AN ABSTRACT OF THE DISSERTATION OF

Gabriela Montaño Moctezuma for the degree of Doctor of Philosophy in Fisheries Science presented on December 20, 2001. Title: Sea Urchin-Kelp Forest Communities in Marine Reserves and Areas of Exploitation: Community Interactions, Populations, and Metapopulation Analyses.

Abstract approved: Redacted for Privacy

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Marine ecosystems can be exposed to natural and anthropogenic disturbances that can lead to ecological failures. Marine reserves have been lately suggested to protect marine populations and communities that have been affected by habitat destruction and harvest. This research evaluates the potential role of two marine reserves established in Oregon in 1967 (Whale Cove) and 1993 (Gregory Point). The red sea urchin (*Strongylocentrotus franciscanus*) was selected as indicator of population recovery since it is the only species that is commercially harvested. Changes in density, biomass, average size, size structure, growth and mortality rates were evaluated through time to assess population recovery. These parameters were also compared between reserves and adjacent exploited areas to evaluate the effect of exploitation. Results from Whale Cove (old reserve) indicate that the population in this area is fully recovered. On the contrary, the population in Gregory Point (new reserve) showed signs of recovery after six years of being protected. The importance of red urchins as source populations to provide larvae to adjacent areas was explored by the analysis of drifter's trajectories. Both reserves might be connected in a network where larvae produced in Whale Cove will provide recruits to Gregory Point and adjacent exploited areas, as well as populations in northern California. Gregory Point releases larvae that become recruits for Whale Cove only when spawning takes place in winter, otherwise larvae travel to central California. No clear trends were found in growth and mortality rates between reserves and non-reserves; differences were more related with food availability, competitors, and age specific mortality.

We applied qualitative simulations to characterize and differentiate the community network inside reserves and exploited areas. Results suggest that communities from a particular site can be represented by a set of alternative models with consistent species interactions. Differences in predator-prey interactions as well as non-predatory relationships (interference competition, mutualism, amensalism) were found among sites. Each set of models represents a hypothesis of community organization that agreed with natural history information. Alternative models suggest that kelp forest communities are dynamic and can shift from one network configuration to another providing a buffer against a variable environment.

SEA URCHIN-KELP FOREST COMMUNITIES IN MARINE RESERVES AND AREAS OF EXPLOITATION: COMMUNITY INTERACTIONS, POPULATIONS, AND METAPOPULATION ANALYSES.

by

Gabriela Montaño Moctezuma

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I understand that my dissertation will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my dissertation to any reader upon request.

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Gabriela Montaño Moctezuma, Author

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CONTRIBUTION OF AUTHORS

Dr. Hiram W. Li was involved in the design and writing of each manuscript. Dr. Philippe Rossignol contributed with the design and writing of Chapters 4 and 5. Neil Richmond assisted in data collection and ideas of Chapter 3.

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CHAPTER 1

INTRODUCTION

Community configurations have changed from how they used to appear several decades ago. The disappearance or reductions of several species that played an important role in community organization have changed the function of persistent community members (Dayton et al. 1998). Understanding how a population and community behave in the absence of anthropogenic disturbances calls for the establishment of protected areas that allow the recovery of lost species and the re-establishment of original communities. A considerable number of coastal marine reserves have been established in different parts of the world. The task then is to probe and assess the recovery of target species that have been released from the disturbance and the direct and indirect effects that this recovery might have on the entire community. Direct observations as well as modeling techniques are helpful tools to perform such an endeavor.

Refuge theory describes areas of relative ecological stability within a disturbed landscape that are of critical importance for long-term species survival. Despite the proliferation of ecosystem theory, there are few if any marine fisheries today that can be pointed to as examples where balance has been achieved in practice.

There are two factors of consideration with refuges: (1) the dynamics of harvested populations, and (2) the effects of harvesting on community structure and stability.

Ecosystems in general encompass three major components: (1) single-species life history strategies, (2) the evolution of communities, and (3) the mechanisms or linkages among species that regulate the systematic functioning of the community.

With a sufficient understanding of ecosystems, one should be able to determine those species that are candidates for efforts at stock stabilization and those that are inherently highly variable.

This thesis puts together the analysis of field observations and modeling approaches to assess the recovery of a target species, the red sea urchin, as well as the kelp forest community where urchins play an important role in the dynamics of the system.

Two marine reserves and their adjacent exploited areas along the Oregon coast were studied to assess the recovery of the red sea urchin population inside the reserves and the status of the kelp forest community. Whale Cove is an old reserve that was established in 1967 and Gregory Point a new reserve instituted in 1993. The effect of exploitation was assessed by comparing populations inside the reserves to those of adjacent exploited areas.

Chapter 2 evaluates the role of adult red urchins inside marine reserves as sources of larvae for outside exploited populations. Signs of recovery were assessed by looking at population parameters such as densities, biomass, average length and maximum sizes. A trend was explored when comparing areas with different protection times (a pristine area and a reserve) and areas with different exploitation rates. The fate of larvae produced inside reserves was inferred by relating drifter's trajectories with plausible larvae courses and final destination points to settle.

In chapter 3, growth and mortality rates of red urchins were estimated using a log-likelihood method (MULTIFAN) based on length frequency information. Comparisons among reserves and non-reserves were explored as well as the effect of food availability, predators and presence of competitors. The importance of marine reserves as potential source of information for stock assessment parameters is emphasized.

Red urchins were incorporated to a community level model in chapter 4 to explore different community structure scenarios in kelp forest communities. We pose the question as whether a community should be represented as a single model or as a set of alternative models that might explain better the dynamics of a system. A novel technique called qualitative simulations was developed to integrate field observations and simulated community models to identify a model or set of models that best describes the community from a particular area.

In chapter 5, we applied qualitative simulations to reconstruct and compare the community interaction networks in two marine reserves and adjacent exploited areas. The effect of different disturbances and different management practices on community stability and organization are explored.

CHAPTER 2

CAPACITY OF OREGON MARINE RESERVES TO SUSTAIN RED URCHIN FISHERIES

Gabriela Montaño Moctezuma and Hiram W. Li

Abstract

Population parameters of the red sea urchin (*Strongylocentrotus franciscanus*), such as density, biomass, average size, and size structure were compared between two marine reserves and adjacent harvested areas to contrast the effect of exploitation with the population recovery among four sites in Oregon. We evaluated the potential role of adult red urchins inside reserves as source populations for adjacent exploited areas, as well as the fate of the produced larvae by using trajectories from drifters released close to the reserves. The population in Whale Cove old reserve showed higher values in adult densities, biomass, average length and maximum sizes compare to the other three study sites. Biomass was a better indicator of the population recovery. Our results indicate that a trend in recovery exists among sites, going from high biomass values in the old reserve, intermediate quantities in the recently established reserve and the exploited area with low harvest rates, to low values in the exploited area with high harvest rates. A trend in density was not as clear, suggesting that considering density as the only parameter to assess recovery might not be appropriate. Differences in mean and maximum sizes were not significant between the new reserve and the low exploited area. These findings suggest that long-lived species may take more than 6 years to show a population recovery. Drifter's trajectories indicated that both reserves may be connected in a network array where larvae produced inside each reserve contribute to the larval pool of each other. Exploited areas will not receive larvae from its adjacent protected area but from the reserve located far away. Reserves along the Pacific Northwest, from Alaska to Baja California, allocated in a network array are necessary to protect source populations and guarantee enough larvae for a successful recruitment.

Introduction

The demand for sea urchin gonads has increased dramatically in Japan and France, the main consumer market. This demand has intensified sea urchins fisheries worldwide and lead to a decline of overexploited stocks as well as opening new fishing grounds (Sloan 1985). In Oregon, the commercial sea urchin fishery for red urchins (*Strongylocentrotus franciscanus)* began in 1986 and reached a peak in 1989-1990. After 1991, harvested areas started experienced heavy fishing pressure. Divers have increased the time spent in deeper waters and the mean harvest depth has increased from 42.5 ft to 52.5 ft (Richmond et al. 1997). Red urchins life history make them susceptible to overexploitation (Tegner and Dayton 1977, Quinn et al. 1993). When older, bigger urchins have been depleted, the recovery of the population relies on recruitment pulses and faster growth rates (Tegner and Dayton 1977; Richmond et al. 1977; Tegner 1989). Since sporadic and uncertain recruitment is common in sea urchins (Tegner and Dayton 1977; Ebert and Russell 1988; Ebert et al. 1994; Wing et al. 1995), more emphasis should be directed to protect adult abundances and critical spawning sites to maximize reproductive successful. Recruitment overfishing is common in broadcast spawners since fertilization success is reduced by adult's fishery removals.

Many marine species distribute in interconnecting patches of planktonic larvae over large spatial scales, simulating a metapopulation array. Harvest can create sink populations by decreasing spawning stocks that are no longer able to replace themselves (Quinn et al., 1993), and by intensifying recruitment overfishing (Carr and Reed 1993). Sink populations will decrease when isolated from a source population supply (Dias 1996). Reserves that protect reproductive stocks, therefore can be useful to regulate the equilibrium of a metapopulation system.

Empirical studies as well as modeling approaches have shown that exploited populations can benefit from protected areas by providing recruits to heavily depleted stocks (DeMartini 1993; Man et al. 1995; Polacheck 1990, Bostford et al. 1993). However, the dispersal properties of the larvae produced inside protected areas is still not well understood. After being released, larvae are exposed to oceanographic events that transport the larvae far away from the spawning stock, becoming recruits of other populations. Because oceanographic conditions are variable, it is difficult to identify how the network is connected and which populations become sources of larval supply to sink populations. This variability confers a spatial dynamic component to larval dispersal (Wing et al. 1998).

Increases in local abundance and mean size (Russ 1985; Alcala 1988; Buxton and Smale 1989; Cole et al. 1990; García-Rubies and Zabala 1990; McClanahan and Shafir 1990; Paddack and Estes 2000), biomass (Polunin and Roberts 1993; Roberts 1995; Paddack and Estes 2000), and reproductive potential (Davis 1977; Weil and Laughlin 1984; Shepherd 1990; Paddack and Estes 2000) have been attributed to the establishment of protected areas. Presumably, these factors increases the reproductive potential of a source population.

Kelp forest communities have been affected by fisheries of different intensities resulting in the extirpation of several species. Sea urchins have been associated with the overgrazing and destruction of kelp beds; however, they also have a positive role in the community since they provide protection from predators to juveniles of several species such as abalones, gastropods, shrimp, crabs, asteroids, snails, chitons, ophiuroids, fishes, and small urchins (Tegner and Dayton 1977; Breen et al. 1985).

The main goals of this study were to: 1) evaluate the trend in recovery of some population parameters of the red sea urchin, such as density, biomass, average size, and size structure. We suggest that a trend can be expected among sites ranging from high signs of recovery in old reserves, intermediate indications in new reserves and low values of the studied parameters in harvested areas, and 2) to assess the role of adult red urchins as sources of larvae for outside populations by evaluating oceanic currents as dispersal corridors. We ask the question of whether larvae produced inside reserves will benefit local populations or whether recruitment is exogenous and reserves are source for distant populations.

Study Areas

We studied two Marine Reserves with different characteristics: 1) Gregory Point is located on the southern Oregon coast, measures 0.22 km^2, and was established in 1993. 2) Whale Cove is located north, measures 0.13 km^2, and was established in 1967. To assess the recovery of the red urchin population and the effect of exploitation, two adjacent exploited areas (Simpson Reef and Depoe Bay, respectively) were studied as well (Fig. 2.1). The four study areas represent a gradient. Whale Cove is a reserve that has been protected for 35 years, Gregory Point, a reserve recovering from harvest for a short time (9 years), Simpson Reef is an exploited area with low average harvest pressure (116.8 thousand ponds), and Depoe Bay is an exploited area with high average harvest rates (337.4 thousand pounds). In the past, the only species commercially harvested in all areas was adult red urchins. In 1967, Whale Cove was established as a habitat restoration site, and in 1993 Gregory Point was set aside as a subtidal reserve. In both protected areas, sport and commercial harvest of subtidal invertebrates are not allowed. The Oregon sea urchin fishery began in 1986. In Simpson Reef, landings peaked in 1991 (322 thousand pounds) and by 1995 landings decreased to 19 thousand pounds. In Depoe Bay, landings were highest in 1990 (1,373 thousand pounds), declining to 157 thousand pounds in 1995. The main management practices that have been used in Depoe Bay and Simpson Reef are based on a limited entry system and a minimum size limit of 8.9 cm (Richmond et al. 1997).

To compare and assess the effectiveness of established marine reserves, the similarities among sites in habitat type need to be documented. Bedrock and boulders constitute the preferred habitat for urchins. Bedrock was the dominant substrate type in both reserves (Whale Cove and Gregory Point) and their adjacent exploited areas (Depoe Bay and Simpson Reef, respectively) (Table 2.1). Percentages of bedrock and boulders were similar between marine reserves and their adjacent exploited areas. Whale Cove and Depoe Bay were characterized by 61.6% and 67.8% of bedrock, and 16.5% and 25.2% of boulders; whereas Gregory Point and Simpson Reef substrate was 72.4% and 76.7% bedrock and 8.5% and 8.3% boulders, respectively (Table 2.1). Although the percentage of sand (15.3% and 13.7%) was the second in importance in

Gregory Point and Simpson Reef, it was found mostly surrounding boulders and bedrock. The percentage of shell (0.6-9.1%) was low in all areas.

Table 2.1. Substrate type (%) in reserves and adjacent exploited areas.

Study Sites	Substrate type			
	Bedrock	Boulders	Sand	Shell
Whale Cove	61.6	16.5	12.8	9.1
Depoe Bay	67.8	25.2	6.4	0.6
Gregory Point	72.4	8.5	15.3	3.8
Simpson Reef	76.7	8.3	13.7	1.3

Methods

Data was collected over 4 years during summer and fall from 1996 through 1999. Density of red urchins was estimated using belt transects, 2m wide by 40m long ($80m^2$), that were systematically allocated in each study site covering the entire area. Each transect was divided in 16 sampling units of $5m^2$ each (quadrats). In each quadrat, SCUBA divers recorded the number of red urchins (*Strogylocentrotus franciscanus*), as well as depth and substrate type (sand, shell, bedrock, and boulders). Red urchin test diameters were taken *in situ* to the nearest 0.1 centimeter with vernier calipers. Along each transect, 10 quadrats were selected randomly to make the length measurements and all urchins inside the $5m^2$ quadrats were measured. Biomass estimates were obtained by a length-weight relationship from red urchins collected in each study site (Fig. 2.2).

