reported that the average size of sea urchins had declined, as had the number of harvestable urchins available on the main urchin beds. In 1999, only 248,283 pounds were landed; however, landings for 2000 rose to 966,287 pounds (figure 1.2). During the period from 1988 to 1990, the average catch per trip was at its peak (approximately 2,300 pounds per trip), but has since leveled out and in 2000 was at 1,300 pounds. Landings and catch-per-unit effort reductions reflect both the fishing process and reduced abundance as well as effort reductions due to permit attrition. In

addition, the Oregon urchin fishery has faced marketing problems since 1996. In 1997-98, Premium Pacific Seafoods of Port Orford shut down the sea urchin processing portion of its facility. The company still purchases urchins for transport to processing plants in California and Washington. At the present time, most divers dive for urchins only under the best ocean conditions and when prices are high enough to make the considerable effort worthwhile (ODFW 2000).

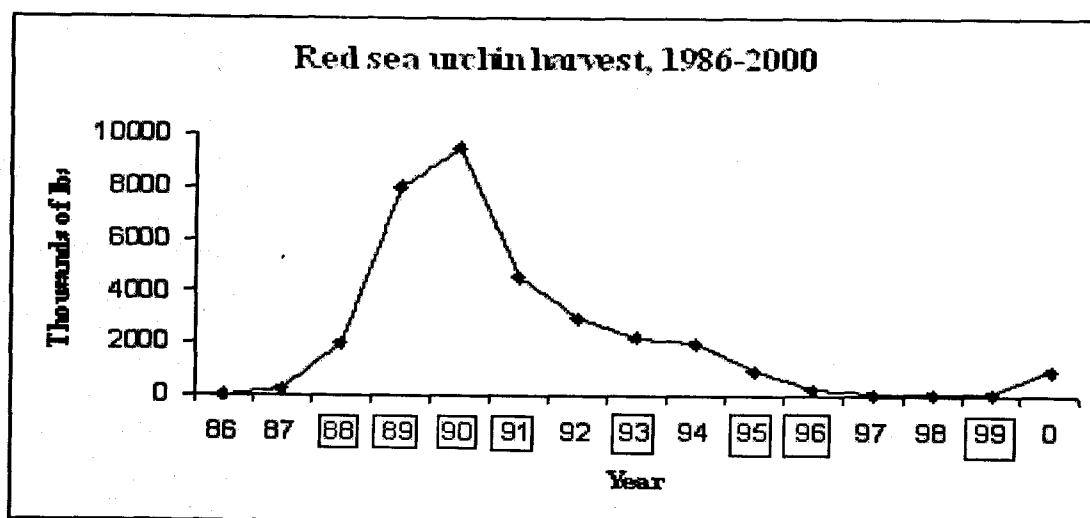


Figure 1.2. Total harvest of red sea urchins in the state of Oregon from 1986 to 2000. Data comes from ODFW (2000). Black boxes indicate years in which management decisions have been made.

Management regulations for the Oregon fishery

Until recently, the principal methods of management of the sea urchin fishery in Oregon have been effort limitation, size restrictions, and time area closures. However, regulations and management strategies have been changing considerably during the past ten years. These changes have shaped the development of the industry and affected the conservation of the species. Total harvest of urchins per year is shown in figure 1.2, with data and years of important management decisions (squares) from ODFW.

Significant management changes

* 1988 - The Oregon Fish and Wildlife Commission develops the legislatively mandated limited entry program. Elements of the program include:

- Maximum of 92 non-transferable permits
- 20,000 lb renewal requirements every two years
- Lottery for unissued permits
- 7.62 cm td minimum size limit
- 3 meters minimum harvest depth
- Logbook requirement which provide depth, fishing time and location
- Maximum of two divers in the water per boat

* 1989 - Changes to control effort made by the Commission due to concerns of economic overharvest. Changes include:

- Set target number of permits to 46, allow reduction through attrition
- Change renewal requirement to 20,000 lb annually
- Restrict the number of non-permit people on a boat to two
- Allow medical transfers of permits with a two-year time limit for transfers

* 1990 - The Commission establishes 300 meters buffer zones around three major sea lion rookeries, areas closed to urchin fishing from May 1 through August 31.

* 1991 - ODFW evaluates the effects of increasing the minimum size of harvest after the industry raises concerns that urchins were being economically overharvested. The Commission makes the following changes:

- Increases the minimum size to 8.9 cm td, with a tolerance of 100 urchins between 5 and 8.9 cm td
- Medical transfer rules specify total allowable harvest by a transferee and a review of each transfer after 90 days

* 1993 - The 1993 legislature mandates a comprehensive review of all limited entry programs in Oregon (Senate Bill 938). As a result of this unfinished process and at the request of the urchin permit holders, the Commission takes action by conference call

in March 1994 to suspend the lottery for unissued permits below the 46 permit ceiling until the legislative permit review is completed.

* 1995 – Two subtidal research reserves are added to complement the existing Whale Cove Research Reserve. In addition, a seasonal closure from May 1 to October 31 at Orford Reef is established.

* 1996 – The Legislature gives the Oregon Fish and Wildlife Commission direction to review permit numbers for the urchin fishery. Beginning in 1996, the Commission sets number of permits to 30 and institutes a system whereby permits could be purchased and combined on a 3 to 1 basis to encourage reduction of permits. Permits would become transferable once the target level of 30 permits was achieved. The permit renewal requirement is reduced to 5,000 pounds of urchin landings.

* 1999 – Permits reach 30 at the end of 1998 and become freely transferable. The medical transfer is eliminated. In 1999 several permit holders that were unable or unwilling to make the minimum 5,000 pounds required to renew their permits, exploited a loophole in the transfer regulations. Permits were transferred to spouses or relatives with the expectation that the permit would be transferred back to their original holders in the following year. In 2000 the permits were transferred back to their original holders, effectively avoiding the 5,000-pound landing permit renewal requirement for two years.

Present Status:

As a result of over-harvesting, abundance of harvestable urchins in the fishery areas has declined and average sizes in the main bed areas have declined below legal size limit (Richmond et al 1997). The ODFW reported reasons for the decline of the fishery, including deterioration of the Asian market due to a collapse of the Asian economy, a decline in urchin roe quality due to recent El Niño events, and low production of kelp. These factors and the reduced amount of fishing effort associated with them diminished any need to implement additional harvest management measures, such as quotas. In 2000, landings totaled 996,287 pounds, a dramatic

increase from the 248,283 pounds in 1999, reversing a nine-year trend of declining harvest. Urchin divers report that urchins are once again at Orford Reef, possible due to depressed fishing efforts and good recruitment. According to ODFW, recruitment has been good but growth is poor along the Oregon coast. However, a study conducted by Montano (2001) in four major areas with sea urchins beds along the Oregon coast stated that recruitment has been low or absent since 1992. My own anecdotal field observations corroborate Montano's findings. Nevertheless, as part of their future research, ODFW is supporting studies that relate urchins to kelp habitat as well as to determine the importance of sea urchin refugia in order to maintain healthy populations.

Management summary for the red sea urchin fishery

Despite the management strategies adopted by the various institutions in charge of managing the urchin fishery in the Pacific Northwest, red sea urchins stocks continue to decline. Management institutions are data limited and industry cannot be controlled solely with restricted quotas when the predictions of abundance are inadequate. A better understanding of the biology of the species and better management strategies need to be implemented to keep the industry alive. Basic biological information is limited. The different management institutions agree that there is a need for a better understanding on growth and recruitment parameters of the species. Reference stock assessment activities are one of the main activities that continue coast wide through biomass transect surveys, experimental harvest sites, and selected study sites; however, the fishery keeps declining due to the dramatic decrease in population sizes (Richmond et al 1997). A new management approach is needed to maintain the red sea urchin fishery and to preserve the species.

As a part of such a new approach, focus on the biological basis of the fishery seems to be warranted. Alternative management tools, including marine reserves, rotational harvesting areas, and the implementation of an upper size limit might be

considered. The purpose of these alternative tools would be to enhance recruitment and survival of juveniles that potentially will enter the fishery as well as to mitigate high fishing mortality rates by providing a refuge for some critical segment of the population, such as spawning adults. Management strategies based on the biology of the species would likely improve assessment of spatial and seasonal growth, survival, and recruitment of juveniles. This information could help managers determine the appropriate level of harvest. Nonetheless, most of these strategies will not provide immediate information to ensure the conservation of the species and the commercial fishery. Other types of analysis also are needed, such as the construction of predictive models that demonstrate the effects of varying fishing mortality rates on population age structure and to identify the most critical life stages for management to ensure a sustainable fishery. These types of models are known as age-structured models, and they are considered relatively simple. However, they still contain a number of unknowns or uncertain parameters; consequently, these models serve mainly as heuristic tools to assess the impacts of different management strategies by providing different scenarios to managers and the identification of critical research needs (Heppell et al reviewed).

2. INFLUENCE OF ADULTS RED SEA URCHINS, *STRONGYLOCENTRATUS FRANCISCANUS* (Agassiz), ON SURVIVAL OF SMALL JUVENILES UNDER THE PRESENCE OF ITS NATURAL PREDATOR

INTRODUCTION

The red sea urchin, *Strongylocentrotus franciscanus*, is one of the three species of strongylocentroids belonging to the phylum Echinodermata found on the west coast of North America from Baja California to Kodiak, Alaska. It has a calcareous shell or test covered with a thin epithelium and armed with spines, and they can regrow broken off spines. The urchins move their feet by a system, which creates suction in the end of the foot by pulling water out. It is one of the largest species of sea urchins, growing to a test diameter of about 17 centimeters. It is considered a long-lived species, with some individuals living for at least 100 years (Ebert, 1998). Red sea urchins occupy shallow waters, from the mid- or low intertidal zone to depths up to 50 meters; however some individuals can be found up to 125 meters. They are free-spawning invertebrates, and produce a large number of eggs. However, their rates of juvenile recruitment are typically low due to the low probability of eggs encountering sperm in the plankton and low survival of juveniles (Pennington, 1985). They are herbivores that profoundly affect the structure of the benthic algal community, thus their absence or decrease has significant consequences for nearshore communities (Pfister and Bradbury 1996, Paine et al 1969). In populations of red sea urchins, large individuals are extremely important due to their high fecundity and because they provide "canopy" habitat for small juveniles. Once the urchins settle into the benthos, they live for at least their first two years as juveniles in association with adults (Breen et al 1985).

Since 1970, red sea urchins have been fished commercially in the Pacific Northwest for their highly valued gonads. As a result, the abundance of harvestable

size urchins has rapidly declined, and the fishing industry has exhibited a dramatic decrease in this relatively short history. At the same time, there has been very low recruitment along the West coast of North America, which is attributed to a lack of suitable shelter for juveniles under the spine canopy of large red sea urchins. This means lower survival of juveniles and subsequently poor recruitment to fishable sizes (Tegner and Dayton 1977, 1981). In Oregon, the commercial sea urchin fishery for this species began in 1986 and reached its peak in 1989-1990. After 1991, divers have increased their diving times and the mean harvest depth has increased from 13 to 16 meters (Montano 2001) due to a reduction in abundance of harvestable urchins. Current management policy for the red sea urchin fishery in the US includes 1) limited entry of fishers 2) limited number of fishing days, 3) harvest quotas, and 4) lower size limits. Some new management strategies have been proposed to restore the population density of red sea urchins, including upper size-limits, individual transferable quotas (ITQs), area rotations, marine reserves and shallow harvest refugia (Rogers-Bennett et al 1998).