To evaluate the spillover effect of adults from the reserve into adjacent exploited areas, we tagged 60 urchins with external anchor tags (Neill 1987). Movement rates were recorded for individuals monitored for 50 days at different time intervals. Two concentric fixed transects were used to record the position of each

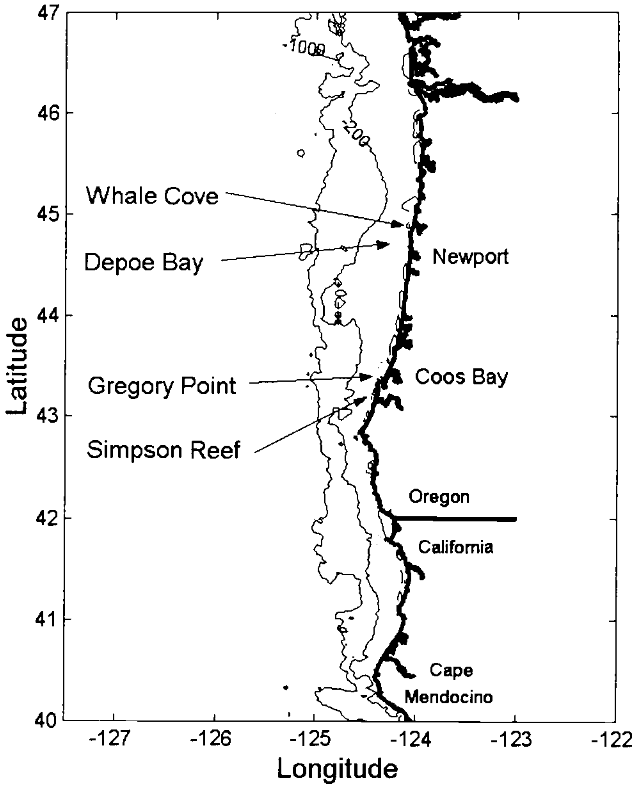


Figure 2.1. Location of the study areas along the Oregon Coast. Marine Reserves: Whale Cove and Gregory Point, and adjacent exploited areas: Depoe Bay and Simpson Reef.

urchin at any given time. Divers swan along concentric circles of 2, 4, 6 and 8m intervals. The transects were located close to the Simpson Reef exploited area.

Larval dispersal patterns were assessed by the analysis of published literature on: 1) satellite-tracked surface drifters (Barth and Smith 1998, Barth et al. 2000, and Barth 2001), and 2) spawning seasons and larvae development (Miller and Emlet 1999).

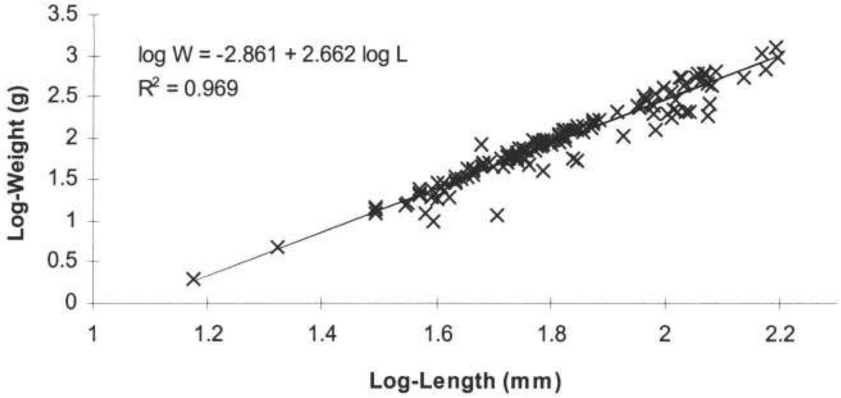


Figure 2.2. Linear relationship between body weigth (g) and length (mm) of red sea urchins. Data from all study sites combined (n = 145).

Results

Urchin Density

Red urchin densities (number of individuals per 5m^2) were higher in the Depoe Bay harvested area compare to the Whale Cove old reserve ($t = 15.1$, $df = 466$, $P < 0.001$, all years combined) and higher than in any other site that we studied. Densities in the Whale Cove and Gregory Point reserves were higher than in the Simpson Reef exploited area ($t = 3.3$, $df = 408$, $P = 0.0006$; $t = 6.5$, $df = 388$, $P < 0.001$, all years combined) (Fig. 2.3). Juveniles and adult red urchin densities were separated to account for the fisheries effect on urchins above 89 mm. In Whale Cove, adult red urchin densities showed a significant increase from 1996 to 1997 ($t = -2.9$, $df = 134$, $P = 0.002$) and from 1997 to 1998 ($t = -2.1$, $df = 109$, $P = 0.019$), and were higher than in Depoe Bay ($t = 5.7$, $df = 402$, $P < 0.001$, all years combined), where adult densities remained the same through time (Fig.2.4a).

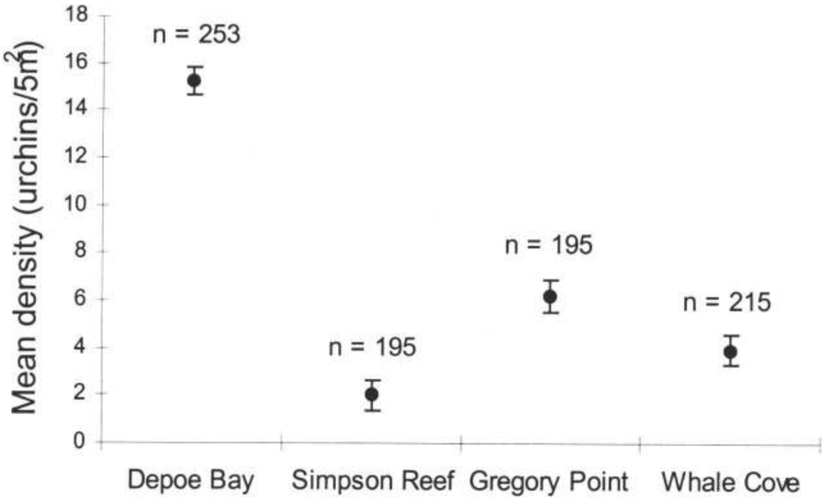


Figure 2.3. Red urchins mean densities (number of urchins per 5m^2) + SE in two marine reserves and adjacent exploited areas for all years combined (1996-1998). (n = number of quadrats per site). Exploited areas: Depoe Bay and Simpson Reef; Reserves: Gregory Point and Whale Cove.

There were more adult red urchins in Gregory Point compare to Simpson Reef in both 1996 ($t = 2.9$, $df = 151$, $P = 0.001$) and 1997 ($t = 1.9$, $df = 154$, $P = 0.02$) (Fig. 2.5a). Juvenile red urchins were more abundant in Depoe Bay compare to Whale Cove ($t = -19.9$, $df = 402$, $P < 0.001$, all years combined) (Fig. 2.4b); and less abundant in Simpson Reef compare to Gregory Point ($t = -5.5$, $df = 387$, $P < 0.001$, all years combined) (Fig. 2.5b). Depoe Bay was the only site where a significant increase in juvenile red urchins from 1996 to 1997 was observed ($t = -4.2$, $df = 187$, $P < 0.001$) (Fig. 2.4b).

Urchin biomass

A trend in red urchin biomass was observed, from higher values in Whale Cove (old reserve), intermediate amounts in Gregory Point (new reserve) and Simpson Reef (low exploited area), and lower quantities in Depoe Bay (high exploited area) (Fig. 2.6). In Depoe Bay, the biomass decreased from 1994 to 1997 ($t = 5.8$, $df = 591$, $P < 0.001$) and 1998 ($t = 4.4$, $df = 399$, $P < 0.001$) (Fig. 2.7a), and was lower than in Whale Cove all years ($t = -45.2$, $df = 1795$, $P < 0.001$) (Figs. 2.6 and 2.7a). In Whale Cove, the biomass has oscillated from 500 to 700 gr/5m^2 since 1996 and no indication of a decline or increase is apparent (Fig. 2.7a). Biomass in Simpson Reef decreased from 1993 to 1997 ($t = 6.0$, $df = 432$, $P < 0.001$) and remained relatively constant from 1997 to 1999 (Fig. 2.7b). In Gregory Point, the biomass has been increasing from 1996 to 1999 ($t = -10.38$, $df = 1281$, $P < 0.0001$). Although in 1997 the biomass in Gregory Point reserve was still significantly lower than in Simpson Reef harvested area ($t = -3.0$, $df = 1170$, $P = 0.001$); by 1999, biomass values in Gregory Point significantly exceeded those of Simpson Reef ($t = 2.4$, $df = 597$, $P = 0.008$) (Fig. 2.7b).

Population structure

A tendency in the size-frequency distribution was detected in the four study areas. Juvenile urchins (average size = 52.6 mm) dominated the population in Depoe Bay. A transition between juvenile and adult urchins was characteristic of Simpson Reef (average size = 83.7 mm) and Gregory Point (average size = 76 mm).

Adult urchins dominated the population in Whale Cove (average size = 122.8 mm) (Fig. 2.8). The length frequency distributions for both reserve-nonreserve comparisons (Whale Cove vs. Depoe Bay and Gregory Point vs. Simpson Reef) were significantly different (Kolmogorov-Smirnov two sample test, $P < 0.001$) (Fig. 2.8). Red urchin maximum size in Whale Cove (old reserve) was 177.6 mm; this length was greater (t-test, $P < 0.0001$) than in any other study site (Fig. 2.9). Although maximum

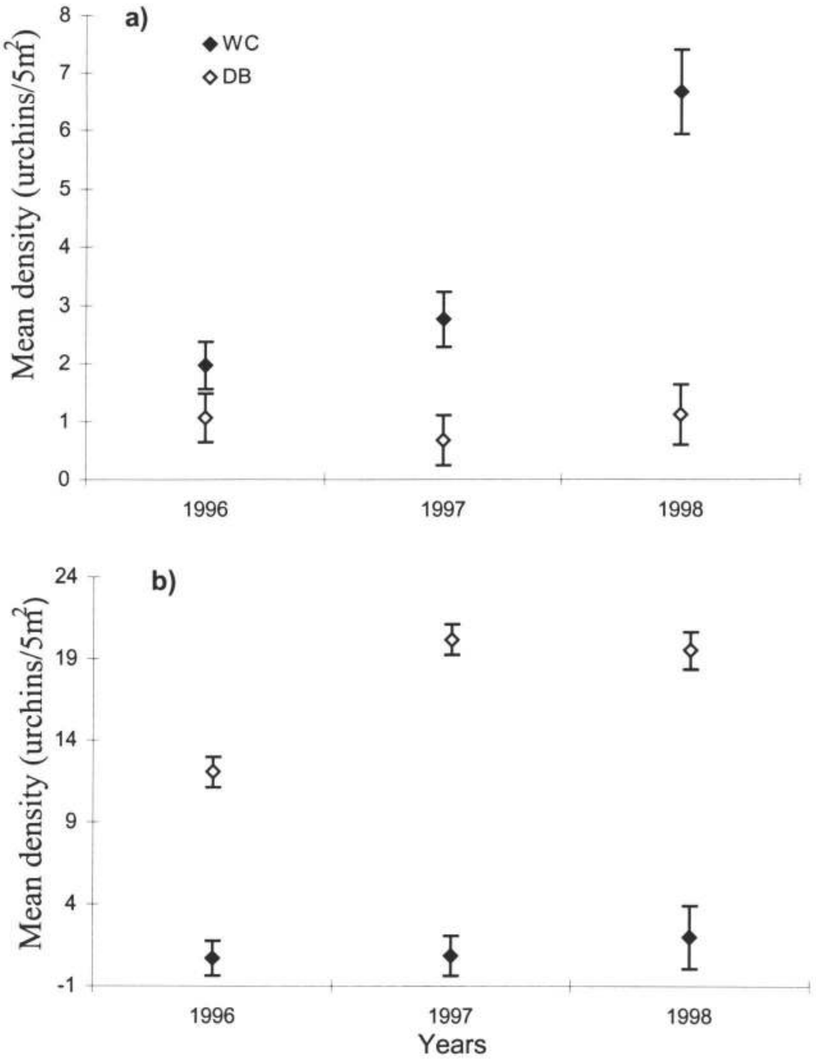


Figure 2.4. Comparison of adult and juvenile red urchin densities between Whale Cove old reserve (◆) and Depoe Bay adjacent exploited area (✧). a) adults and b) juveniles. Standard error bars are indicated.

sizes at Gregory Point (new reserve) were higher than those of Simpson Reef (136.88 mm and 134.90 mm), the differences were not significant (t-test, $P = 0.37$). Red urchin maximum size in Depoe Bay was smaller than those of other studied sites (t-test, $P < 0.001$) (Fig. 2.9).

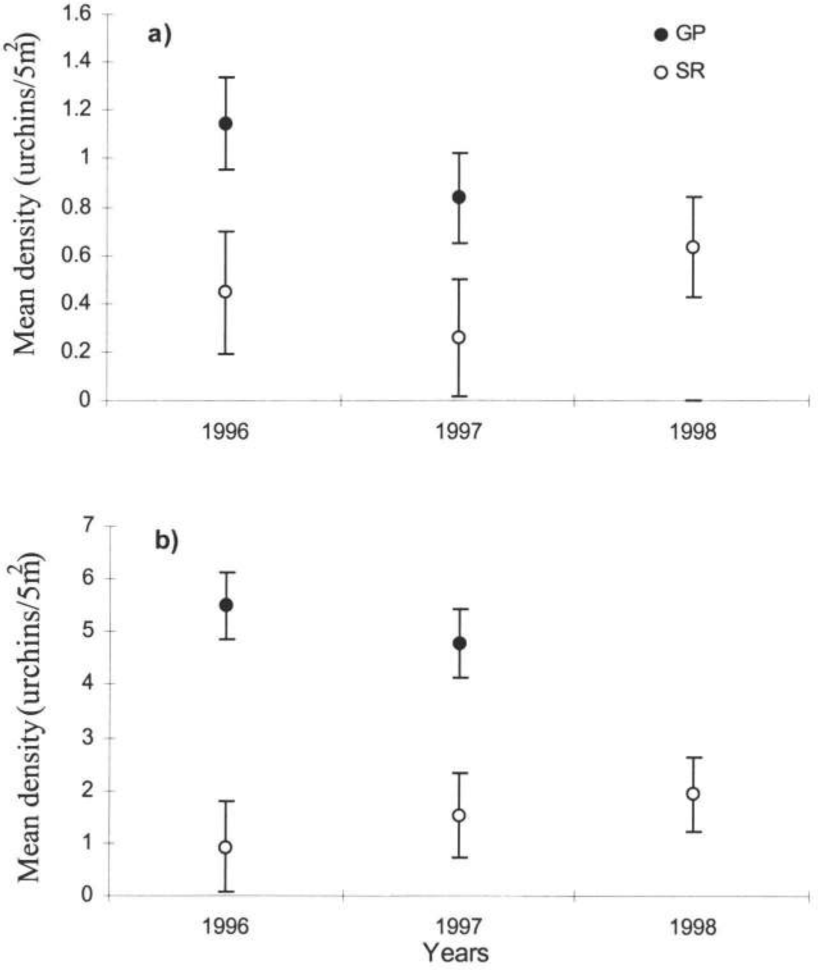


Figure 2.5. Comparison of adult and juvenile red urchin densities between Gregory Point new reserve (•) and Simpson Reef adjacent exploited area (o). a) adults and b) juveniles. Standard error bars are indicated.

The movement experiment showed that urchins moved on average 2.3 ± 1.73 m (S.D.) during the first week. From 7 through 50 days movements fluctuated around 2 to 4 m. The maximum average distance observed was 4 m, and the minimum 0.63 m (Fig. 2.10).

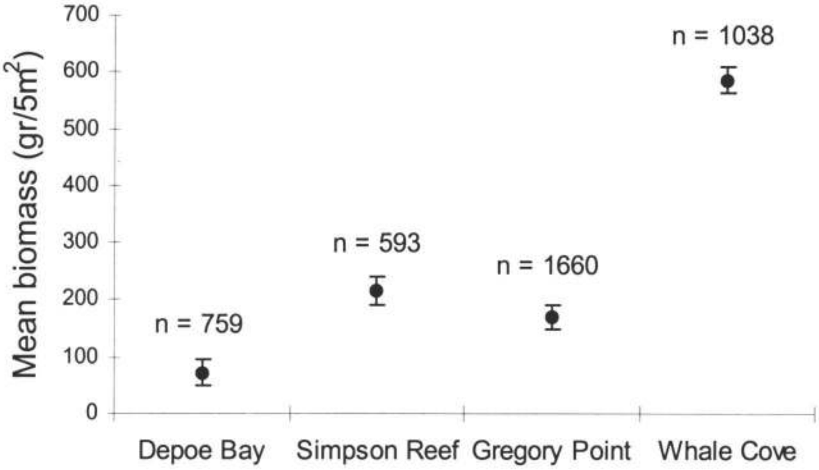


Figure 2.6. Red urchins mean biomass + SE in two marine reserves and adjacent exploited areas for all years combined (1996-1999). (n = number of quadrats per site).

Larval transport

The role of adult red urchins as source of larvae for outside exploited populations is related to the fate of larvae released inside the reserves. Planktonic larval stages in marine invertebrates can range from 1 week (snails, polychaetes, tunicates) to 3-4 months (starfish, urchins) (Strathmann 1978). The time larvae spend in the water column is related to the distance traveled and how much it disperses.

Several factors, such as currents, eddies, water velocity, offshore transport, ENSO events, and storm regimes, can affect larval transport and distance traveled by each individual larvae (Palmer 1988, Palmer et al. 1996). Current patterns in Oregon have winter and summer flow regimes that are primarily influenced by winds. The winter regime is characterized by a Northward current generated by Southwest winds.

Winds from the North create a Southward flow during the summer (Huyer 1977). From late March to early April there is a spring transition period characterized by small shifts in currents direction between the winter and summer flows (Huyer et al. 1979, Strub et al. 1987). Ocean circulation patterns off the Oregon coast have been studied by satellite-tracked surface drifters released along the coast (Barth and Smith 1998, Barth et al. 2000).

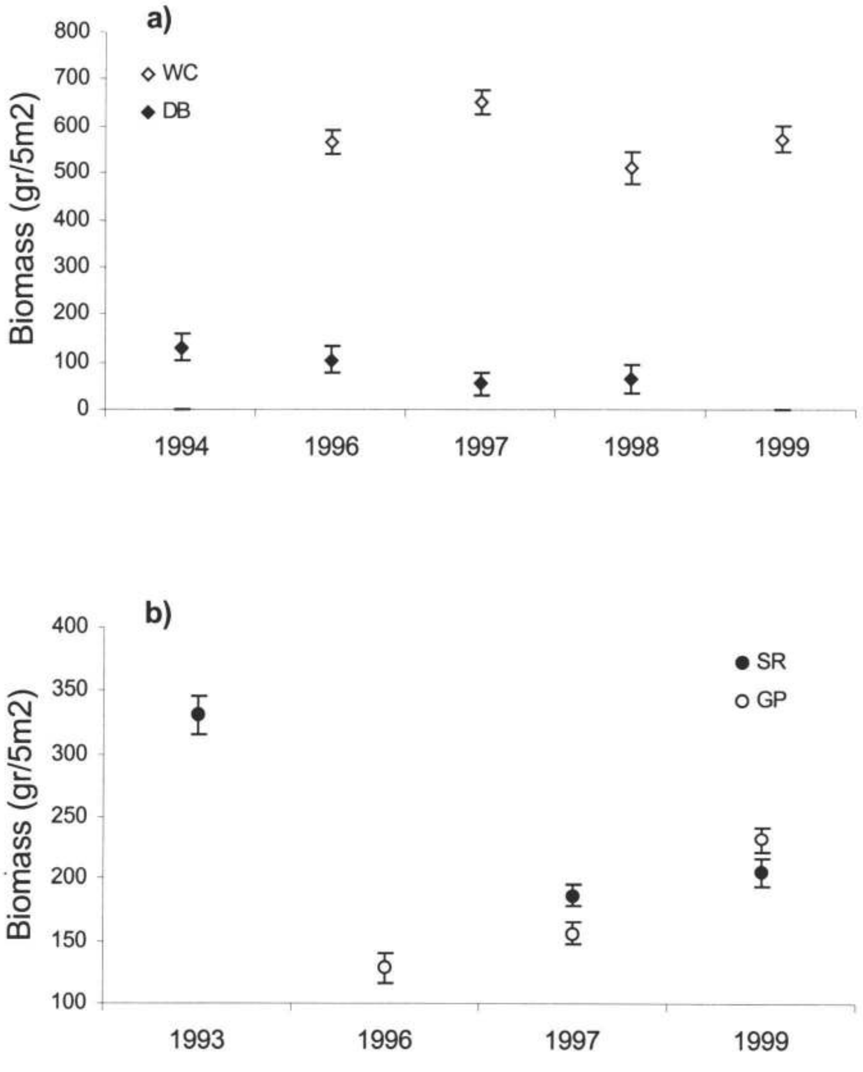


Figure 2.7. Changes in mean urchins biomass through time in a) WC = Whale Cove and DB = Depoe Bay, b) GP = Gregory Point and SR = Simpson Reef. Standard error bars are indicated.

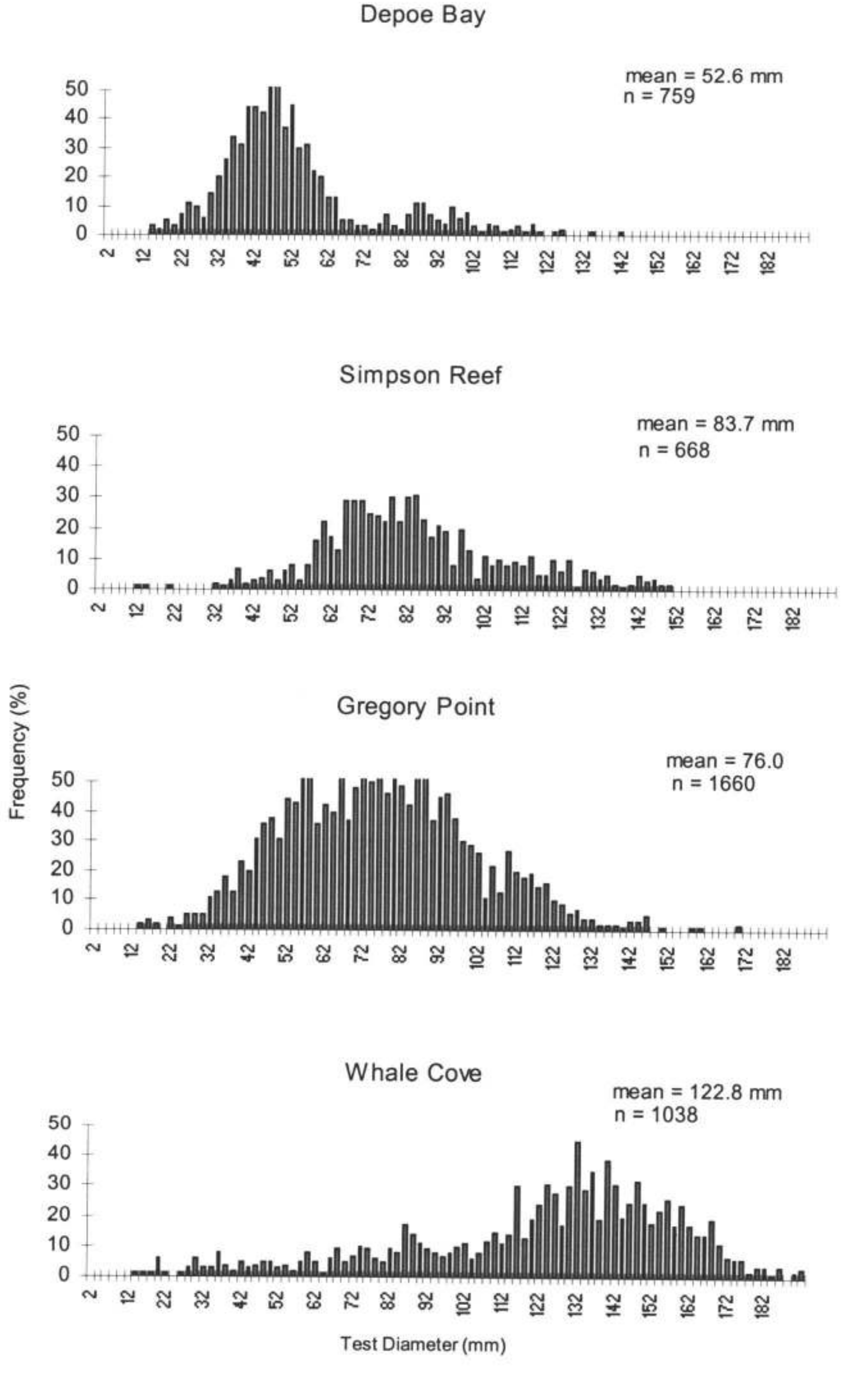


Figure 2.8. Length frequency distributions of red sea urchins in two marine reserves (Gregory Point and Whale Cove) and two non-protected areas (Depoe Bay and Simpson Reef). Pooled data from 1996 through 1999.

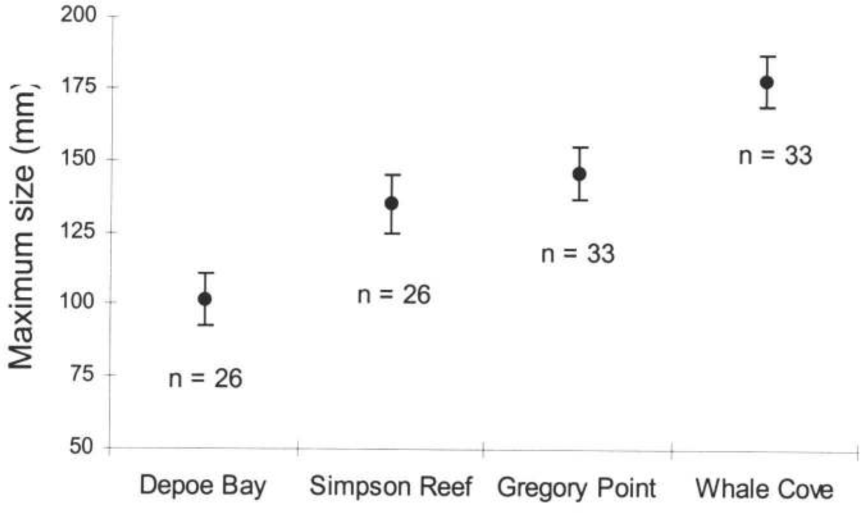


Figure 2.9. Maximum red urchin sizes for two marine reserves and adjacent exploited areas for all years combined (1996-1999). (n = number of transects per site). Standard error bars are indicated.

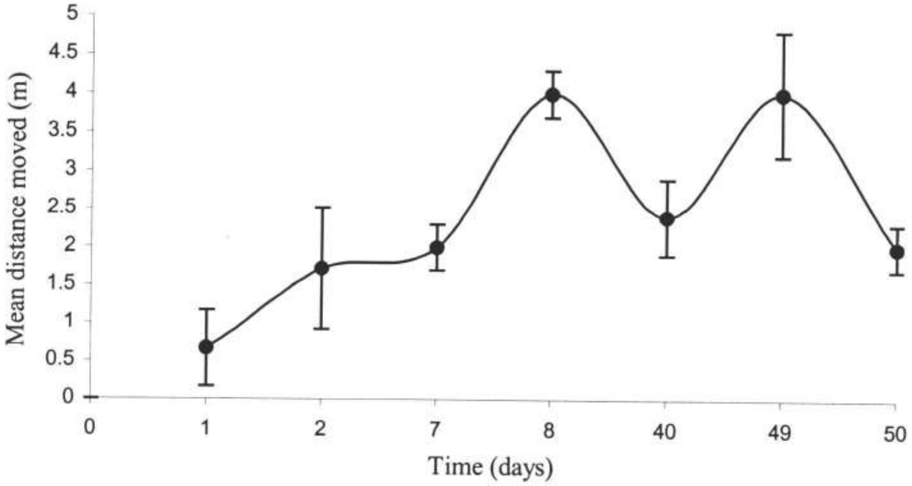


Figure 2.10. Mean Distance moved (meters) by tagged red sea urchins during 50 days.

Drifter's trajectories can indirectly indicate the distance and time a larvae can travel and the final location where it can possibly settle and recruit. In Oregon, red urchins spawn from March through July and released larvae can spend approximately 40 days in the water column before they become competent to settle (Miller and Emlet 1997, Miller and Emlet 1999). The fate of larvae released in Whale Cove and Gregory Point reserves may be inferred by looking at drifters trajectories released during the urchin's spawning season. Drifters that were released over the continental shelf on March and April off Newport, traveled south following a path close to shore (Fig 2.11). Due to the spring transition that causes oscillations in the current direction, drifters can be trapped in eddies and gyres. After 35 days on average, the drifters were located in front of Coos Bay (Fig 2.11) (Barth 2001). Drifters released later in the spawning season (June-July) traveled faster in a straight line because the spring transition was over. It took 15 days for these drifters to get to Coos Bay, arriving at Crescent City (California border) in 40 days on average (Fig 2.11) (Barth 2001). Drifter's trajectories suggest that larvae produced in Whale Cove early in the spawning season (March-April) might be competent and ready to settle by the time they arrive at Coos Bay. Larvae released later in the spawning season will become recruits for populations in northern California. This pattern suggests that protected adult urchins from Whale Cove can serve as a source of larvae for populations in Gregory Point, since this reserve is located in Coos Bay. Drifters released south of Coos Bay in May traveled south, fast ($0.6\ m \cdot s^{-1}$), and in a straight direction (Fig. 2.12). In one week, they crossed the California border and by 30-40 days they reached the north of San Francisco (Barth 2001). This trajectory suggests that adult urchins from Gregory Point might provide larvae to populations in northern California.