The upper size-limit regulation has been proposed to promote recruitment and survival of young urchins (Rogers-Bennett et al 1998, Breen 1984). This alternative by itself might not increase the number of adults since the fishery will concentrate on the "slot" and abundance may or may not increase. This management regulation has to be combined with other regulations such as quotas and reduction in fishing mortality in order to be effective. The upper-size limit regulation is based on the hypothesis that the recruitment and survival of juvenile urchins is enhanced by the presence of larger adults that provide a spine canopy habitat against predators (Tegner and Dayton 1977, Breen et al 1985, Rogers-Bennett et al 1995). If this hypothesis is correct and an upper size limit is established, this management strategy would not have a major effect on the value of the fishery since gonads of larger urchins (> 13 cm test diameter) generally lose their bright color and smooth texture, which lower their value in the market (Campbell et al 1999). However, the evidence in support of this hypothesis is circumstantial and based mainly on field observations. The only laboratory experiment

to look at the social behavior of juveniles concluded that the primary function of the association of juveniles with adults is avoiding predation (Breen et al 1985). This conclusion was based on observations of juveniles looking for refuge under adults on the presence of predators. However, this study consisted of a single, unreplicated treatment and did not include measurement of survival over time.

The benefit the adult-juvenile association may provide juveniles is still uncertain (Rogers-Bennett et al 1998). Despite this uncertainty, some states in North America are considering the implementation of an upper-limit assuming that the adult-juvenile association in fact increases the survival rate of juveniles. However, it is important to test this hypothesis as well as to know if there is a relationship between the amount of protection and the size of the adult before implementing an upper limit. To investigate this, I tested the hypotheses that 1) survival of juvenile urchins is enhanced by the presence of adult spine canopy in the presence of a natural predator, and 2) the predation rate on juveniles is related to the size of the adults present. Using six tanks, I conducted manipulation experiments of red sea urchins (adults and juveniles) and its natural predator, the sunflower star (*Pycnopodia helianthoides*), in order to observe the association between juvenile-adult and survival of juveniles over time in the presence of predators.

METHODS

In November 2002, using SCUBA equipment, I conducted field surveys were at two Oregon coast locations: Depoe Bay (44° 48'N: 122° 04'W) and Port Orford (42° 44.4'N: 124° 29.8'W). In Depoe Bay, no juvenile urchins were found. In Port Orford, I observed the use of adult spine canopies by juveniles in the Kelp forest habitat. Juveniles (n = 225) were collected (between 1.1 cm to 4.3 cm td) for the experiment (figure 2.1); individuals of this size are <2 yr old (Breen et al 1985). I also collected 40 adults (above 7 cm td). Collection depth ranged from 5 to 12 meters.

Urchins were measured in situ using Vernier calipers and care was taken not to break spines, and not to damage tube feet when removing sea urchins from their habitat.

Predator: *Pycnopodia helianthoides*

For the predator, I used large sunflower stars (*Pycnopodia helianthoides*). This species is the red sea urchins' major predator along the Oregon coast (Montano 2001). In fact, between Oregon and the northern Gulf of Alaska, the abundant starfish is the only organism that has been considered an important sea urchin predator (Duggins 1983, Montano 2001). This predator coexists with its prey without decimating urchin populations, with the exception of some areas with a high population of sea otters that tend to reduce significantly populations of urchins like in British Columbia (Duggins 1983). Duggins (1983) states that *Pycnopodia* eats in average 0.12 urchins per day, or 44 urchins per year, preferring urchins 6-8 cm in test diameter size in normal years when recruitment does not occur. However, *Pycnopodia* predation upon small red urchins might be more important in those sporadic years when good recruitment occurs, as well as in subsequent years until the cohort reaches the size refuge (> 8 cm td) (Duggins 1983).

I collected *Pycnopodia* from Boiler Bay, Oregon during a negative low tide. This rocky beach is a protected area with several tide pools inhabited by urchins and *Pycnopodia*. I measured the *Pycnopodia* in the field in order to collect individuals of approximately the same size and that were a good representation of the average size (25.7 cm) observed in the subtidal zone of this rocky beach. I determined the average size by collecting and measuring all the *Pycnopodia* that I observed ($n = 27$). *Pycnopodia* from subtidal areas were preferred since they can reach sizes greater than 25 cm in maximum diameter (maximum diameter measured from ray tip to opposite ray tip), plus *Pycnopodia* less than 25 cm maximum diameter rarely feed on urchins (Duggins 1983).

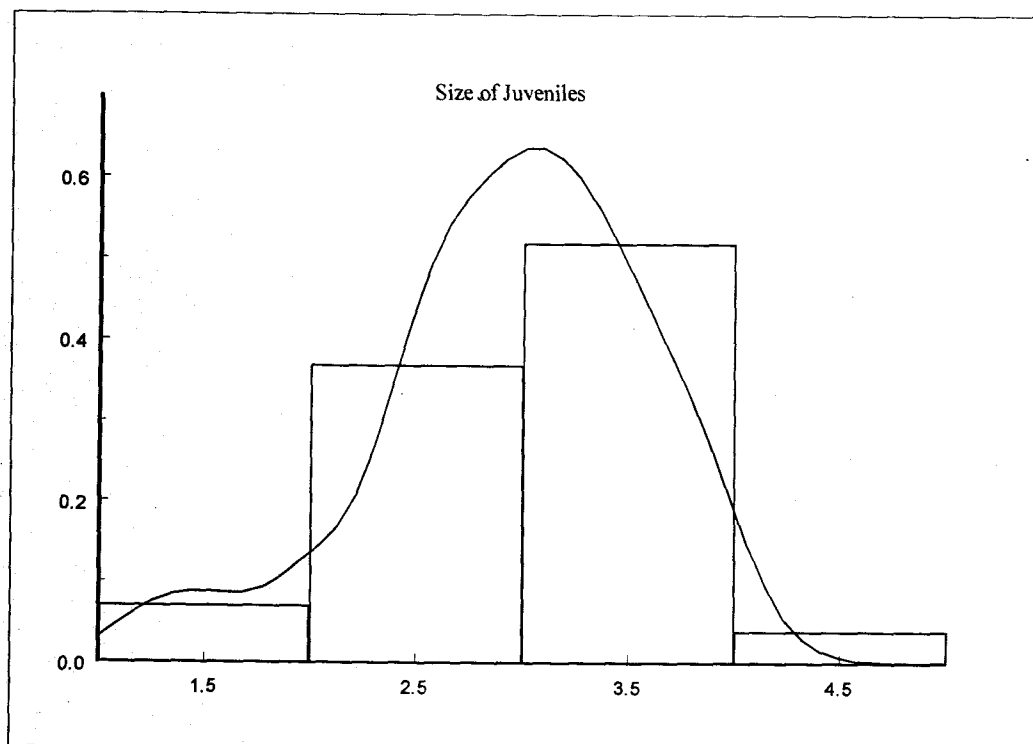


Figure 2.1. Size distribution of juvenile urchins collected from Port Orford field site.

Prey: *Strongylocentrotus franciscanus*

Urchins were held in round fiberglass tanks (191 cm in diameter x 96 cm in depth), with flow-through seawater system at the Oregon State University - Hatfield Marine Science Center (HMSC), in Newport, Oregon. Tanks were covered with fiberglass lids during the time of the experiment. Urchins were fed with fresh blades of the kelp *Nereocystis luetkeana* during the acclimation period. I used two different size classes for the adults in order to examine protection based on test diameter. The size classes for the adults were from 7 to 9 cm td (small adults) and from 13 to 15 cm td (large adults). A hollow concrete cinder block brick (19 x 19 x 15 cm) was placed in each tank in order to provide structure; however it has been shown that juveniles have a preference to hide under adults than under rocks when a predator is present (Breen et al. 1985). The brick was placed in the same location in every tank.

I placed twenty-five juvenile and four adult urchins into the tanks for one week prior to the onset of the experiment in order to observe behavior and adaptation to their new environment. The number of adults and juveniles were chosen based on the association of adults and juveniles observed in the field. Both juveniles and adults moved around the tank and up the sides until they reached the air-water interface; however the urchins chose no particular area. Temporary clusters of approximately four and five juveniles per adult urchins were formed during the 7 days. Very little use of the bricks if any was observed. Urchins were fed twice during this part of the experiment.

Experiment: Survival of juveniles under the presence of predatory sunflower star

I used three different treatments with three replicates each for this experiment (figure 2.2). The first treatment (NO ADULTS) consisted of 25 juvenile urchins per tank with no adults, the second treatment was 25 juvenile urchins per tank with 4 small adults (between 7 and 9 cm td) (SMALL), and the third treatment was 25 juveniles per tank with 4 large adults (between 13 and 15 cm in td) (LARGE). The size distribution of sizes of the juveniles was almost the same for every tank except for one tank (NO ADULTS 1) (figure 2.3). Due to limited availability of tanks; two treatments (LARGE and SMALL) were run first; 11 days later the third treatment (NO ADULTS) was run. Experimental conditions were held the same for all treatments, so this should not affect my results.

I placed the predators ($n = 18$) in empty tanks to observed behavior and adaptation to the experiment environment. The sunflower stars moved freely through the tanks, and were able to reach any part of the tank that could be reached by the urchins. Sunflower stars were held in the staging tank for one week, during which time they were fed with small purple urchins (*S. purpuratus*) in order to observe changes in feeding behavior due to enclosure; the Sunflower stars appeared to adapt well to the confined environment, as their hunting behavior was the same as that observed under

natural conditions. Following one week of confinement, *Pycnopodia* were starved for the 5 days preceding the onset of the experiment.

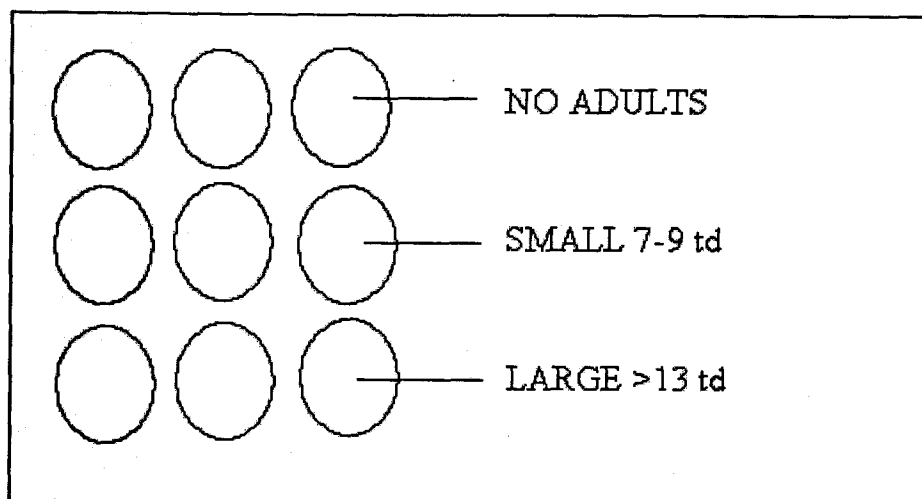


Figure. 2.2. Illustration of the experimental design: three treatments were used (NO ADULTS = no adults, SMALL = adults 7-9 cm td and LARGE = adults 13-15 cm td) with three replicates per treatment.