Miller and Emlet (1997) have observed early spawning (February) in populations from Gregory Point. Larvae produced early in the spawning season will be affected by winter currents characterized by a northward flow. Drifters released off Newport in winter traveled north and arrived in Washington and Vancouver Island in 21-30 days (Fig. 2.13) (Barth 2001), suggesting that early spawners from Whale Cove might provide recruits to populations in Washington and British Columbia. Larvae released in Gregory Point during winter will also travel north supplying recruits to Whale Cove reserve and Depoe Bay exploited area (Fig. 2.13) (Barth 2001).

Other factors such as upwelling strongly affect the probabilities of competent larvae to settle. Offshore transport is strong during the summer upwelling season (Huyer et al. 1974, Smith 1981) and can transport larvae to deeper waters where no suitable habitat is available. When winds relax during the summer a relaxation event creates an onshore transport (Huyer et al. 1974, Smith 1981), favorable for larval recruitment (Fig. 2.13).

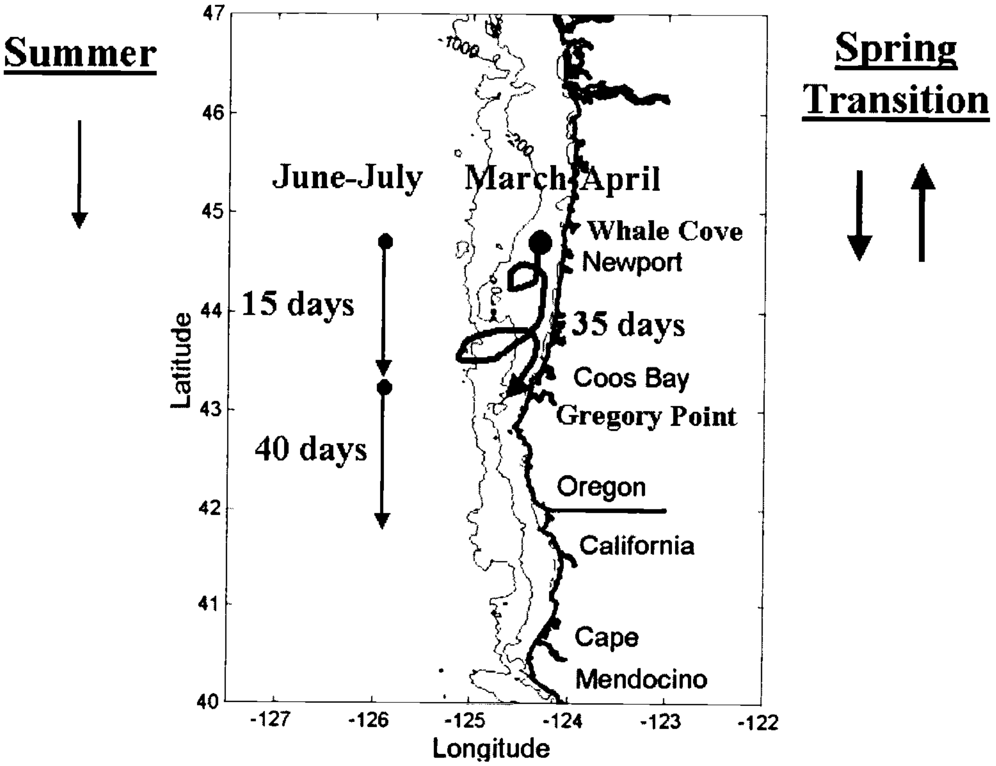


Figure 2.11. Diagram of drifter's trajectories released off Newport, Oregon during the spring transition on march-april (thick curve) and during the summer on june-july (thin line). All drifters were released close to the shoreline but were placed offshore in this figure for clarification of the drawing. Information obtained from Barth (2001).

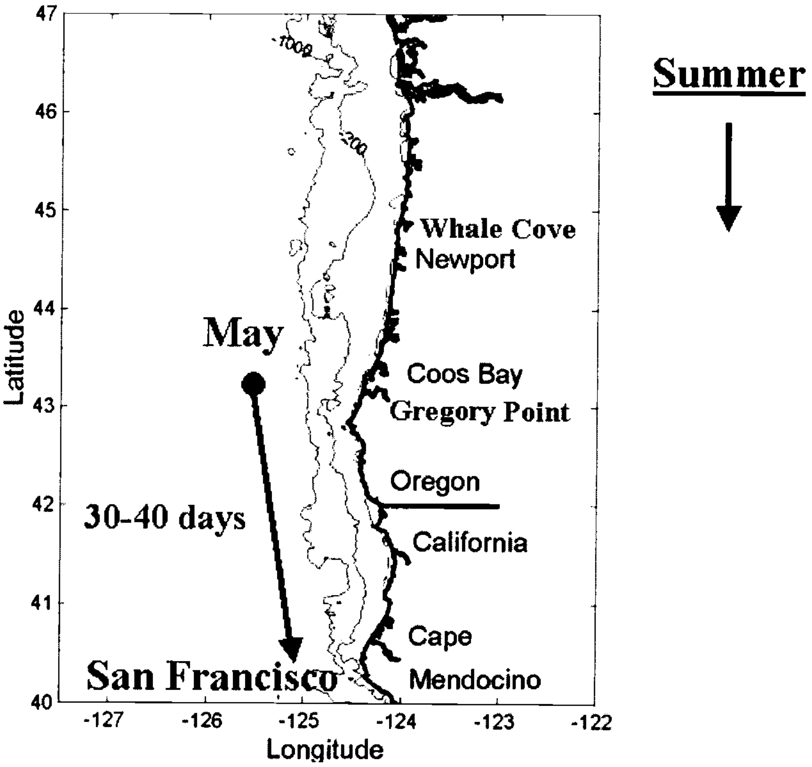


Figure 2.12. Diagram of drifter's trajectories released off Coos Bay, Oregon on May. All drifters were released close to the shoreline but were placed offshore in this figure for clarification of the drawing. Information obtained from Barth (2001).

Discussion

The response of the red urchin population in Whale Cove and Gregory Point marine reserves suggests that populations inside the reserve have the potential to recover. Biomass showed a clearer trend among sites going from low values in the heavy exploited area (Depoe Bay), intermediate amounts in Gregory Point (short recovery time) and Simpson Reef (low harvest rates), and very high biomass values in Whale Cove (old reserve).

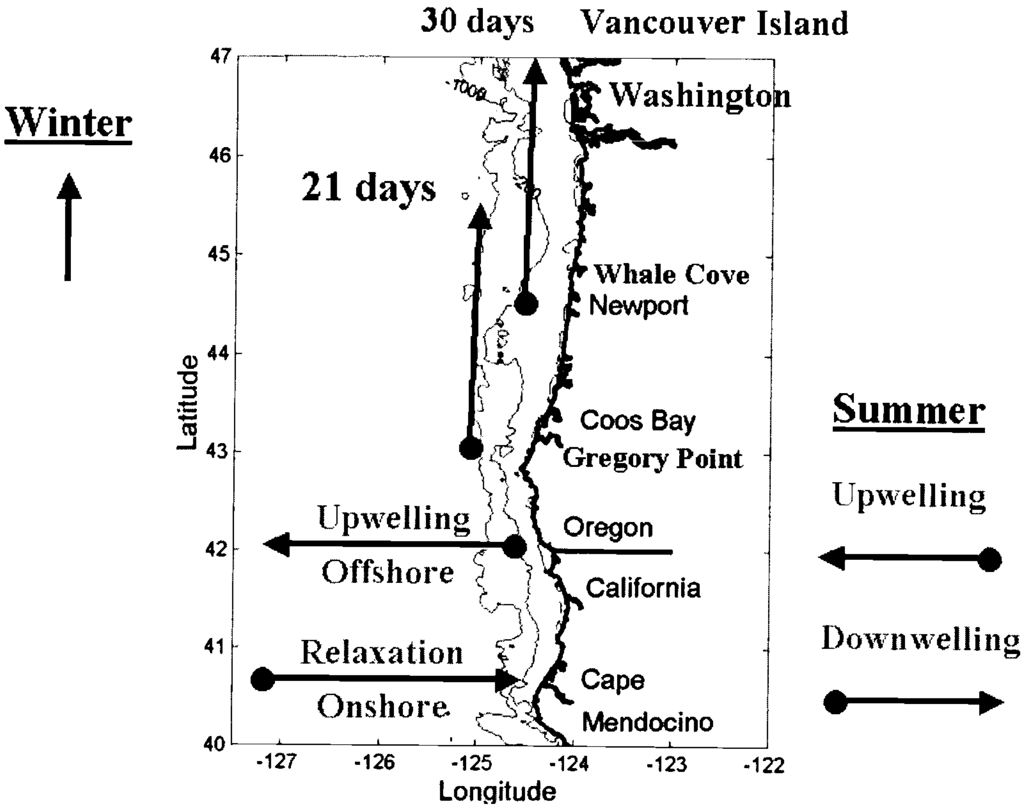
Although greater biomass values were not observed in Gregory Point (new reserve) compare to Simpson Reef (less heavy fished area), when all years were combined (Fig. 2.6), an increase in biomass was clear in Gregory Point from 1996 to 1999. By 1999, after six years of being protected, a significant difference was finally observed in the reserve compared with the adjacent harvested area (Fig. 2.6b). The trend in biomass in Whale Cove suggests that perhaps after 35 years of protection, the population has reached the carrying capacity of the system since biomass values remained within the same boundaries from 1996 through 1999. The effect of the fishery was clear in Depoe Bay and Simpson Reef where the biomass has been continuously decreasing since 1993.

Unexpectedly, red urchin densities were higher in Depoe Bay where harvest rates are high. Although higher densities were found in this area, the population was mostly represented by juvenile urchins under the minimum harvestable size (8.9 cm).

In contrast, densities of adult urchins were low in this area compare to both protected areas. This result suggests that biomass is a better indicator than density to assess the recovery rate of protected populations. Other studies also failed to find significant differences in fish densities between reserves and exploited areas (Paddack and Estes 2000, García-Rubies and Zabala 1990, Buxton and Smale 1989, Cole et al. 1990, Roberts 1995); yet, they found increases in fish biomass, reproductive potential (Paddack and Estes 2000), and individual sizes (García-Rubies and Zabala 1990, Larson 1980, Paddack and Estes 2000). Since density can be strongly influenced by sporadic recruitment, years with favorable recruitment conditions can mistakenly show a recovery in the population if density is the only parameter considered as an indicator.

Differences in mean size were clear between the old reserve (Whale Cove) and the heavy exploited area (Depoe Bay); however, urchins from Simpson Reef (low harvest rates) were significantly bigger than urchins inside Gregory Point (new reserve). Urchin's growth rates in these areas are very low (Chapter 3) and apparently six years of protection have not been sufficient to show an increase in average size.

For long-lived species such as sea urchins and numerous species of rockfish, several years of protection are necessary before a recovery can be observed. It is important to consider the life history strategies of different species when assessing the importance of marine reserves, since short-lived species will show a recovery in few years after the establishment of a reserve, while long-lived ones will take more time.



2.13. Diagram of drifter's trajectories released off Newport and Coos Bay, Oregon during winter. Offshore and onshore transport during the upwelling and downwelling summer events are indicated. All drifters were released close to the shoreline but were placed offshore in this figure for clarification of the drawing. Information obtained from Barth (2001).

Maximum sizes showed the opposite trend as mean sizes, being greater in the new reserve (Gregory Point) compared to the low exploited area (Simpson Reef). Although urchins have not attained a significantly greater maximum size in Gregory Point compared to Simpson Reef, the shift in trend indicates that urchins above harvestable sizes that remain protected, will be allowed to grow and reach significant maximum sizes in few years. Size distributions were more similar between the reserve that had been protected for a short time (Gregory Point) and the area with low harvest rates (Simpson Reef). Extreme size distributions were observed between the old reserve (Whale Cove) and the heavy fished area (Depoe Bay), where giant and very small urchins were found, respectively.

An interesting result was the low abundance of small urchins found inside Whale Cove. The observed high abundance of adult urchins inside the reserve may limit the available space making settlement difficult for juveniles. In addition, sunflower stars (*Pycnopodia*) predation on juvenile red urchins is strong in this area since adult red urchins have attained sizes big enough to escape predators (Chapter 5). The abundance of juvenile urchins outside the reserve (Depoe Bay) was approximately six times higher than inside. It is possible that larvae found more space available to settle outside the reserve, since adult urchin densities were very low in this adjacent exploited area. Although adult urchins enhance recruitment by providing protection and food to small urchins (Tegner and Dayton 1977; Duggins 1981), a threshold must exist where too many big urchins can limit recruitment, a reverse of the Allee effect (positive density dependence). We found patches where adults were very close together leaving almost no space for even a small urchin.

Based on the potential larval trajectories described, Whale Cove and Gregory Point seem to be connected in a network array where larvae produced in each reserve may contribute to the recruits of each other in certain times of the year. Drifter trajectories suggest that urchins in the reserves will not provide larvae to adjacent exploited areas but to distant populations. Whale Cove might provide larvae to exploited sites close to Coos Bay (Simpson Reef) and northern California, while Gregory Point will supply larvae to central California and to Depoe Bay, when an early spawning takes place. These findings suggest that reserves may be inadequate for sustaining local populations and adjacent exploited areas for species with long larval stages; however, they will be important source of recruits for reserves and exploited areas located within the dispersal range of larvae. This metapopulation array suggests the establishment of a network of reserves along the Pacific Northwest to assure the maintenance of source populations. Movement of adults and propagules among patches has been poorly studied due to the lack of established network reserves. The design of marine reserve networks will depend on the dispersal patterns of different species (Carr and Reed 1993; Allison et. al. 1998). Low dispersal species produce larvae that settle within the reserve and replenish themselves, with no need of immigration from other sources. The lack of balance between colonization and extinction in these isolated areas can drive populations to perish (Levins 1970). These species may or may not be part of a network; establishing a small reserve in one of these areas will be limited to protecting a single population without any effect on others. Different dispersal rates will create distinct network patterns going from limited connections between populations to a series of source and sink assemblages (Carr and Reed 1993; Allison et. al. 1998). It is important to identify habitats that serve as sink or source for different species and assess the connection between close and faraway sites. Long-term studies about site-specific demographic parameters are important to discern between a self-sustaining population without emigration and a local population increase due to an anomalous good year in a sink population (Harrison 1991, Dias 1996). In order to establish a reserve network, a combination of sink and source locations should be chosen to create a stable source-sink system that will ensure the persistence of the population in a specific region. Allocating reserves in isolated sink areas will probably render population extinctions since they may not prevail without supply from source populations (Harrison 1991, Dias 1996).

Yearly variations in the dominant pattern of these components will make dispersal patterns even more difficult to predict. A network of reserves along a specific geographic area will provide a higher probability of protecting several source populations even when shifts in physical conditions prevail. A rocky reef with suitable habitat located offshore can reinforce the reserves network by providing a suitable location for settlement when upwelling conditions prevail.

Adult urchins movement rates indicate that a spillover of adults from the reserves into adjacent harvested areas might be limited to urchins located at the edge of the reserves.

To what extent a particular reserve will enhance recruitment to adjacent exploited areas or other reserves is still a difficult challenge due to the complex task of tracking larvae. New techniques, such as mark and recapture (Levin 1990), molecular analysis (Waples and Rosenblatt 1987; Powers et al. 1990; Doherty et al. 1995; Palumbi 1995), and modeling (Siddall et al. 1986; Johnson and Hess 1990; Possingham and Roughgarden 1990; Black et al. 1991; Bostford et al. 1994) appear promising, but more research needs to be done to accurately relate larvae to source populations (Sammarco and Andrews 1988). Indirect techniques such as enzyme electrophoresis and DNA-based analysis show potential to evaluate genetic differences between populations and indirectly infer dispersal and gene flow capabilities (Palumbi 1995). Populations with low larval dispersal might be genetically different compare to populations whose larvae disperse broadly. But the fact that certain populations have larvae with high dispersal capabilities does not imply that genetic differentiation between close populations is not possible. Some examples show that despite the long larval periods of some intertidal species, genetic differences exist between populations few kilometers apart (Berger 1973; Burton and Feldman 1982; Saavedra et al. 1993;).

Fertilization success can be greatly enhanced if the density and size of reproductive adults increases. Broadcast spawners rely on dense aggregations of individuals to assure fertilization (Denny and Shibata 1989; Shepherd 1990; Pennington 1985; Levitan et al. 1992). Minimum size limits has been used as management tool to allow urchins to reach sexual maturity and spawn at least twice before being harvested. However, recruitment overfishing is a common problem in red urchins since spawning stocks that produce recruits are not well protected. The lack of spawning adults in the exploited areas might have contributed to decrease the frequency of recruitment events and increase their variability. Population levels can be strongly affected by stochastic recruitment events as suggested by Sale (1978, 1990) in the "lottery hypothesis". The bottleneck of most marine populations recovery is the sporadic and irregular recruitment that might not be sufficient to support heavy exploitation rates (Bostford et al. 1993). A combination of maximum size limits and the establishment of reserves ensure the protection of source populations that can increase recruitment in the adjacent areas. Larger individuals with enhanced reproductive potential can provide a buffer against non-favorable recruitment conditions that can increase the availability of larvae in the column water and the probabilities of settlement when oceanographic conditions become propitious.

CHAPTER 3

ASSESSMENT OF GROWTH AND MORTALITY OF RED SEA URCHINS (*Strongylocentrotus franciscanus*) IN KELP FOREST RESERVES AND ADJACENT EXPLOITED AREAS.

Gabriela Montaño Moctezuma, Hiram W. Li, and Neil T. Richmond

Abstract

Differences in growth and mortality rates in red sea urchins (*Strongylocentrotus franciscanus*) were assessed among two marine reserves and adjacent exploited areas off Oregon. Growth rates and number of age classes were estimated by length frequency analysis using a maximum likelihood method (MULTIFAN). Growth parameters generated by the program were compared with parameters estimated by growth increments from urchins reared in laboratory conditions. Instantaneous mortality rates were calculated using catch curve analysis applied to length at age data. Mortality rates estimated with MULTIFAN were compared with catch curve analysis results. Growth increments suggest that the time it will take a specific cohort to recruit to the fishery is 9-10 years, suggesting a low recovery rate after exploitation. Mortality rates were higher in marine reserves compared to exploited areas. Growth and mortality rates were affected by food availability, competitors, and sporadic recruitment more than by reserve non-reserve effects.

Introduction

Spatial management in combination with protected areas have been lately suggested as practices to protect marine ecosystems and perhaps to enhance fisheries (Quinn et al. 1993, Botsford et al. 1993, Polacheck 1990, De Martini 1993, and Man et al. 1995). Models proposed by these authors indicate possible preventions of high variability in population levels as well as extinctions when spatial management is utilized. These models incorporate life history information such as growth, mortality, maturity, emigration-immigration rates as well as different exploitation characteristics to evaluate different closure size scenarios.

Spatial variations in red urchins (*Strongilocentrotus franciscanus*) growth and mortality rates have been studied from Alaska to California (Ebert et al. 1999, Morgan 2000). Differences in growth rates were common in populations few kilometers apart, but a pattern associated with latitude was not evident (Ebert et al. 1999). Morgan (2000) found no differences in growth and natural mortality rates between sites in northern California; however, he found significant differences in alongshore fishing mortality that were strongly correlated with recruitment variability.

Growth and mortality estimations have been difficult because techniques to determine age in red sea urchins are not well developed. Several previous attempts did not lead to conclusive results. Without aging techniques, determining population parameters relies on analyzing length frequency data to infer population age structure. Length frequency methods are based on the presence of modes in all size distributions, but it is often the case that modes occur only at small sizes (Smith et al. 1998). The lack of modes is common when recruitment is sporadic or variability in growth is strong enough to obscure age modes (Barry and Tegner 1990, Ebert 1993, Bostford et al. 1994). Length frequency distributions can depict different forms depending on the effect that mortality, growth, recruitment, predation or sampling selectivity have on populations (Bostford et al. 1994). Red urchin size distribution can vary among populations (Tegner and Dayton 1981, Ebert and Russell 1992, Ebert et al. 1999, Morgan 2000), but it is usually bimodal, with one mode at small sizes and another mode at adult sizes. Annual pulses in recruitment create periodic consecutive modes with all sizes well represented (multimodal distribution). When K (von Bertalanffy growth parameter) varies, mode pulses at small sizes and close together are removed. Changes in these parameters can create differences in size distributions among sites (Bostford et al. 1994).

Several approaches have been taken to estimate growth and mortality rates in red sea urchins. Growth rates have been estimated by following size increments in laboratory conditions (Leighton 1967, Bostford et al. 1993), in caged field experiments (Swan 1961, Schroeter 1978), and by tagging wild urchins with tetracycline (Ebert et al. 1999). Smith et al. (1998) introduced the idea to determine growth and mortality parameters in red urchins from length frequency data and growth increments. Maximum likelihood methods have been used to estimate population parameters from size frequency data (MacDonald and Pitcher 1979, Hasselblad 1966, Rao 1973). These techniques utilize single length frequencies that can overestimate or underestimate some parameters (Schnute and Fournier 1980, Fournier and Breen 1983). Better estimations can be derived when a sequence of length frequencies from different months or years are analyzed together (Fournier et al. 1990). These authors developed a likelihood-based model (MULTIFAN) that simultaneously analyzes a sequence of length frequencies. The model has been applied to obtain parameters for long-lived species such as tuna (Fournier et al. 1990), sea turtles (Bjorndal et al. 1995), abalone (Fournier and Breen 1983), as well as short-lived species like shrimp (Fournier et al. 1991) and prawns (Baelde 1994).

Spatial management as well as the design of marine reserves require information about spatial variation in growth and mortality rates among locations within the same region. In Oregon, red urchins growth and mortality rates have been estimated by Ebert et al. (1999) for two exploited populations in the south, but no information has been gathered for northern or non-harvested areas. Populations inside marine reserves can provide natural mortality estimates and give insights about differences in growth rates between fished and non-fished areas. This study looks at differences in growth and mortality rates in red sea urchins (*Strongylocentrotus franciscanus*) among two marine reserves and adjacent exploited areas off Oregon. We propose that slow growth might be common inside the reserves due to lower red urchin densities; on the contrary, natural mortality possibly will be more driven by predation.

Methods

Size frequency information was collected during the summer and fall from 1994 through 1999 at four locations in Oregon. Two marine reserves: Whale Cove and Gregory Point, and two harvested areas: Simpson Reef and Depoe Bay. Whale Cove has been protected since 1967, and Gregory Point since 1993. The average harvest over ten years is 116.8 thousand pounds in Simpson Reef and 337.4 in Depoe Bay

(Richmond, et al. 1977). Red urchins test diameters were recorded *in situ* with vernier calipers to the nearest 0.1 cm. Ten $5m^2$ quadrats per transect were selected at random along belt transects, 2m wide by 40m long ($80m^2$), and all urchins inside the quadrats were measured. On average six transects were located in each study site. Abundances of annual kelp (*Nereocystis luetkeana*), perennial kelp (*Pterygophora californica* and *Laminaria sp.*), and the starfish *Pycnopodia helianthoides* were estimated by counting all the individuals found in each $5m^2$ along all transects. Kelp abundances were estimated by the analysis of video transects that were recorded at the same time in all transects.

Length frequency data from each site was analyzed with a nonlinear statistical model (MULTIFAN) that incorporates hypothesis testing to calculate von Bertalanffy growth parameters (K, L_∞, t_0), and the number of age classes present in a set of length data (Fournier et al. 1989, Fournier et al. 1990). A maximum value of the log-likelihood function is calculated for each proposed initial K values and presumed age modes present in the data. Each time a new age class is proposed, the increase in the maximum log-likelihood is calculated. An additional age class is added until there is not a significant increase in the maximum log-likelihood function. Each increase is tested for significance by a χ^2 test. The best fit is found when the addition of a new parameter does not improve the previous fit of the model. To assess the sensitivity of MULTIFAN to initial conditions, we tested different constraints, standard deviations, range of K values and age modes. Each condition was tested independently, leaving the others fixed. 50 model runs per study area were performed and the effect of changing initial conditions was assessed. Because initial standard deviation was the most important factor that controlled the estimates of K, L_∞, and age classes, we set the same standard deviation values (2.5) for all sites based on the width of a well-defined mode in the length data.

To validate growth estimations obtained with MULTIFAN, we followed growth increments from urchins held in tanks with flowing seawater at the Hatfield Marine Science Center (OSU). 40 red urchins were individually tagged with passive integrated transponder (PIT) tags, and increments in size were recorded every 2-3 months for one year. Size intervals were: 2-4 cm, 4-6 cm, 6-8 cm, and 9-16 cm. Urchins were fed regularly with a mixture of 3 parts of kelp (*Nereocystis leutkeana* and *Laminaria sp.*) and 1 part of fish supplement (squid, krill, herring, trout, and vegetables). Von Bertalanffy growth parameters (K, L_∞, and t_0) were calculated by a Ford-Waldford plot (Waldford 1946).

Instantaneous mortality rates were estimated by catch curve analysis using the age frequency distributions obtained by MULTIFAN. The instantaneous rate of total mortality (Z) is the slope of the regression line fitted to points greater than the age of full recruitment. To make comparisons among sites, mortality rates were calculated in each study area for urchins above 8.9 cm, the harvestable size limit. Mortality estimates for both exploited areas represent the total mortality (Z) of the population, and encompasses fishing (F) and natural (M) mortality. Estimates from the reserves correspond only to natural mortality, since populations in these areas are not affected by harvest. Mortality estimates from the catch curve analysis were verified with estimates obtained by MULTIFAN.

Results

Growth

Growth parameter estimations from red urchins reared in laboratory conditions provided information to validate the performance of length frequency analysis. The increments in size during 1 year were higher for small urchins compare to large urchins. Small urchins (2-3 cm test diameter) had an average growth of 1.15 cm (S.D. = 0.31), medium size urchins (6-8 cm) grew 0.68 cm (S.D. = 0.40), and bigger urchins (9-16 cm) had small increments of 0.26 cm (S.D. = 0.40). Increments were mostly observed from November through July (Fig. 3.1). Growth increments derived from length frequency analysis also showed greater increases in size for small urchins compare to larger individuals (Table 3.1).

Von Bertalanffy growth parameters for urchins kept in the lab were: $K = 0.075$; $L\infty = 14.6$ cm, and $t_0 = 0.97$ (Figure 3.2). These estimations were within the range of parameters calculated by length frequency analysis and were very similar to the ones from Gregory Point ($K = 0.067$, $L\infty = 20.4$ cm, and $t_0 = 0.68$).

Growth coefficient comparison among sites suggested faster growth in Gregory Point ($K = 0.067$), intermediate growth in Depoe Bay ($K = 0.042$) and Simpson Reef ($K = 0.027$), and lower growth in Whale Cove ($K = 0.014$) (Table 3.2). The percentage of younger individuals in Gregory Point and Depoe Bay (Ages 2-6) may have contributed to faster growth rates in this areas, Whale Cove is mostly represented by old urchins (> 12 years) that grow slower than young individuals.

Length frequency distributions used for the length frequency analysis (MULTIFAN) show the fits selected by the maximum likelihood function to best represent the data in each study site (Figs. 3.3-3.6). Each mode was assigned a year class to generate the mean length at age and the corresponding standard deviations per age class. 20 year classes were selected by the model to represent the population in Whale Cove, Depoe Bay and Simpson Reef, and 19 year classes for the population in Gregory Point.

We followed the predominant modes through time from the length frequency distributions of Depoe Bay and Gregory Point to compare the differences in growth suggested by MULTIFAN between these two sites. Mode changes in time agree with the K values obtained for the two sites that suggest faster growth rates for Gregory Point compared to Depoe Bay. The first mode in Depoe Bay corresponds to urchins that were 2 years old in 1994. The same cohort was 4 and 5 years old in 1996, and 6 years old by 1998 (Fig. 3.3). In Gregory Point, red urchins that were 4 and 5 years old in 1996 had approximately the same sizes as urchins from Depoe Bay in the same year (1996); however, by 1997, 5 and 6 year old individuals from Gregory Point were the same size as urchins the same age (5 and 6 years) from Depoe Bay in 1998, suggesting fast grow during 1997 in Gregory Point (Fig. 3.4). By 1999 the same cohort from Gregory Point (8 years old) attained 8.1 cm, while urchins from Depoe Bay would have been 7.5 cm, has the same growth rate prevailed in Depoe Bay from 1998 to 1999.

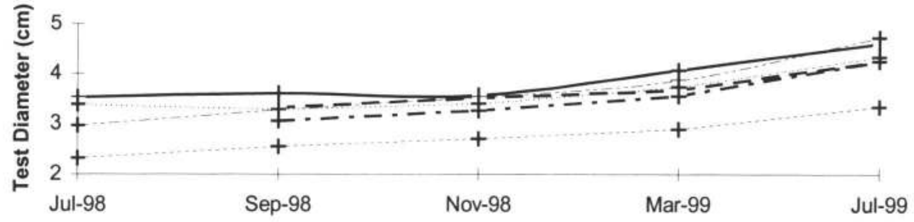
Table 3.1. Annual growth increments (mm) at different size intervals for red sea urchins in two reserves (Whale Cove and Gregory Point) and adjacent exploited areas (Depoe Bay and Gregory Point).