Two *Pycnopodia* were allocated to each of the treatments tanks at the onset of the experiment; they were held in the experimental tanks with the urchins for 2 days in a sealed plastic bucket with small holes in order to observe change in behavior on the urchins. Urchins moved up to the air-water interface as soon as the bucket with *Pycnopodia* were introduced into the tanks. During the second day, urchins moved freely along the tank, apparently ignoring the presence of the enclosed predators. After 2 days, the predators were released into the tanks and survivors were counted every 24 hours for 11 days for each treatment (figure. 2.6).

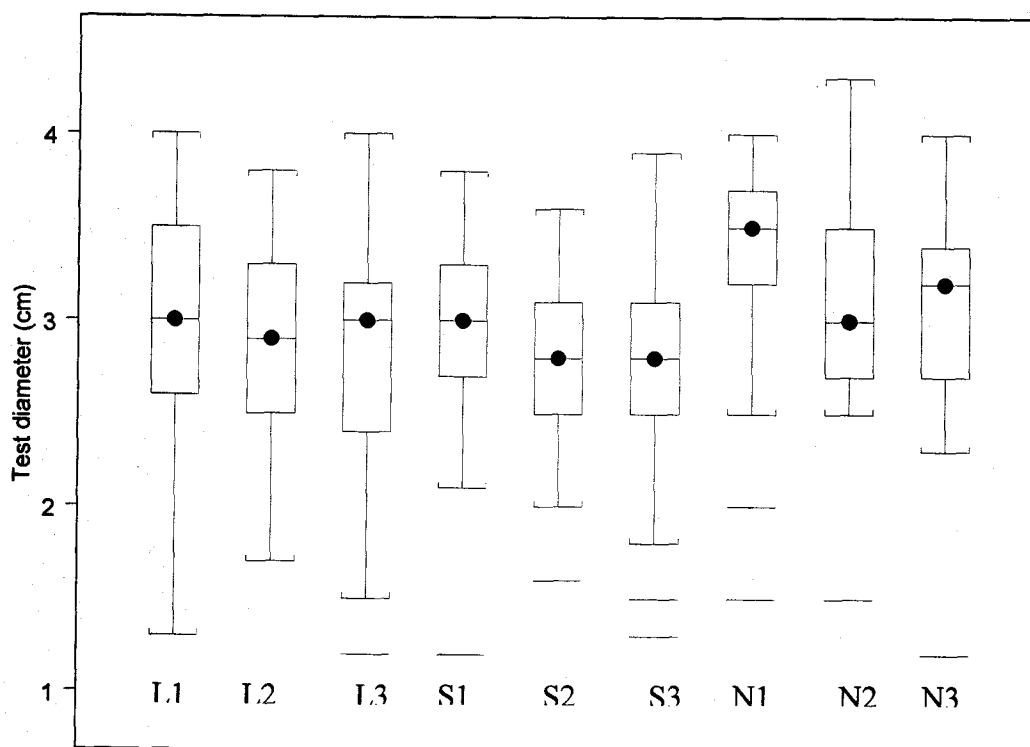


Figure 2.3. Juvenile urchins for each tank; sizes ranges were from 1.1 to 4.3 cm td. L# = treatments with LARGE adults, S# = treatments with SMALL adults, and N# = treatments with NO ADULTS.

RESULTS

An analysis of variance (ANOVA) was performed testing the null hypothesis that there is no difference between the sizes of juveniles among the tanks (Table 2.1). The null hypothesis was rejected (p -value = 0.018). However, an analysis of variance was performed again removing CONTROL 1 since this tank seemed to have slightly bigger juveniles than the others. In this case, the null hypothesis was that there is no difference between the sizes of juveniles among the tanks (Table 2.2). The null hypothesis was not rejected this time (p -value = 0.28). However, the tank (CONTROL 1) might have affected the results of the experiment.

Table 2.1. A single factor analysis of variance, H_0 = mean of juvenile urchins is the same for every tank.

Anova: Single Factor

SUMMARY

<i>Groups</i>	<i>Count</i>	<i>Sum</i>	<i>Average</i>	<i>Variance</i>
SMALL1	25	69.5	2.78	0.235
SMALL2	25	73.9	2.956	0.3042333
SMALL3	25	68.9	2.756	0.4842333
LARGE1	25	71.1	2.844	0.3359
LARGE2	25	72.8	2.912	0.4569333
LARGE3	25	69.7	2.788	0.5494333
NO ADULT 1	25	77.3	3.092	0.3691
NO ADULT 2	25	77.8	3.112	0.3794333
NO ADULT 3	25	83.2	3.328	0.3821

ANOVA

<i>Source of Variation</i>	<i>SS</i>	<i>df</i>	<i>MS</i>	<i>F</i>	<i>P-value</i>	<i>F crit</i>
Between Groups	7.3688	8	0.9211	2.3710042	0.0182192	1.9814479
Within Groups	83.9128	216	0.3884852			
Total	91.2816	224				

Table 2.2. A single factor analysis of variance, H_0 = mean of juvenile urchins is the same for every tank, excluding tank: NO ADULT 1.

Anova: Single Factor

SUMMARY

<i>Groups</i>	<i>Count</i>	<i>Sum</i>	<i>Average</i>	<i>Variance</i>
SMALL1	25	69.5	2.78	0.235
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NO ADULT 2	25	77.3	3.092	0.3691
NO ADULT 3	25	77.8	3.112	0.3794333

ANOVA

<i>Source of Variation</i>	<i>SS</i>	<i>df</i>	<i>MS</i>	<i>F</i>	<i>P-value</i>	<i>F crit</i>
Between Groups	3.3926	7	0.4846571	1.2449984	0.2800798	2.0575328
Within Groups	74.7424	192	0.3892833			
Total	78.135	199				

Behavior of juveniles was also recorded every 24 hours for 2 hours at a time (from 3 to 5 pm) for the two treatments containing adults and classified into three different categories: under adults (totally under spine canopy or less than 2 cm apart from adults), cluster of juveniles or alone. Observations were recorded for each treatment by pooling the total of number of juveniles of each replicate into the different categories (figure 2.4). The mean number of juveniles looking for refuge under adults is shown in figure 2.5. A chi-square goodness of fit test was used to test the hypotheses that there is no difference between the two treatments for juveniles looking for refuge under adults under the presence of its natural predator. The hypothesis was not rejected; there is no difference in behavior between the two treatments (Table 2.3).

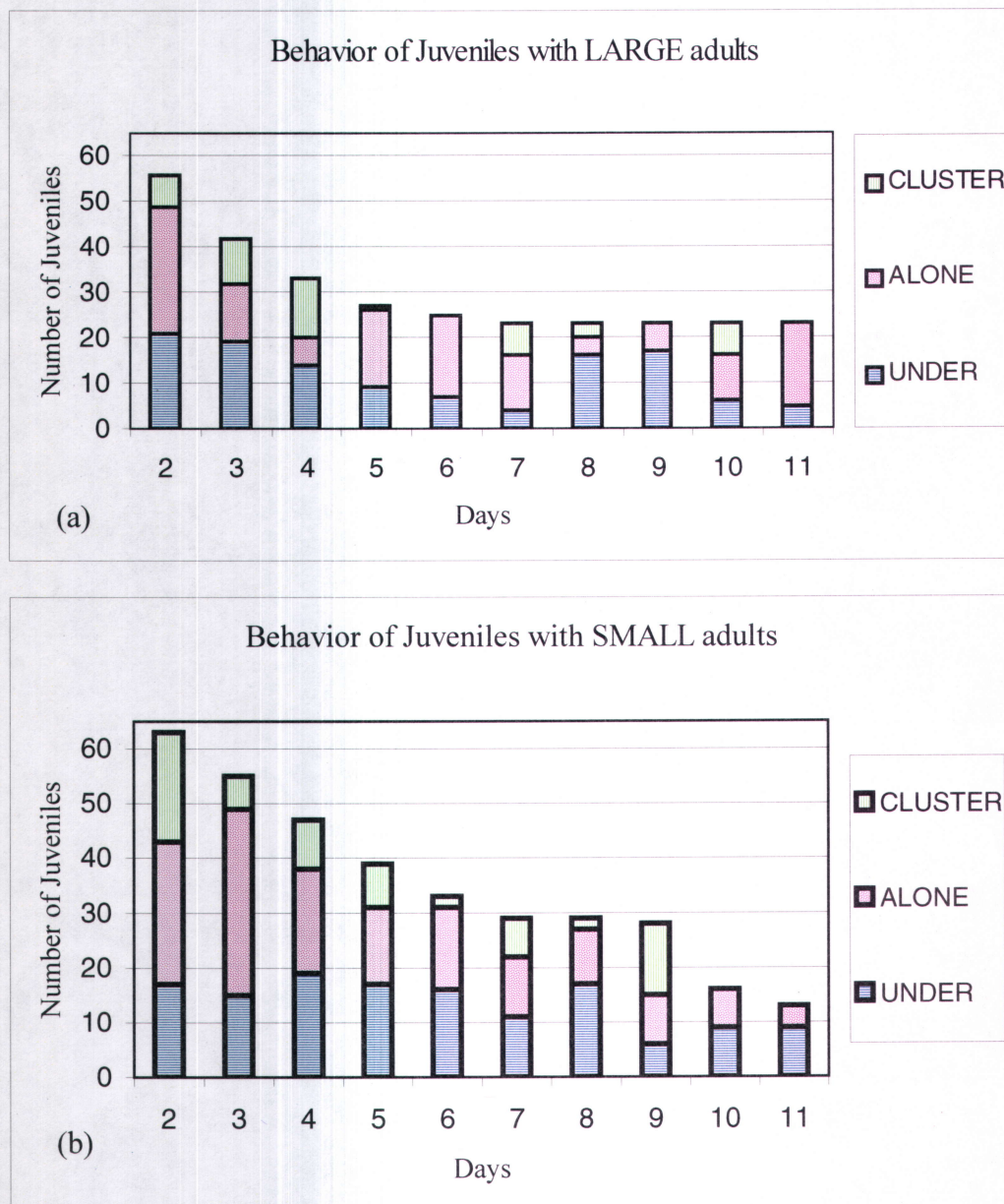


Fig. 2.4. Behavior of juveniles in the presence of adults and its natural predator over 10 days. (a) Behavior of juveniles with LARGE adults. (b) Behavior of juveniles with SMALL adults. Pooled data for 3 replicates.

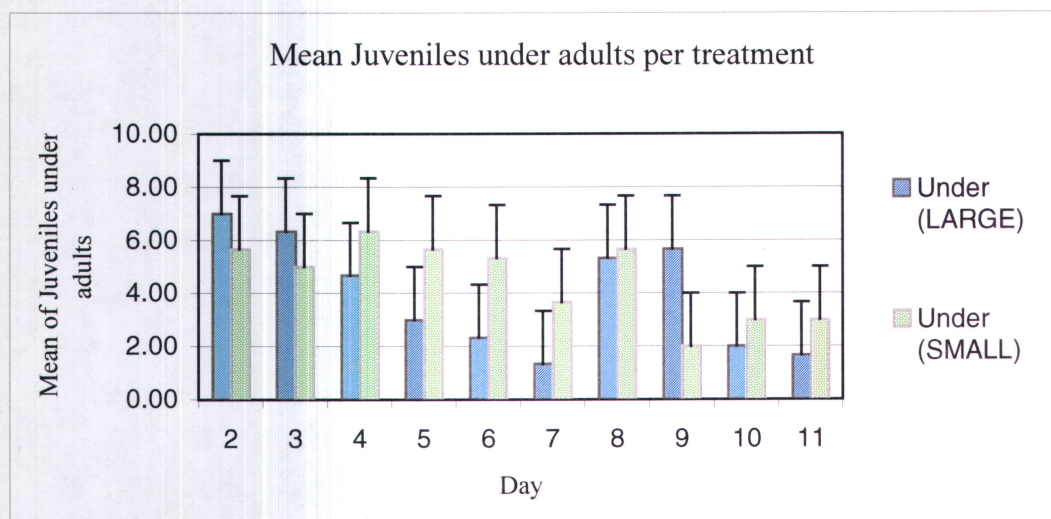


Figure 2.5. Mean number of juveniles looking for refuge under the spine canopy habitats provided by the adults in the different treatments.

Table 2.3. Chi-square analysis for behavior of juveniles for both treatments (Large and Small)

	Day 2	Day 3	Day 4	Day 5	Day 6	Day 7	Day 8	Day 9	Day 10	Day 11	Total
Under Large	21	19	14	9	7	4	16	17	6	5	118
Under Small	17	15	19	17	16	11	17	6	9	9	136
Total	38	34	33	26	23	15	33	23	15	14	254

Degrees of freedom: 9

Chi-square = 16.7416769400318

Critical Chi-square = 16.92.

The distribution is not significant.

RESULT: NO SIGNIFICANT DIFFERENCE

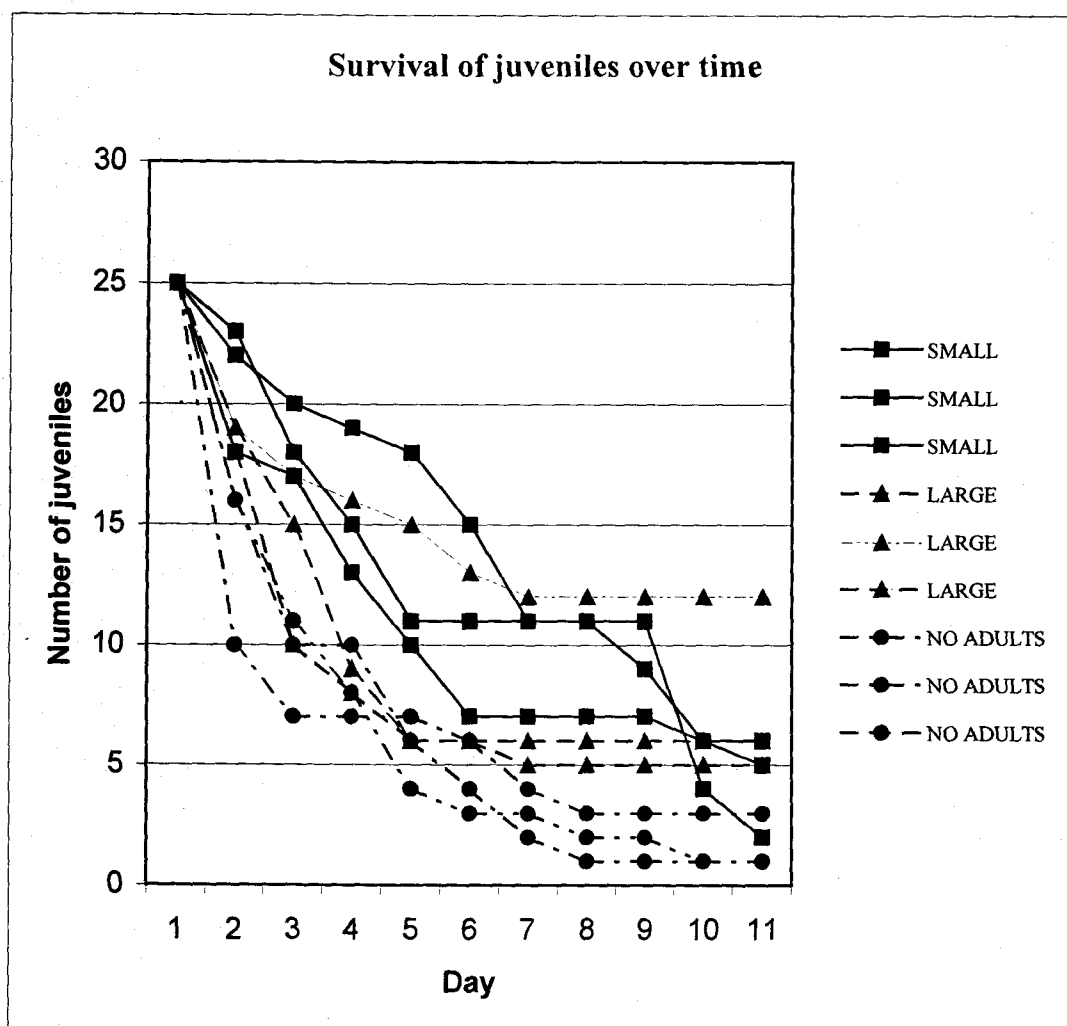


Figure 2.6. Survival of juvenile urchins over time for the three different treatments under the presence of red urchins' natural predator, the sunflower star.

There was a rapid decline in the number of juveniles in the first five days of the experiment; where the treatment with SMALL adults seemed to have a lower rate of decline compared to the other treatments. After day 6, the number of juveniles preyed by the sunflower star in those treatments containing adults, decreased compared to the treatment with no adults. Mortality of juveniles associated with LARGE adults level off after day 6; none of the juveniles were eaten during this part of the experiment (figure 2.6).

A chi-square goodness of fit test was used to test the hypotheses that (1) survival of juvenile urchins is enhanced by the presence of adult spine canopy under the presence of its natural predator (NO ADULTS vs. SMALL and LARGE), and that (2) the rate of survival of juveniles is related to the size of the adult under the presence of its natural predator (SMALL vs. LARGE). There was not a significant difference among replicates (Table 2.4, 2.5 and 2.6), and therefore data for each treatment were pooled. The null hypothesis that survival of juvenile urchins was not enhanced by the presence of adults was rejected, indicating that there was a significant difference on survival of juveniles among treatments (Table 2.7).

Table 2.4. Chi-square analysis within treatment (LARGE) of number of surviving juvenile urchins.

	Day 1	Day 2	Day 3	Day 4	Day 5	Day 6	Day 7	Day 8	Day 9	Day 10	Day 11	Total
L. 1	25	19	15	9	6	6	5	5	5	5	5	105
L. 2	25	19	17	16	15	13	12	12	12	12	12	165
L. 3	25	18	10	8	6	6	6	6	6	6	6	103
Total	75	56	42	33	27	25	23	23	23	23	23	373

Degrees of freedom: 20

Chi-square = 12.9618138973744

Critical Chi-square = 31.41

The distribution is not significant

RESULT: NO SIGNIFICANT DIFFERENCE

Table 2.5. Chi-square analysis within treatment (SMALL) of number of surviving juvenile urchins.

	Day 1	Day 2	Day 3	Day 4	Day 5	Day 6	Day 7	Day 8	Day 9	Day 10	Day 11	Total
S. 1	25	22	20	19	18	15	11	11	11	4	2	158
S. 2	25	23	18	15	11	11	11	11	9	6	5	145
S. 3	25	18	17	13	10	7	7	7	7	6	6	123
Total	75	63	55	47	39	33	29	29	27	16	13	426

Degrees of freedom: 20

Chi-square = 9.11437297711987

Critical Chi-square = 31.41

The distribution is not significant

RESULT: NO SIGNIFICANT DIFFERENCE

Table 2.6. Chi-square analysis within treatment (NO ADULTS) of number of surviving juvenile urchins.

	Day 1	Day 2	Day 3	Day 4	Day 5	Day 6	Day 7	Day 8	Day 9	Day 10	Day 11	Total
NO A. 1	25	10	7	7	7	6	4	3	3	3	3	78
NO A. 2	25	16	10	10	6	4	2	1	1	1	1	77
NO A. 3	25	16	11	8	4	3	3	2	2	1	1	76
Total	75	42	28	25	17	13	9	6	6	5	5	231

Degrees of freedom: 20

Chi-square = 10.8891638373402

Critical Chi-square = 31.41

The distribution is not significant

RESULT: NO SIGNIFICANT DIFFERENCE

Significant difference in survival over time was found for both groups of adults when compared to the control; however there was not a significant difference between LARGE and SMALL adults (Table 2.8, 2.9, and 2.10).

Table 2.7. Chi-square analysis for the three different treatments (LARGE, SMALL and NO ADULTS)

	DAY 1	DAY 2	DAY 3	DAY 4	DAY 5	DAY 6	DAY 7	DAY 8	DAY 9	DAY 10	DAY 11	Total
L.	75	56	42	33	27	25	23	23	23	23	23	373
S.	75	63	55	47	39	33	29	29	27	16	13	426
NO A.	75	42	28	25	17	13	9	6	6	5	5	231
Total	225	161	125	105	83	71	61	58	56	44	41	1030

Degrees of freedom: 20

Chi-square = 45.5411855953068

Critical Chi-square = 31.41

p is less than or equal to 0.001

The distribution is significant

RESULT: SIGNIFICANT DIFFERENCE

Table 2.8. Chi-square analysis for the two treatments (LARGE and NO ADULTS)

	DAY 1	DAY 2	DAY 3	DAY 4	DAY 5	DAY 6	DAY 7	DAY 8	DAY 9	DAY 10	DAY 11	Total
L.	75	56	42	33	27	25	23	23	23	23	23	373
NO A.	75	42	28	25	17	13	9	6	6	5	5	231
Total	150	98	70	58	44	38	32	29	29	28	28	604

Degrees of freedom: 10

Chi-square = 29.4057401024911

Critical Chi-square = 18.31

The distribution is significant

RESULT: SIGNIFICANT DIFFERENCE

Table 2.9. Chi-square analysis for the two treatments (SMALL and NO ADULTS)

	DAY 1	DAY 2	DAY 3	DAY 4	DAY 5	DAY 6	DAY 7	DAY 8	DAY 9	DAY 10	DAY 11	Total
S.	75	63	55	47	39	33	29	29	27	16	13	426
NO A.	75	42	28	25	17	13	9	6	6	5	5	231
Total	150	105	83	72	56	46	38	35	33	21	18	657

Degrees of freedom: 10

Chi-square = 30.1443371881884

Critical Chi-square = 18.31

The distribution is significant

RESULT: SIGNIFICANT DIFFERENCE

Table 2.10. Chi-square analysis for the two treatments (LARGE and SMALL)

	DAY 1	DAY 2	DAY 3	DAY 4	DAY 5	DAY 6	DAY 7	DAY 8	DAY 9	DAY 10	DAY 11	Total
L.	75	56	42	33	27	25	23	23	23	23	23	373
S.	75	63	55	47	39	33	29	29	27	16	13	426
Total	150	119	97	80	66	58	52	52	50	39	36	799

Degrees of freedom: 10

Chi-square = 10.1571500947319

Critical Chi-square = 18.31

The distribution is not significant

RESULT: NO SIGNIFICANT DIFFERENCE

DISCUSSION

The association of juvenile urchins with adults in order to avoid predation has been previously reported (Tegner and Dayton 1977, 1981, Breen 1984, Breen et al 1985). However, the importance of this association with regard to survival of juveniles over time has not been investigated, nor observed in the field (Duggins 1983). Among the reasons for this is the absence of research during good recruitment years, which are sporadic events (Duggins 1983, Montano 2001). The experiment conducted here is intended to represent a year of good recruitment followed by those years of growth of juveniles by having juvenile urchins under 4.5 cm td. However, it is not possible to replicate natural environments in a laboratory experiment. Enclosure of urchins in a confined environment where they cannot escape by migrating away from the predators is something to consider before making any type of conclusion. It is clear that natural survival rates over time could not be calculated from this type of experiment, but if predator avoidance is the more important function of the adult-juvenile association (Breen et al 1985), a higher survival of juveniles should be expected by having adults associated with juveniles. A slower decline was expected over time of juvenile urchins associated with LARGE adults (13 to 15 cm td) than with the SMALL adults, since LARGE adults can provide a bigger canopy habitat for the juveniles. This appears not to be the case. While juveniles look for refuge under adult spine canopies when threatened with predation, there is not a significant difference in survival of juveniles based on the size of the adults. Therefore, an upper size limit based on the assumption that larger adult association will provide a greater protective habitat to protect juvenile urchins from natural predation compared to small adults is not supported. However, there is a greater survival of juveniles when associated with adults of any size (LARGE and SMALL). An experimental study of survival of juveniles under different densities of adults was intended, but it could not be done due to limitation of finding and collecting juveniles below 5 cm in td.