Size Interval	Depoe Bay	Gregory Point	Simpson Reef	Whale Cove	Laboratory
(2-3 cm)	9.00	11.77	9.06	10.13	11.5
(4-6 cm)	7.77	9.64	8.24	9.72	7.6
(6-8 cm)	6.71	7.89	7.59	9.40	6.8
(>8 cm)	5.25	5.36	6.46	8.60	2.6

Table 3.2. von Bertalanffy growth parameters ± S.D. for red urchins estimated by length frequency analysis and laboratory conditions.

Study Site	K (yr^{-1})	$L\infty$ (mm)	t_0 (yrs)
Depoe Bay	0.042 ± .0007	246.7 ± 2.6	1.76 ± .03
Simpson Reef	0.027 ± .0007	362.8 ± 7.4	1.71 ± .02
Gregory Point	0.067 ± .0009	204 ± 1.5	0.68 ± .03
Whale Cove	0.014 ± .001	764.2 ± 64.1	1.21 ± .03
Laboratory	0.075	146	0.97

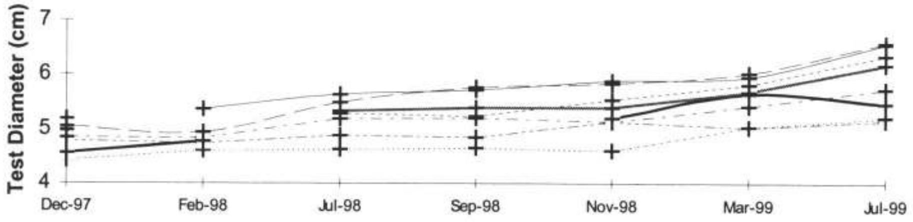
Length Interval 2-4 cm



Average growth (1Year)=1.15 cm

Average Slope=.003

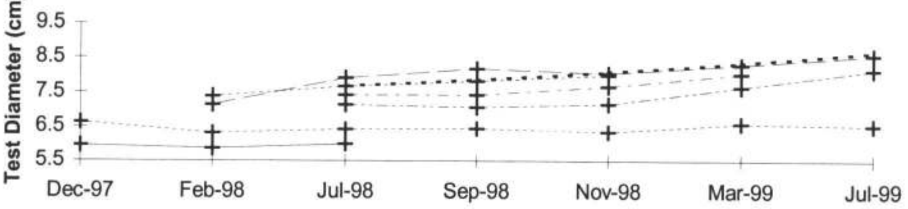
Length Interval 4-6 cm



Average growth (1 Year)=.76cm

Average slope=.0019

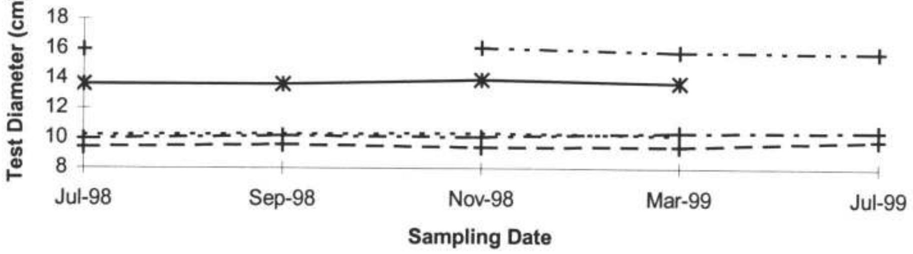
Length Interval 6-8cm



Average growth (1 Year)=.68 cm

Average Slope=.002

Length Interval 9-16 cm



Average growth (1 Year)=.26 cm

Average Slope=.005

Figure 3.1. Changes in length through time for different length intervals of red urchins reared in laboratory conditions. Each line represents and individual.

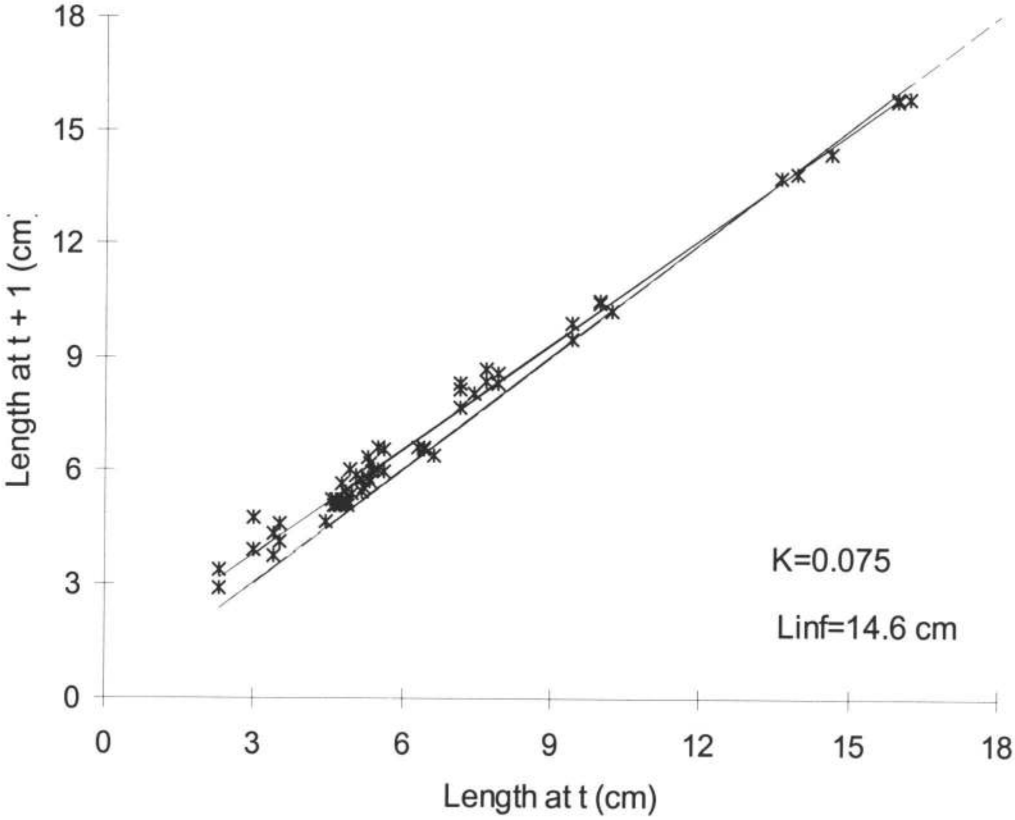


Figure 3.2. Ford-Waldford plot of red urchins reared in laboratory conditions for 1 year. Regression: $y = 0.97 + 0.93x$; $K = - \ln 0.93 = 0.075$; $L\infty = 14.6$ cm. Dashed line = no growth.

Mean length at age (Table 3.3) was used to estimate the years after settlement that it takes red urchins to attained 8.9 cm, the minimum harvestable size limit. In Whale Cove and Gregory Point it will take around 9 years to reach 9 and 8.9 cm, respectively; it will take 10 years in Depoe Bay and Simpson Reef to get to 8.9 and 9.1 cm, respectively. Urchins from Depoe Bay that appear as 6 years old in 1998 will recruit to the fishery in 2002 (Fig. 3.3). Urchins from Simpson Reef that were 8 years old in 1997 and measured 7.6 cm, by 1999 were 10 years old and attained harvestable sizes (9.1 cm) (Fig. 3.5).

Length frequency information from Depoe Bay suggests that urchins that were 2 years old in 1994 came from a recruitment episode that took place in 1992. None of the length frequency series suggests that a significant recruitment event has occurred from 1994 through 1999 (Figs. 3.3-3.6).

Mortality

Based on mean length-at-age results (Table 3.3), that indicate the age of urchins that have reached harvestable sizes (8.9 cm), total mortality estimates were calculated for urchins 9 years old in Gregory Point and 10 years old in both exploited areas. Mortality estimates in Whale Cove were calculated for urchins above 13 years because is the age where the slope starts descending (Figs. 3.8 to 3.11).

In Depoe Bay, total mortality (Z) decreased from 0.26 yr^{-1} (1994) to 0.21 yr^{-1} (1996) (Fig 3.8). This decline corresponds to declines in catch per unit effort from 381 lb/dive (1994) to 321 lb/dive (1996). Total mortality increased to 0.31 yr^{-1} in 1998, suggesting a 47.6 % increase in fishing pressure from 1996 through 1998. In Simpson Reef, Z increased 71.4 % from 1997 through 1999 (Fig. 3.9). In both exploited areas fishing pressure has increased through time. In Gregory Point, natural mortality decreased from 0.33 yr^{-1} in 1996 to 0.29 yr^{-1} in 1997, and increased to 0.50 yr^{-1} by 1999 (Fig. 3.10). Natural mortality in Whale Cove oscillated between 0.24 yr^{-1} and 0.52 yr^{-1} from 1996 through 1999 (Fig. 3.11).

Average annual mortality rates were low in Depoe Bay (0.26 yr^{-1}), intermediate in Simpson Reef and Gregory Point (0.29 yr^{-1} and 0.37 yr^{-1}, respectively), and high in Whale Cove (0.42 yr^{-1}) (Tables 3.4-3.7). These results suggest higher mortality rates in both marine reserves compare to both exploited areas; however, the difference between Simpson Reef and Gregory Point is small (0.08 yr^{-1}). High mortality in Whale Cove indicate that the survival of adult red urchins from this area may decrease with age. This area is mostly represented by old urchins.

Mortality estimates obtained by catch curve analysis were the same as those obtained by MULTIFAN (Tables 3.4-3.7).

Table 3.3. Mean and standard deviation of lengths-at-age (mm) for red urchins calculated by length frequency analysis (MULTIFAN).

Age	Depoe Bay	Gregory Point	Simpson Reef	Whale Cove
1	17.38 ± 3.67	9.0 ± 3.38	16.5 ± 2.43	12.58 ± 2.50
2	26.76 ± 3.53	21.57 ± 3.18	25.81 ± 2.43	22.86 ± 2.57
3	35.75 ± 3.41	33.32 ± 3.01	34.87 ± 2.43	32.99 ± 2.64
4	44.38 ± 3.30	44.31 ± 2.85	43.68 ± 2.43	42.99 ± 2.71
5	52.65 ± 3.19	54.6 ± 2.71	52.26 ± 2.43	52.85 ± 2.78
6	60.58 ± 3.09	64.23 ± 2.59	60.61 ± 2.43	62.58 ± 2.85
7	68.19 ± 3.00	73.23 ± 2.48	68.74 ± 2.43	72.17 ± 2.92
8	75.48 ± 2.91	81.66 ± 2.38	76.65 ± 2.43	81.64 ± 2.99
9	82.48 ± 2.83	89.54 ± 2.29	84.34 ± 2.43	90.97 ± 3.06
10	89.19 ± 2.76	96.91 ± 2.21	91.83 ± 2.43	100.17 ± 3.14
11	95.63 ± 2.69	103.81 ± 2.14	99.11 ± 2.43	109.25 ± 3.21
12	101.8 ± 2.63	110.27 ± 2.07	106.2 ± 2.43	118.21 ± 3.29
13	107.72 ± 2.57	116.31 ± 2.01	113.1 ± 2.43	127.04 ± 3.36
14	113.4 ± 2.51	121.96 ± 1.96	119.81 ± 2.43	135.75 ± 3.44
15	118.85 ± 2.45	127.25 ± 1.91	126.35 ± 2.43	144.35 ± 3.52
16	124.07 ± 2.40	132.19 ± 1.87	132.71 ± 2.43	152.82 ± 3.59
17	129.08 ± 2.36	136.82 ± 1.82	138.89 ± 2.43	161.18 ± 3.67
18	133.88 ± 2.31	141.15 ± 1.79	144.91 ± 2.43	169.42 ± 3.75
19	138.49 ± 2.27	145.2 ± 1.75	150.77 ± 2.43	177.56 ± 3.83
20	142.91 ± 2.23		156.47 ± 2.43	185.58 ± 3.91

Food, predators, and competitors abundance

Perennial kelp showed higher abundances in Gregory Point compare to Simpson Reef and Depoe Bay (F = 9.07, P = 0.01, df = 287) but not a significant difference was found between Whale Cove and all other sites (F = 1.47, P = 0.22, df = 287). Annual kelp was more abundant in Gregory Point than all other sites, and it was also more abundant in Simpson Reef compare to Whale Cove and Depoe Bay (F = 36.12, P < 0.001, df = 287) (Fig. 3.7).

The starfish *Pycnopodia helianthoides* was more abundant in Simpson Reef than in any other site, and densities in Whale Cove were higher than those of Gregory Point and Depoe Bay (F =7.75, P < 0.0001, df = 329). Purple urchins were more abundant in Gregory Point. Depoe Bay presented higher abundances than Whale Cove and Simpson Reef (F = 16.28, P < 0.0001), df = 329) (Fig. 3.7).

Table 3.4. Annual natural mortality rates (M) and survival (e^{-M}) for Whale Cove marine reserve from 1996 through 1999.