At the beginning of the experiment, when *Pycnopodia* were introduced into the tanks, urchins (juveniles and adults) moved away from the enclosed predators to the

air-water interface. This suggests that the urchins can detect the presence of predators. However, urchins started to move freely along the tank during the second day. This suggests that red sea urchins can distinguish between active and inactive *Pycnopodia* as Breen et al (1985) suggested. When predators were released, juvenile urchins associated immediately with adults. This supports the hypothesis that juveniles associate with adults to avoid predation. However, when *Pycnopodia* approached, not all juveniles remained under the spine canopies; some individuals moved away from the adults or behind the adults, forming temporarily clusters or sitting alone.

Pycnopodia paid little attention to the adults when this occurred and chased the juveniles. This created a faster dispersion of juveniles along the tank, which increased mortality. This could be related to the number of juveniles than an adult can protect under threatening conditions, or that adults reject some juvenile urchins when threatened by predators. However, no analysis has been conducted to test these ideas. High mortality could be related to the artificial environment. Even though juveniles sought refuge under or behind spine canopies, *Pycnopodia* could go around the adults and forced some of the juvenile urchins out of their protection. Three adults (two LARGE and one SMALL) were eaten by *Pycnopodia* during the experiment. These adults were replaced for other adults of the same size. I believed that this did not affect the results of the experiment since *Pycnopodia* kept chasing juveniles during the 11 days. However, any report of predation on red sea urchins larger than 8 cm td by *Pycnopodia* has been reported before.

Contrary to my expectations of low mortality of juveniles due to protection of adults, I observed a high mortality of juveniles in all treatments and no difference between the SMALL and LARGE treatments. These results differed from Breen et al. (1985), where 4 adults and 40 juveniles were placed with 5 different starfish (3 of them were *Pycnopodia*) and only one juvenile was eaten. However, their predators were all smaller than 20 cm and it has been reported that *Pycnopodias* smaller than 25 cm in maximum diameter rarely feed on red sea urchins (Duggins 1983). Even though I did not find a significant difference in protection based on the size of the adults, there

was a slower decline in juvenile urchins with SMALL adults at the beginning of the experiment (figure 2.6). I observed that small adults tended to move away, followed by juveniles, when predators approached. Large adults tended to stay in one place, and not all juveniles stayed with them when predators approached. This could explain why for the last five days of the experiment, mortality of juvenile urchins associated with larger adults remained almost at the same level. It is possible that larger adults that stayed in the same place facing predators are more effective protecting a smaller number of juveniles than smaller adults that run away. This could explain why at the last 6 days of the experiment *Pycnopodia* did not eat any juvenile associated with LARGE adults. However, more work needs to be done in order to better understand this behavior and its benefits, if there is one.

3. EVALUATION OF MANAGEMENT STRATEGIES FOR THE RED SEA URCHIN *STRONGYLOCENTRATUS FRANCISCANUS* (Agassiz): MATRIX MODELS OF POPULATION GROWTH

INTRODUCTION

The red sea urchin, *Strongylocentrotus franciscanus*, is one of the three species of strongylocentroids belonging to the phylum Echinodermata found on the west coast of North America from Baja California to Kodiak, Alaska. It has a calcareous shell or test covered with a thin epithelium and armed with spines, and they can regrow broken off spines. The urchins move their feet by a system, which creates suction in the end of the foot by pulling water out. It is one of the largest species of sea urchins, growing to a test diameter of about 17 centimeters. It is considered a long-lived species, with some individuals living for at least 100 years (Ebert, 1998). Red sea urchins occupy shallow waters, from the mid- or low intertidal zone to depths up to 50 meters; however some individuals can be found up to 125 meters. They are free-spawning invertebrates, and produce a large number of eggs. However, their rates of juvenile recruitment are typically low due to the low probability of eggs encountering sperm in the plankton and low survival of juveniles (Pennington, 1985). They are herbivores that profoundly affect the structure of the benthic algal community, thus their absence or decrease has significant consequences for nearshore communities (Pfister and Bradbury 1996, Paine et al 1969). In populations of red sea urchins, large individuals are extremely important due to their high fecundity and because they provide "canopy" habitat for small juveniles. Once the urchins settle into the benthos, they live for at least their first two years as juveniles in association with adults (Breen et al 1985).

In populations of red sea urchins, large individuals are believed to be extremely important due to their high fecundity and because they provide "canopy" habitat for small juveniles. This nursery association of adult and juvenile urchins offers two probable advantages to the smaller animals: increase ability of adults to

acquire food for juveniles and protection from predators (Tegner et al 1977, Breen et al 1985). However, the population level benefits of this association have not been explored empirically, nor theoretically.

Since 1970, red sea urchins have been fished commercially for their highly valued gonads; as a result, the abundance of harvestable size urchins has rapidly declined in a relatively short period of time. This susceptibility to population collapse with an increase in mortality due to harvesting has been attributed mainly to (1) the loss of spine canopy for small urchins and (2) decrease in fecundity by removal of big adults. In other words, reduced recruitment and depensation (low densities limiting reproductive output by reducing the probability of fertilization) affect long-term population trajectories. Some models that incorporate these dependencies have been made (Pfister and Bradbury 1996, Ebert 1998); but their conclusions differed in the importance of these dependencies in relation to population growth rates. Differences are mainly due to the importance given to the survival of juveniles urchins enhance by the adult spine canopy and contribution of reproductive adults to the population. Pfister and Bradbury (1996) included a strong relationship between juvenile (new recruit) survival and adult abundance in relation to the population growth rate; on the contrary, Ebert (1998) concluded that these dependencies are not that important. Also, Ebert (1998) explored this dependency by assuming that survival of urchins under natural conditions remain constant for all size classes ($s = 0.95$; 95 % annual survival); however, it has been reported that red sea urchins between 6 and 8 cm td have a lower survival rate due to predation than those reported by Ebert (Duggins, 1983). Plus, prior to this work, no experimental study that evaluates survival of juveniles as a function of density or size of adults had been done.

Based on the experimental study of *Pycnopodia* predation presented in part 2, there is a high mortality of juveniles (from 1 to 4.5 cm td) when adults are present and there is not a difference in protection based on the size of the adults; however, survival is much lower when no adults are present. This suggests that survival of juveniles

urchins is less than that reported by Ebert. Based on these results, an analysis of population growth could be made by incorporating the information obtained in the experimental study into a mathematical model. The objectives of this paper are (1) to incorporate the information obtained in the predation experiment and create two size-class structured models based on an analysis of the red sea urchin life cycle under different survival rates, (2) to identify the sensitivity of λ to changes in survival rates of different size classes (3) to measure changes in population growth rate under various harvest scenarios that include both a lower and upper size limit, and (4) to compare the population growth rate of the two models to see how important is the association between adult-juveniles with respect to population growth.

The first model (Model 1) is a linear deterministic model, while Model 2 is a non-linear deterministic model. The linear deterministic model, assumes stable age distribution where the proportion of individuals in each age class is constant over time. It also assumes that juvenile survival remains constant through time and that juvenile survival is not dependent on the presence of adults. The Model 2 assumes that survival of juveniles depends on the association between juveniles and adults, so it examines at differences in survival of juveniles based on the ratio between juveniles and adults. Both models focus on relative changes in population responses as certain parameters in the population model are changed. Population growth rate, which is represented by λ , is used as population response. The growth rate is related to the intrinsic rate of increase (r) obtained for Lotka's equation $r = \ln \lambda$, where λ is the dominant eigenvector of a matrix. Sensitivity analysis can reveal how changes in size-classes vital rates (e.g. survival, growth, or fecundity) affect λ (Ferson and Burgman 2000). These models are relatively simple; however, they still contain a number of unknowns or uncertain parameters. Consequently, these models serve as heuristic tools to assess the impacts of different management strategies and to identify critical research needs.

METHODS

The importance of an upper size limit was explored by using an analysis of the red sea urchin life cycle (figure 3.1). Size was used to define categories, and so transitions mean transfer from one size class to another, g_x , remaining in a size class, r_x , or reproducing and contributing back to the smallest size class, f_x . Each of these transitions has the same time period of one year and so f_x values include egg production, fertilization, survival in the plankton, and early survival up to the age of one year from the time of spawning. By modifying survival of adults that reach the harvestable size, the importance of an upper size limit and its contribution to the population growth was investigated. The steps in analysis were to assemble all of the transitions into a matrix that could be analyzed using the techniques presented by Caswell (1989).

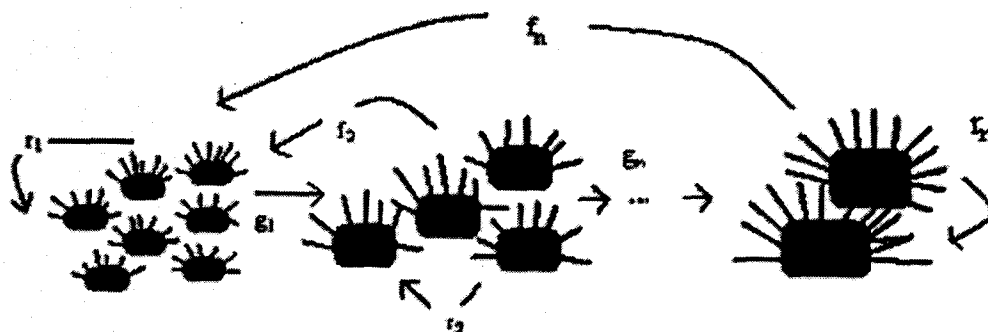


Figure 3.1. Life cycle based on size classes; g_x = the probability of growth from one size class to another multiplied by the annual survival rate; r_x = the probability of staying in that size class multiplied by the annual survival rate; f_x = size-specific fecundity, m_x , multiplied by p_0 where p_0 = first year survival and includes: fertilization rate, survival in the plankton, and, post-settlement survival up to the age of 1 year. After Ebert (1998).

Each pre-breeding census matrix, where individuals are “counted” just prior to the breeding season (Heppell 1998), consists of 1 cm size classes (Ebert 1998). The

data in the matrix (same for both models) included growth, survival and reproduction. Growth, calculated by Ebert, was determined by mark-recapture of wild sea urchins tagged with tetracycline (Ebert 1998). Natural survival rates (s_x) were estimated for animals older than one year (Duggins 1983, Ebert 1998), and assumptions made based on the experiment presented in chapter 2 of this document (Table 3.1). Survival to age 1, s_0 , is included in the fertility terms and chosen from trial values until the population growth rate (λ) of both models was slightly above 1.0. A $\lambda = 1$ means that the populations would be neither increasing nor decreasing. In this case, the baseline (= unharvested) populations are increasing ($\lambda = 1.07$) by 7 % per year. While somewhat arbitrary, this increase is probably reasonable for unexploited populations at low density (populations that have not yet reached their carrying capacity). Reproduction was calculated by converting size-specific spawn mass to egg number using the relationship between volume and egg number (7.764×10^5 eggs cm^{-3}) (figure 3.2) (Levitan 1993). Using the software program Mathcad™, the final transition matrix ($M_{x,y}$) for the unexploited populations of red sea urchin was calculated with the growth times survival transitions along the diagonal and f_x values in the first row which included early survival, s_0 , and fecundity, m_x . In other words, $f_x = s_0 m_x$ (Table 3.2). Where m_x is the number of eggs produced by females. These models are female-based; I assumed these populations have a 50:50 sex ratio and multiplied m_x by 0.5 in order to incorporate this ratio into the model.

The values for survival for each size class are presented in the table 11. A lower survival rate was given to juvenile urchins in the 1-2 cm td size class compared to the rest of juveniles, which assumes high mortality rates at that stage. Lower survival rates for the rest of juveniles, when compared to Ebert's values, were given based on the high mortality observed under the predation experiment. Assuming high predation on urchins between 6 and 9 cm td as reported by Duggins, a lower survival rate was given to those adults compared to the rest of the adults under unexploited conditions.

Table 3.1. Natural annual survival rates (s) for urchins older than one year in two unexploited populations (Populations for Model 1 and 2), where $s_0 = 0.5 \times 10^{-7}$.

cm	0-1	1-2	2-3	3-4	4-5	5-6	6-7	7-8	8-9	9-10	10-11	11-12	12-13	13-14	14-15	15-16	≥ 16.1
S	5×10^{-7}	0.5	0.85	0.85	0.85	0.85	0.75	0.75	0.75	0.95	0.95	0.95	0.95	0.95	0.95	0.95	0.95

In order to identify to which size class or size classes have the biggest impact on λ , I determined the stable age distribution (w_x) and age-specific reproductive values (v_x), which are the right and left eigenvectors associated with the dominant eigenvalue, λ . The Elasticity matrix ($E_{x,y}$), which shows the proportional change in λ given a proportional change in each matrix parameter ($M_{x,y}$) is given by:

$$E_{x,y} = \delta \log \lambda / \delta \log M_{x,y} = (M_{x,y} / \lambda) * ((v_x * w_x) / \sum (v_x * w_x)) \quad (1)$$

Elasticities of matrix elements sum to 1.0; thus, the elasticities can be interpreted as proportional contributions of fecundity and annual survival to the population growth rate, λ (Heppell 1998).

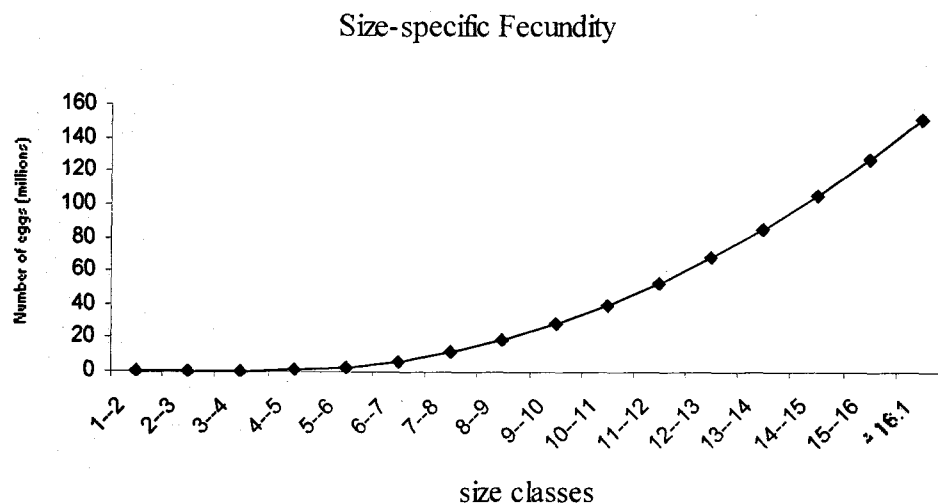


Figure 3.2. Relationship between test diameter and number of eggs (m_x).

Table 3.2. Transition matrix for an unexploited population of red sea urchins with growth x survival transition in a band along the diagonal and f_x values in the first row.

[illegible]

Dependency of juvenile survival based on the presence of adults was modeled by using a relationship that is determined by the ratio of juveniles to adults. Juveniles that were included in this ratio were urchins from 1 to 4 cm td and they were chosen based on the sizes of juveniles used in the experimental study presented in chapter 2. The adults were greater than 9 cm td, representing only the adults that are above the harvest lower size limit (8.9cm td). Consequently, population growth rates under harvest are affected by this relationship. This relationship is integrated into the model by using the equation:

$$P = 1/(1 + \exp^{(-a+bX)}) \quad (2)$$

where P is a multiplier for juvenile survival. The parameters a and b determine the shape of the relationship, and X represents the ratio of juveniles to adults. Parameter b determines the slope of this relationship. We do not know the true shape of this relationship, nor the exact ratio of juveniles to adults that provides the maximum survival rate for the juveniles. For the purpose of this heuristic exercise, knowing the exact value of this relationship is not crucial since the model is looking at changes in λ under different ratios of juveniles to adults (levels of dependency) in order to evaluate the importance of this association.

The initial population growth rate (λ) was obtained from the final transition matrix. By performing sensitivity analyses that are changes in size-classes vital rates (e.g. survival, growth, or fecundity) under different scenarios (different upper size limits and fishing mortalities), I made projections of adults over time (100 years) for an imaginary population of 1 million red sea urchins. The slopes of these projections were used to obtain the population growth rates, where λ is given by the equation:

$$\lambda = e^{\text{slope}} \quad (3)$$

however, the first 20 years of these projections were ignored in order to avoid initial conditions that could affect the population growth rates.

Mortality estimates represent the total instantaneous mortality (Z) of the population, and encompasses instantaneous fishing (F) under harvest conditions and instantaneous natural (M) mortality:

$$Z = M + F \quad (4)$$

Where: $e^{-Z} = \text{survival } (s_x) \quad (5)$

RESULTS

Sensitivity analysis:

I calculated the elasticities for a population of red sea urchins based on the baseline population, where the population is slightly increasing ($\lambda = 1.07$), there is not harvesting, and there is not a dependency on survival of juveniles based on the direct association juveniles to adults. I separated the size classes into three different categories: juveniles (1-5 cm td), young adults (reproductive adults under lower size limit) and old adults (reproductive adults larger enough to enter the fishery). I summed size class-specific elasticities within these categories (figure 3.3) in order to evaluate the proportional contribution of fecundity and annual survival to λ . There is a greater elasticity of old adults. This means that λ would be more sensitive to changes in survival of adults between 9 and 16 cm td.

In order to explore which size class among this group has a greater proportional contribution of fecundity and annual survival to λ (figure 3.4), elasticities

of older adults were examined. This could help me to determine if an upper size limit that intends to protect larger adults would be beneficial to increase or maintain λ at a healthy level. By looking at the graph, those urchins that are between 9 and 12 cm td have greater elasticities than the rest of the old adults. This means that λ could be more sensitive to changes in survival of adults between 9 and 12 cm td. Therefore, an upper size limit that protects adults larger than 13 cm td may not be that beneficial than an upper size limit that protects smaller adults within this category.

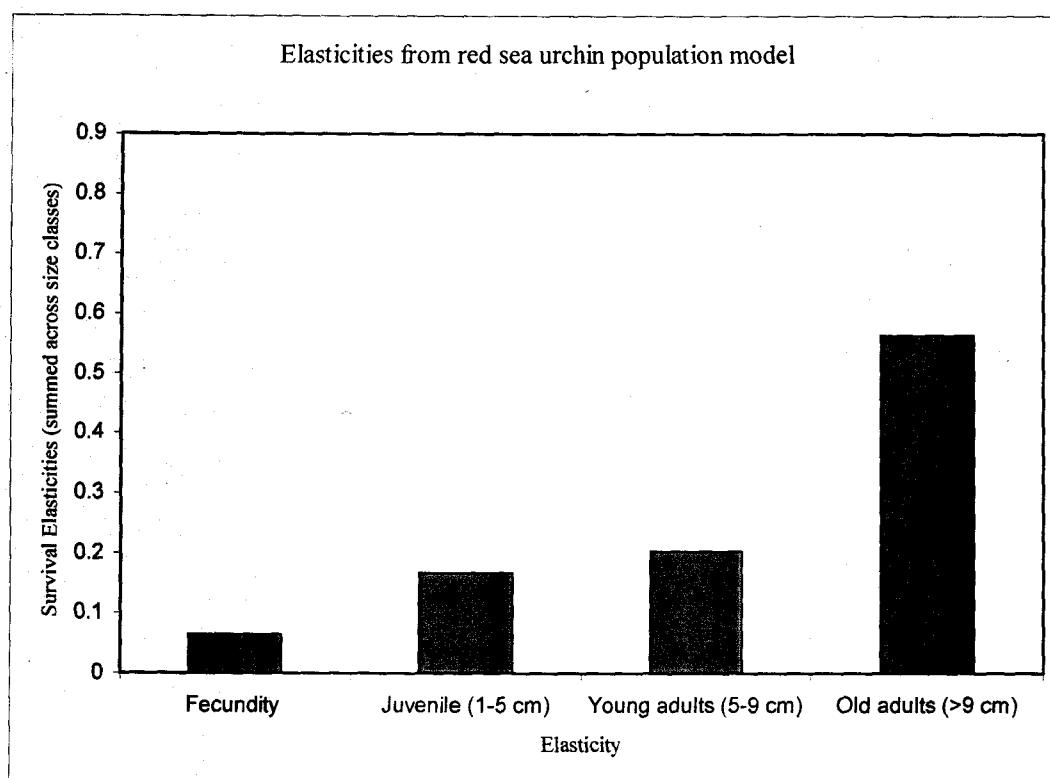


Figure 3.3. Elasticities from a red sea urchin population model. Elasticity = proportional contribution of fecundity or annual survival to λ , the population growth rate.