Method	1996	1997	1998	1999	Average	
					Mortality	Survival
Catch Curve	0.39	0.24	0.51	0.52	0.42	0.66
MULTIFAN	0.39	0.25	0.50	0.55	0.42	0.66

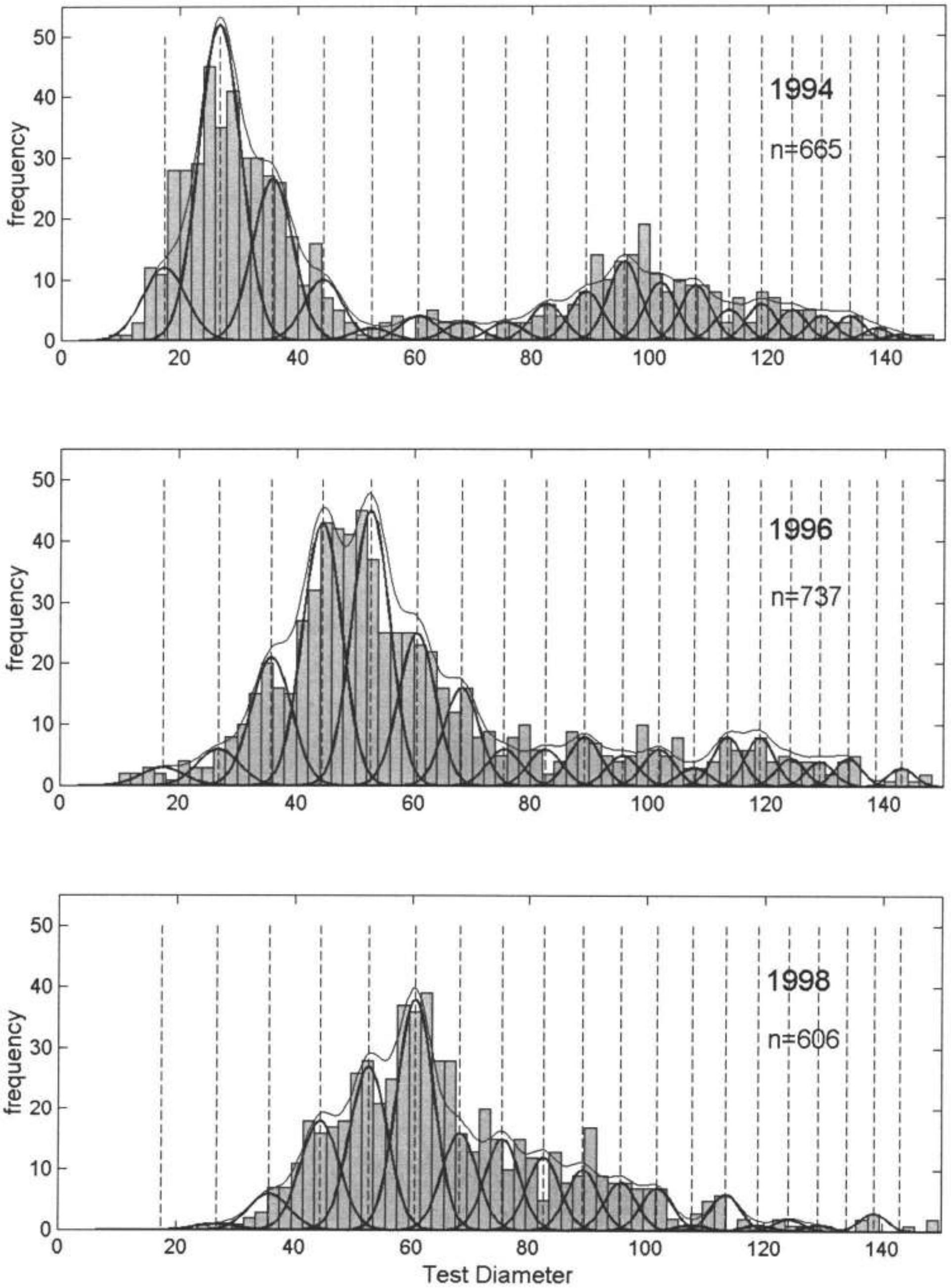


Figure 3.3. Length frequency distributions used for the length frequency analysis (MULTIFAN) for Depoe Bay harvested area for 1994, 1996, and 1998. Modes show the fits selected by the maximum likelihood function to best represent the data. Each mode represents an age class. Vertical dashed lines correspond to mean length at age values.

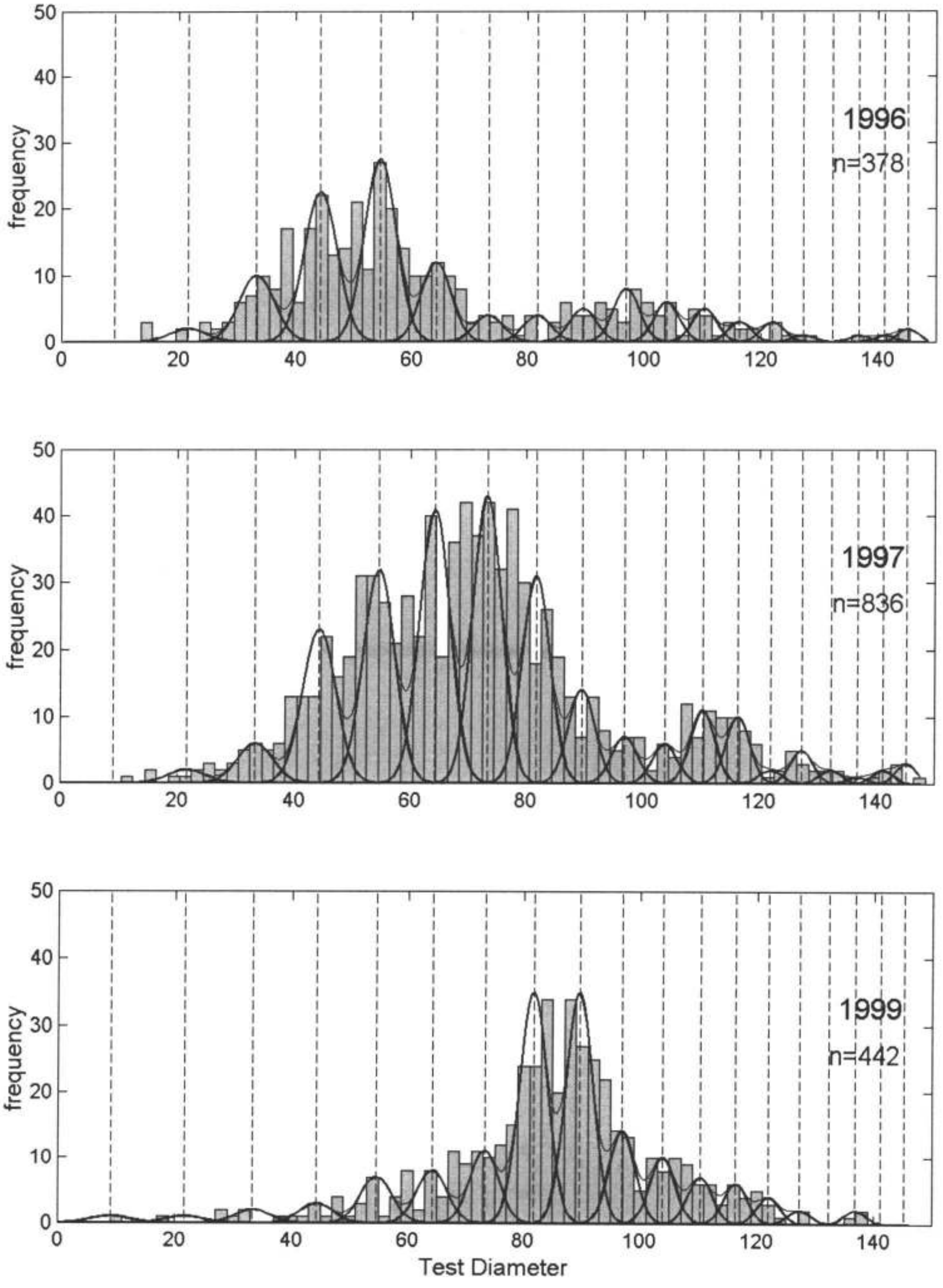


Figure 3.4. Length frequency distributions used for the length frequency analysis (MULTIFAN) for Gregory Point marine reserve for 1996, 1997 and 1999. Modes show the fits selected by the maximum likelihood function to best represent the data. Each mode represents an age class. Vertical dashed lines correspond to mean length at age values.

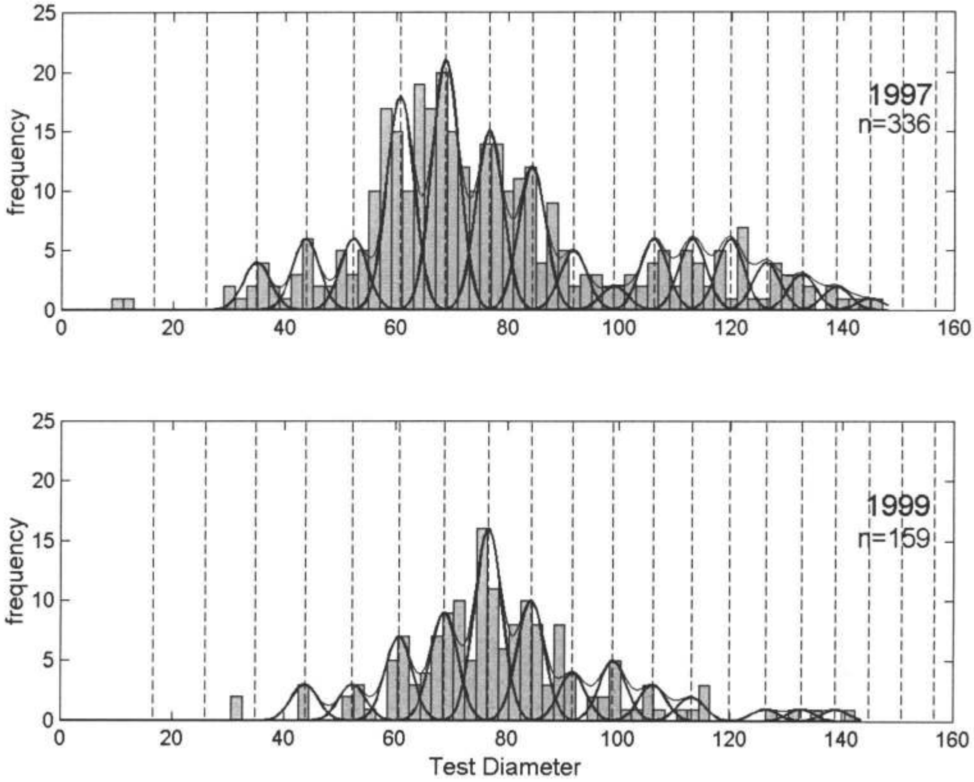


Figure 3.5. Length frequency distributions used for the length frequency analysis (MULTIFAN) for Simpson Reef harvested area for 1997 and 1999. Modes show the fits selected by the maximum likelihood function to best represent the data. Each mode represents an age class. Vertical dashed lines correspond to mean length at age values.

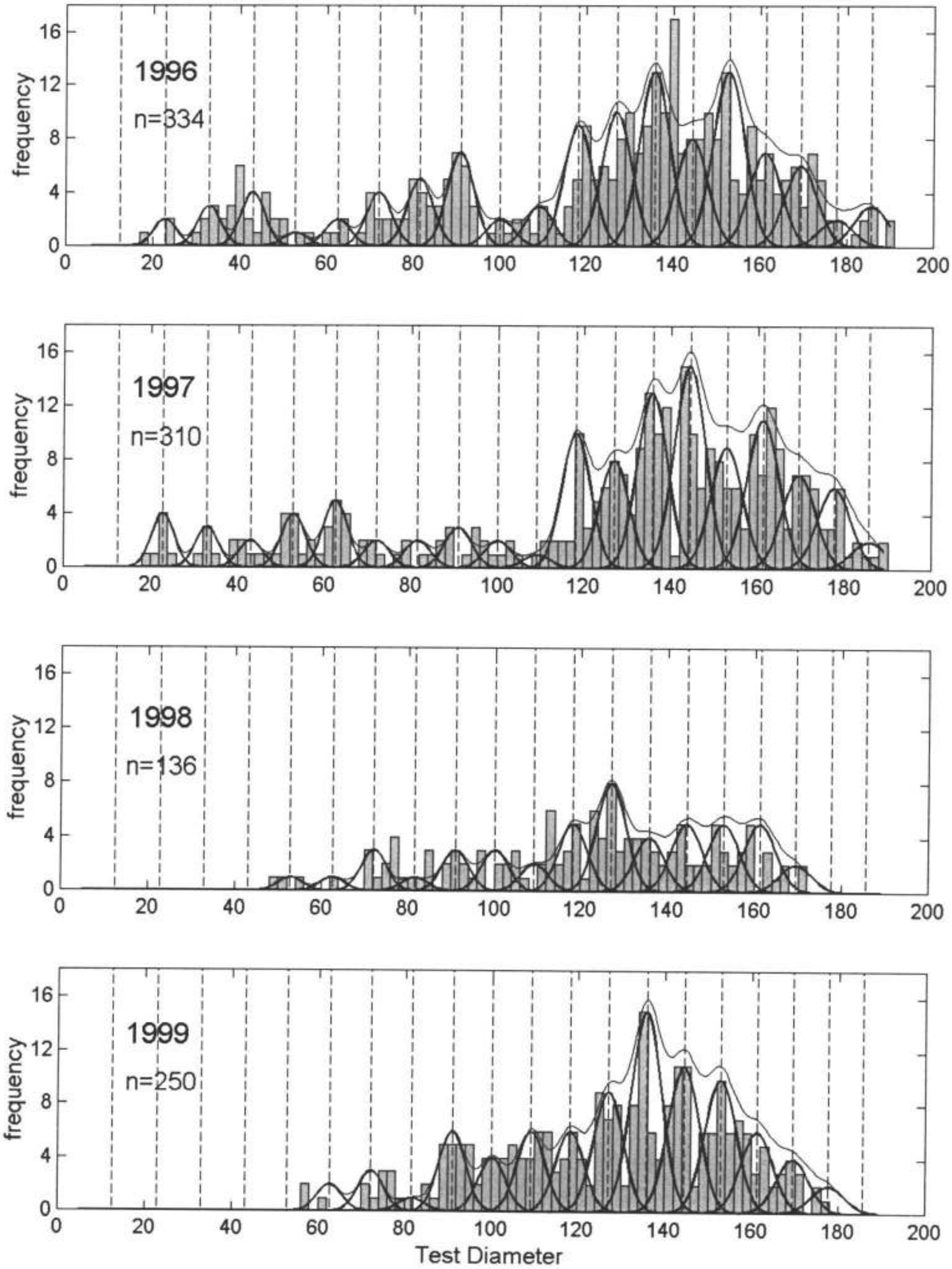


Figure 3.6. Length frequency distributions used for the length frequency analysis (MULTIFAN) for Whale Cove marine reserve from 1996 through 1999. Modes show the fits selected by the maximum likelihood function to best represent the data. Each mode represents an age class. Vertical dashed lines correspond to mean length at age values.

Table 3.5. Annual natural mortality rates (M) and survival (e^{-M}) for Gregory Point marine reserve from 1996 through 1999.

Method	1996	1997	1999	Average	
				Mortality	Survival
Catch Curve	0.33	0.29	0.50	0.37	0.69
MULTIFAN	0.29	0.33	0.47	0.36	0.70

Table 3.6. Annual total mortality (Z), and survival (e^{-Z}) for Simpson Reef exploited area in 1997 and 1999.

Method	1997	1999	Average	
			Mortality	Survival
Catch Curve	0.21	0.36	0.29	0.75
MULTIFAN	0.23	0.39	0.28	0.76

Table 3.7. Annual total mortality (Z), and survival (e^{-M} or e^{-Z}) for Depoe Bay exploited area from 1994 through 1998.