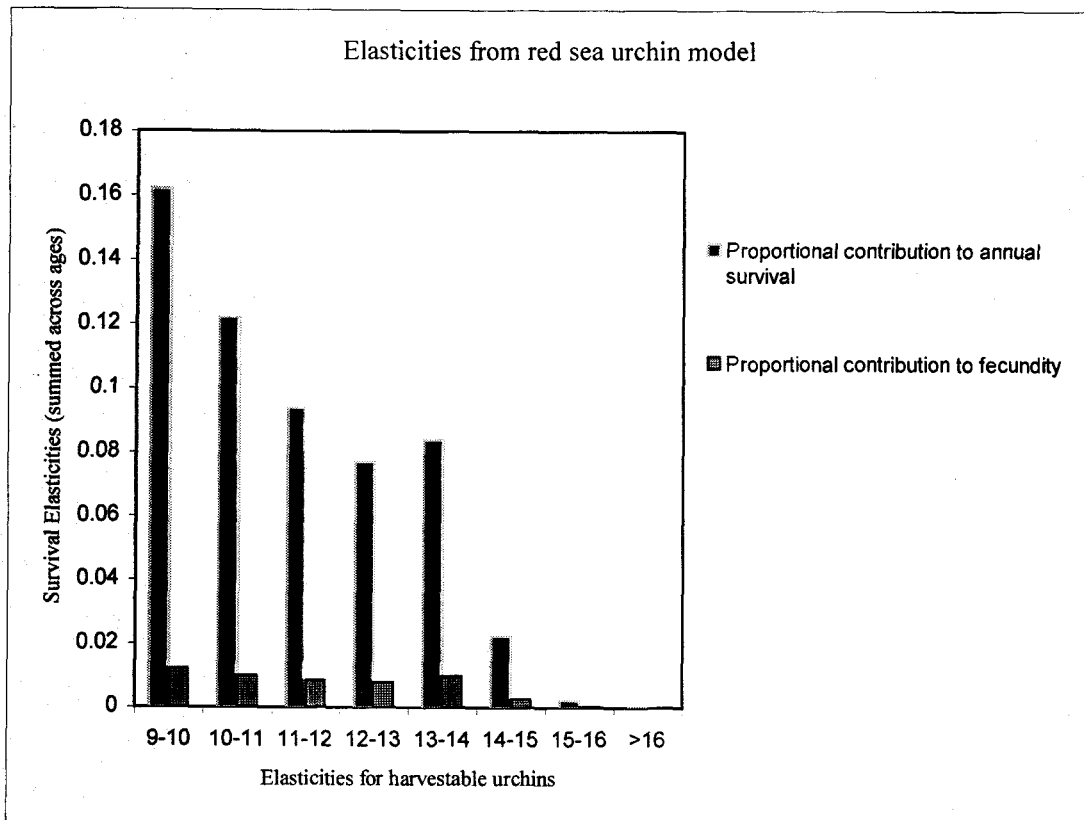


Figure 3.4. Elasticities from a red sea urchin population model for those adults under the category of “old adults” (from 9 to >16 cm td). Proportional contribution of annual survival and proportional contribution of fecundity are represented for each size-class.

Effects of harvest on λ :

In the linear deterministic model (Model 1), assuming that survival of juveniles remains constant through time and that there is not a dependency on survival of juveniles based on the direct association between juveniles and adults, the population growth rate was calculated for the unexploited population to be $\lambda = 1.07$. Applying different upper size limits and by adding different values for fishing mortality (F) I explored changes on λ (figure 3.5). As expected, there was a decrease in λ when fishing mortality was increased, because F decreases survival rates of harvested size

classes. Also, there was a decrease in λ when a greater upper size limit was applied, which resulted in a higher mortality of older adults. For this model at a fishing mortality of 0.2, upper size limits above 13 cm td will create a decline of the population at a rate of approximately 2.3 % ($\lambda = 0.977$). However, any dependency on survival of juveniles based on the presence of adults was included in this analysis, which is unrealistic for a population of red sea urchins.

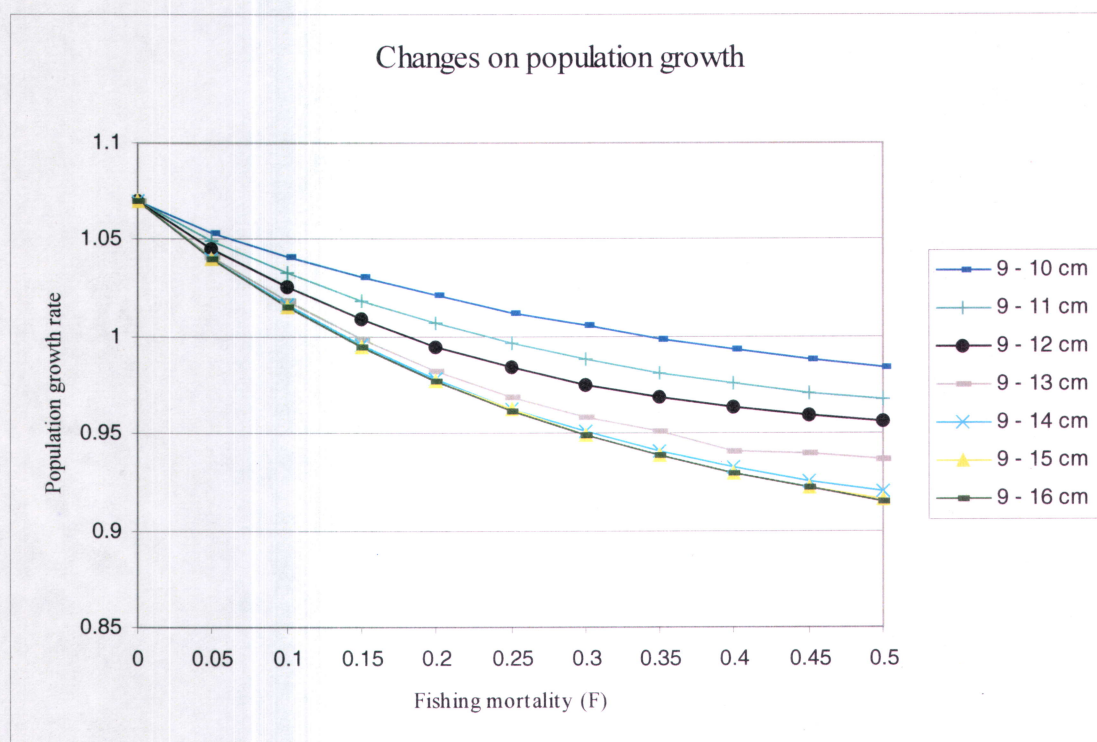


Figure. 3.5. Changes on population growth rate (λ) under different fishing mortality and different upper size limits for the linear deterministic model.

In the non-linear deterministic model (Model 2), the construction of the matrix and the parameters are almost identical to Model 1; however, in the non-linear deterministic model, survival of juveniles is directly associated with the number of adults. In order to compare the two models and measure the population-level importance of the association between juveniles and adults, I explored the effects of increasing parameter b in Equation 2. For each simulation, the parameter a was

adjusted until λ of the baseline model was the same as in Model 1 under no harvest conditions ($\lambda = 1.07$). In other words, a and b were adjusted to assume that $P = 1.0$ for the ratio juveniles to adults obtained in Model 1 (figure 3.6).

For Model 2, with $a = 12$ and $b = 3$, the decrease of λ , when fishing mortality was increased, was greater than Model 1 because harvest increases the ratio juveniles to adults (figure 3.7). This means that when there is a removal of adults in this case due to an increase in fishing mortality, there is a negative effect on survival of juveniles, and this decreases λ . Considering a very high fishing mortality 0.5, an upper size limit of 13 cm in td or below would create a rate of decline of approximately 8% per year. Under this dependency and with a fishing mortality of 0.2, an upper size limit of 13 cm td would generate a $\lambda = 0.977$ (a rate of decline of 2.3 % per year).

I conducted further exploration of how critical is the ratio juveniles to adults with respect to λ by increasing the slope of this relationship under different scenarios (figure 3.8). By increasing the value of parameter “b” a much higher dependency of juvenile urchins on adults was created, and parameter a was adjusted in order to have the same λ as in initial population ($\lambda = 1.07$). As the dependency on survival of juveniles based on density of adults increases, and less size classes of adults are protected by the upper size limit, there is a significant decline in population growth as fishing mortality increases to the point of extinction if no other management strategies are implemented.

Another way to explore how critical is the association juveniles on adults, I graphed the P multiplier versus the ratio juveniles to adults for each change in parameter a and b presented above under no fishing mortality (figure 3.9). I adjusted the parameter a for each scenario until λ of the baseline model was the same as in Model 1 under no harvest conditions ($\lambda = 1.07$). As expected, the multiplier for

juvenile survival P decreases rapidly as the dependency of juvenile survival on adults increases.

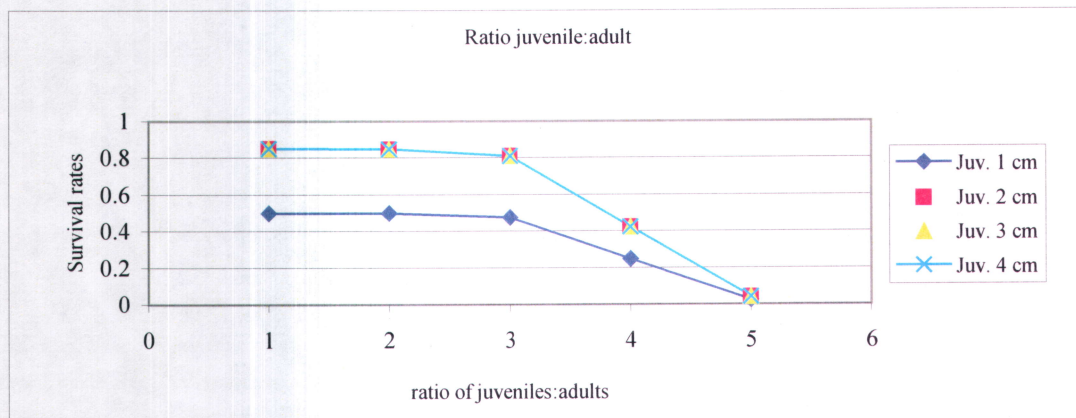


Figure 3.6. The Ratio juvenile:adult for an unexploited population using a non-linear deterministic model, $a = 12$ and $b = 3$. 1 and 2 juveniles per adult will maintain the starting survival rates given to this model, with 5 juveniles per adult there is a rapid decline in survival rates for juveniles. The slopes for juveniles between 2 and 4 cm td are the same since they have the same starting survival rates.

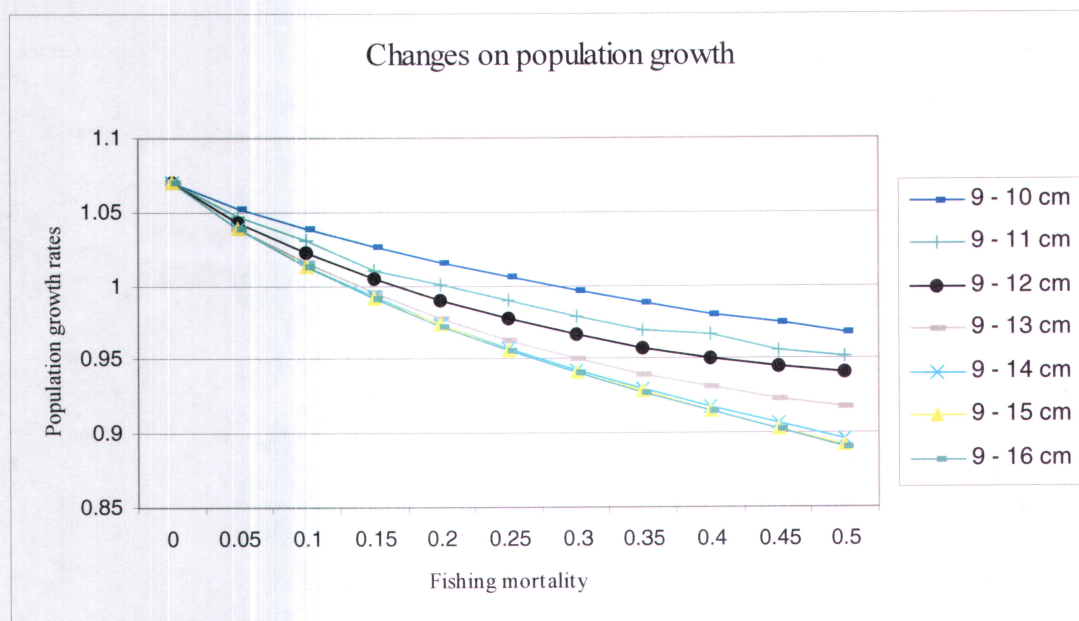


Figure 3.7. Changes on population growth rate (λ) under different fishing mortality and different upper size limits for the non-linear deterministic model, $a=12$ and $b=3$.

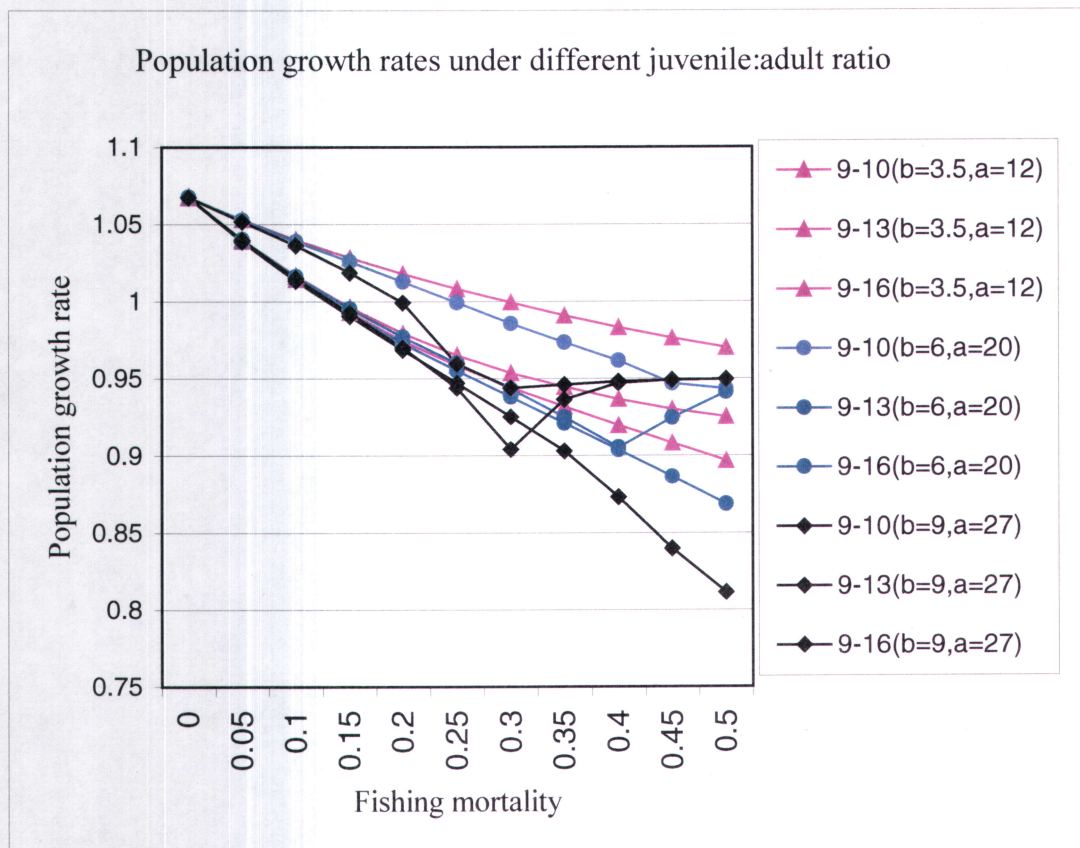


Figure 3.8. Changes on population growth rates under different: juvenile to adult ratio, fishing mortality and upper size limits for the non-linear deterministic model.

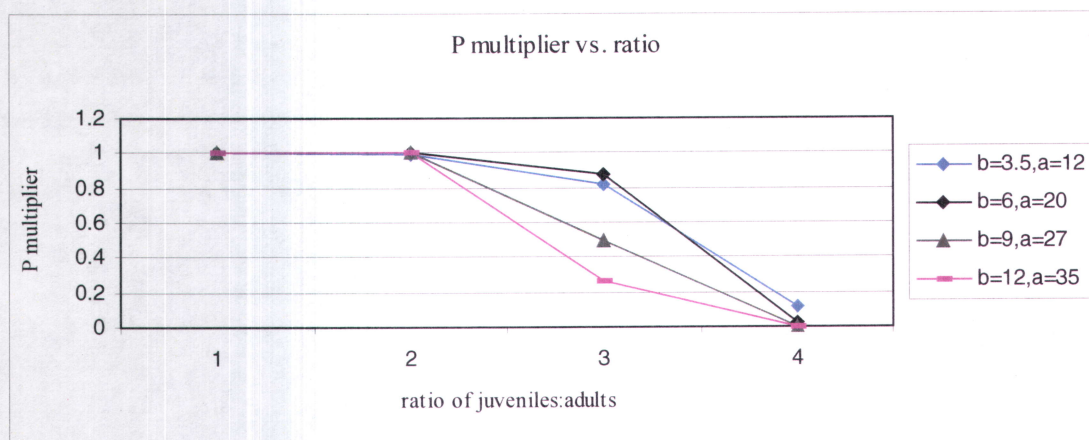


Figure 3.9. P multiplier vs. ratio juvenile:adult with different a and b parameters.

DISCUSSION

Size-structured models, which allow us to evaluate management alternatives as hypotheses, are very useful tools to manage marine resources even when demographic data are limited. There is no objection that more sophisticated quantitative models could be more beneficial to address management problems, but accurate information on the life history of this species does not exist. In the mean time, the use of sensitivity analyses to qualitatively compare the impact of stage-specific survival, growth, and fecundity on population growth allow us to screen among arrays of management alternatives and to decide which are most likely to enhance threatened populations.

Based on these models, there is clear evidence that larger adults greater than 9 cm td play an important role in the population growth. Therefore, an upper size limit will benefit population growth rates regardless of the existence of the potential beneficial relationship between juveniles and adults. The lower the size assigned as an upper size limit, the greater the benefit for the population growth under different fishing mortality rates. This is due to the protection of reproductive adults that eventually will produce more eggs and increase fertilization success. However, this benefit for a population based on the linear deterministic model where survival rates of juveniles remain constant through time may be overly optimistic. In my experiments, there was a positive association between juveniles and adults since there is a higher mortality of juveniles without the presence of adults. This could be corroborated by studies that demonstrate that good recruitment of juvenile urchins is a sporadic event that does not occur every year, and is dependent mainly on suitable oceanographic conditions such as upwelling relaxation that allow larvae to settle near to the coast in suitable habitats (Miller et al 1997, Montano 2001). Unfortunately, in the Pacific Northwest, no major recruitment events occurred during the past ten years (Pearse and Hines 1987, Montano 2001, Carter and VanBlaricom 2002) and this is increasing the risk of depletion of the species.

Growth increments of red sea urchins suggest that the time it takes for a specific cohort to recruit to the fishery is 9-10 years, suggesting a low recovery rate after exploitation (Montano 2001). If survival of juveniles depends on the density of adults, as presented in the non-linear deterministic model, removing protective adults due to harvesting might aggravate population decline. Therefore, based on the two models presented here, the implementation of an upper size limit would benefit the species as well as the fishery industry. The upper size limit, which has been proposed by the different institutions in charge of managing the red sea urchin fishery, is 13 cm td. Based on the non-linear deterministic model, the 13 cm td upper size limit seems a very reasonable size for this management strategy. A lower upper size limit would be more beneficial for the conservation for the species, but it will be hard for managers to implement. However, more research has to be conducted in order to understand the association juvenile:adult and survival as a function of density. Comparing my results with Pfister and Bradbury (1996), we agreed that overfishing reduces the magnitude of recruitment due to decrease in fertilization success and protective adults. However, my models are more realistic and unique since Pfister and Bradbury (1996) ignored the decreases in fertilization when spawner density is low.

4. CONCLUSION

In the Pacific Northwest, the harvest of red sea urchins started as a project to develop fisheries for underutilized species. The fishery developed relatively quicker due to high abundance of harvestable urchins and due to increasing demand from Japan fueled by rising prices based largely on a more favorable export currency exchange rate. The stock assessment methods for this fishery have been based on a combination of fisheries dependent data and population surveys. The main management policies established are harvest quotas, individual quotas, size limits, and license restrictions. However, these management strategies have been ineffective in maintaining a sustainable fishery; as a result, density of harvestable urchins has decreased very rapidly and the fishery is declining.

One of the main reasons that these management strategies have not been able to restore stocks is the lack of information about the biology of the species. This has lead managers to the application of management strategies based on limited information. As a part of a new approach, a biologically-based fishery has been suggested along with management tools such as marine reserves, rotational harvest, and an upper size-limit regulation have been proposed. The upper size-limit regulation has been anticipated to promote recruitment and survival of young urchins. In order to analyze the importance of this strategy, this study tested the hypotheses that (1) survival of juvenile urchins is enhanced by the presence of adult spine canopy under the presence of a natural predator, and that (2) the rate of survival of juveniles is related to the size of the adult under the presence of a natural predator, the sunflower star (*Pycnopodia helianthoides*), and (3) this protection by adults can translate into population-level impacts, such as population growth rates. Based on an experimental study, survival of juvenile is enhanced by the presence of adult spine canopy; however there is not a significant difference on survival of juveniles based on the size of the adults. Therefore, an upper size limit based on the assumption that larger adults association will provide greater protective habitat to juvenile urchins from natural

predation is not supported. However, an experimental study of survival of juveniles under different densities of adults is necessary in order to have a better understanding of this relationship (juvenile-adult) and to analyze how important an upper size limit could be to restore red sea urchins stocks.

By creating a non-linear deterministic model, I was able to simulate this relationship, where survival of juvenile urchins was directly associated with different densities of adults. Changes in population growth rates were explored as a response of this association. This exercise demonstrates that a higher density of larger adults would benefit population growth. And if there were not enough larger adults, the population would collapse under this dependency of juvenile urchins on adults.

To conclude I am listing management recommendations that I considered crucial to maintain a sustainable fishery.

- Further research to protect the species and insure a sustainable fishery. Field observations and experimental studies on age, growth, mortality and recruitment rates are required to have a better understanding of this species.
- I recommend more modeling that integrates new research data, and that investigates which demographic variables need the greatest research.
- There is a need to keep compiling existing research on red sea urchins in order to make available for the different institutions in charge of managing this resource.
- Surveys for abundance estimates and more accurate estimates of bed areas holding viable populations of red sea urchins are required, particularly in Oregon.

- An adaptive management approach should be considered to respond to those sporadic years in which good recruitment occurs, such as the implementation of a small slot limit and lowering harvesting quotas in order to protect new recruits following a recruitment pulse.
- Experimental studies on repopulation of suitable areas for red sea urchin with red sea urchin larvae from artificially spawned and fertilized eggs, under laboratory conditions, should be considered. This type of experiment is very easy to do and since recruitment process is a rare event in this species, this might contribute to enhance recruitment for those areas where population of red sea urchins is declining.
- To monitor harvested red sea urchins at ports and processing plants, this will provide temporal changes and area differences in size frequency, mean weights, and gonad quality of harvestable size individuals, and will provide a tool to assess the appropriate size range to set quotas in the future.
- Set quotas based on a low fishing mortality until a better understanding of the life cycle of the species is achieved.
- Promote studies that investigate the relationship of urchins to kelp forest as well as research that relates gonad quality based on availability of food. This could enhance protection of crucial habitat for red sea urchins and could benefit the fishery by having urchins with gonads of higher quality for the urchin market. This could decrease the number of landings without decreasing the profits for the industry.

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