Method	1994	1996	1998	Average	
				Mortality	Survival
Catch Curve	0.26	0.21	0.31	0.26	0.77
MULTIFAN	0.29	0.21	0.32	0.27	0.76

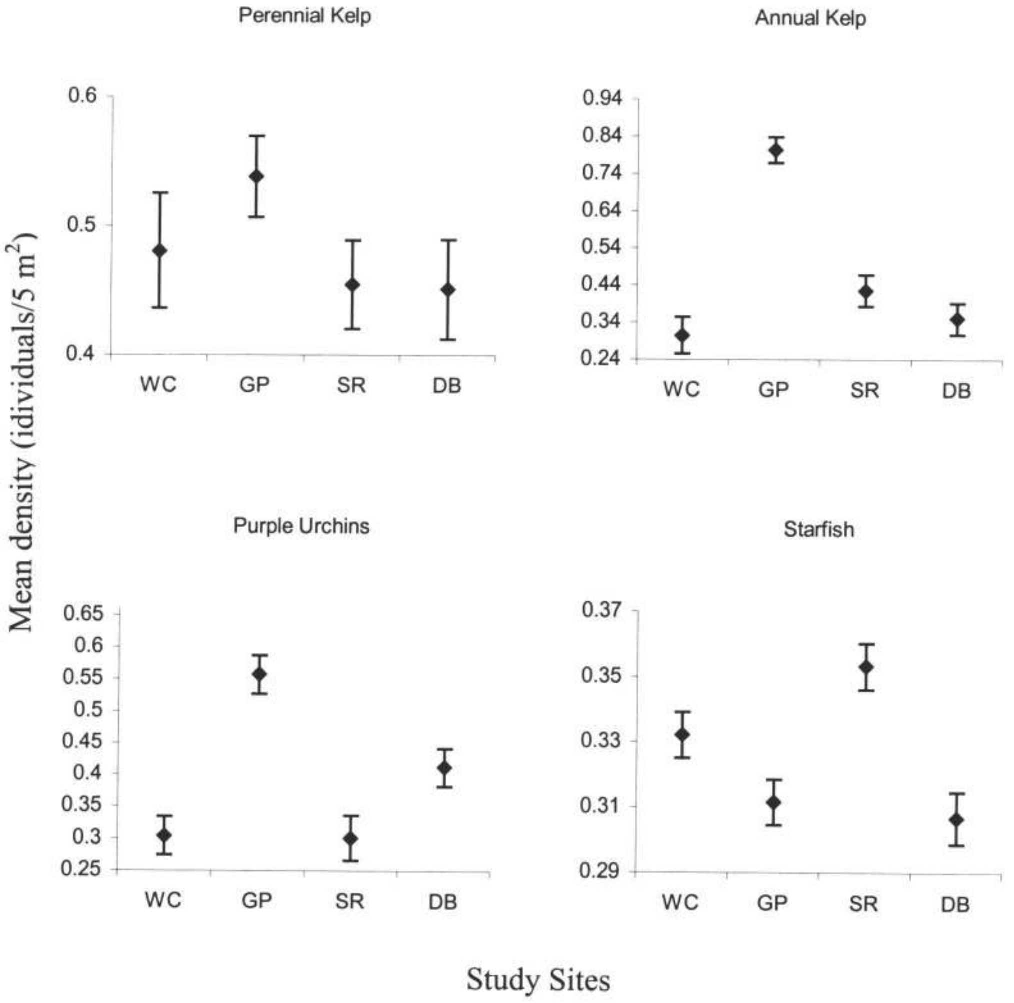


Figure 3.7. Mean densities of food (annual and perennial kelp), predators (starfish), and competitors (purple urchins) in two marine reserves: Whale Cove (WC) and Gregory Point (GP), and adjacent exploited areas: Simpson Reef (SR) and Depoe Bay (DB). Standard error bars are indicated.

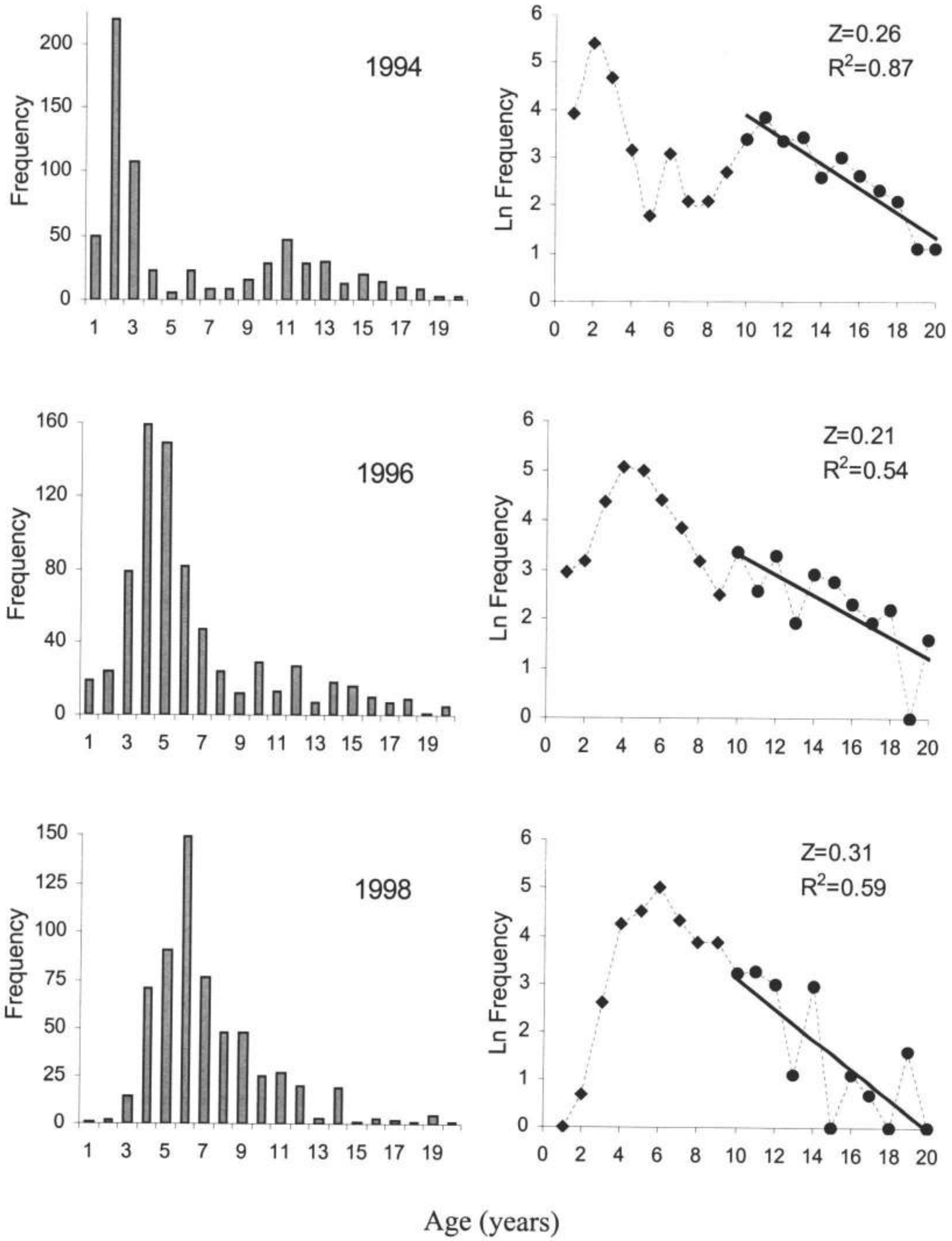


Figure 3.8. Red urchins age distribution for Depoe Bay exploited area between 1996 and 1999. Catch curve analyses for each year are indicated on the right panel. The slope of the descending part of the curve corresponds to the total mortality rate (Z). In a fished area, Z is equal to natural mortality (M) + fishing mortality (F).

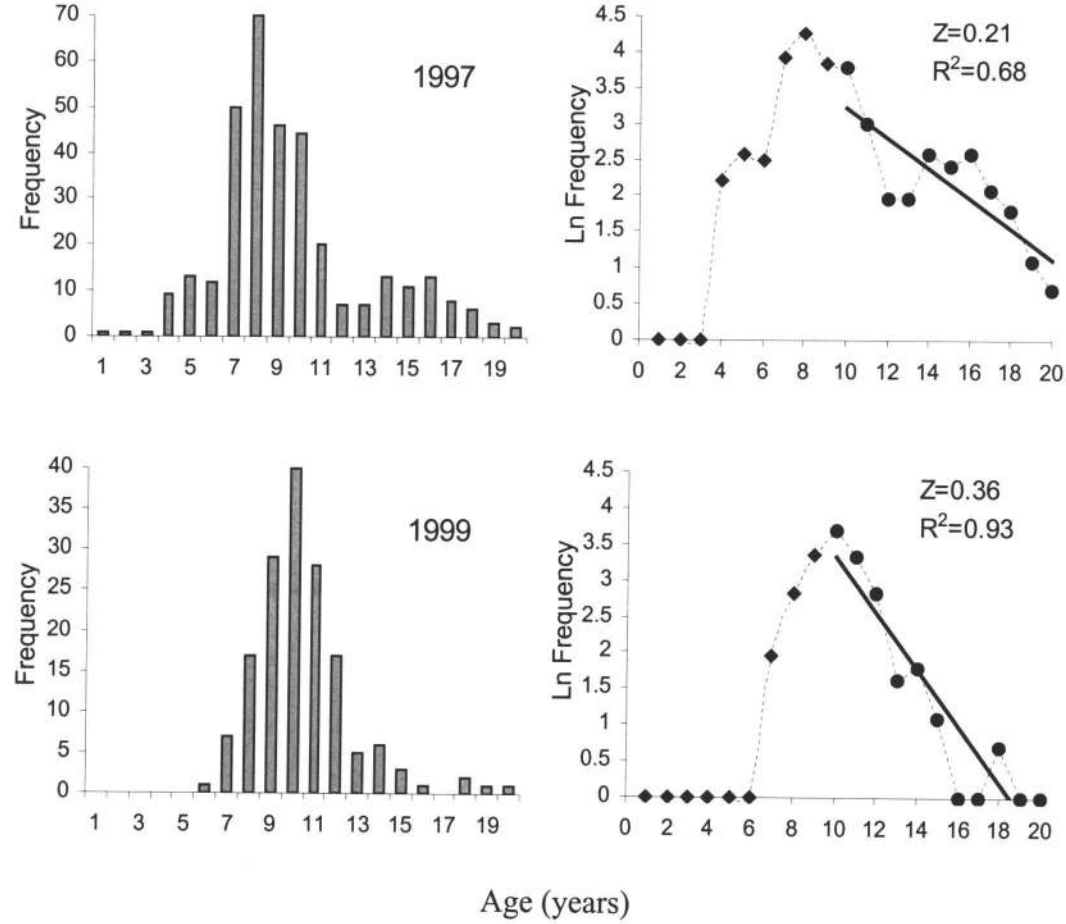


Figure 3.9. Red urchins age distribution for Simpson Reef exploited area between 1996 and 1999. Catch curve analyses for each year are indicated on the right panel. The slope of the descending part of the curve corresponds to the total mortality rate (Z). In a fished area, Z is equal to natural mortality (M) + fishing mortality (F).

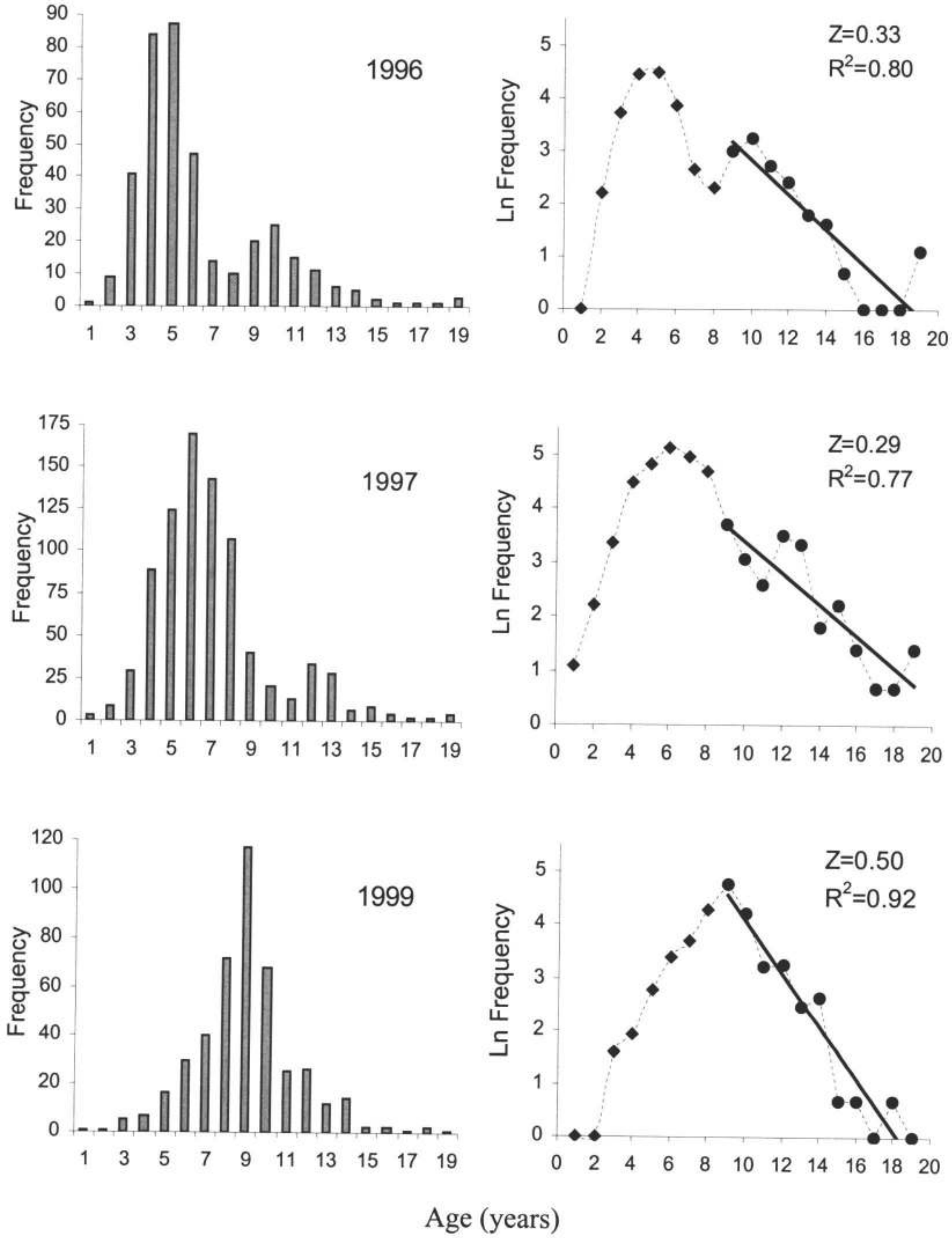


Figure 3.10. Red urchins age distribution for Gregory Point marine reserve between 1996 and 1999. Catch curve analyses for each year are indicated on the right panel. The slope of the descending part of the curve corresponds to the natural mortality rate (M). In a reserve, total mortality (Z) is equal to natural mortality (M).

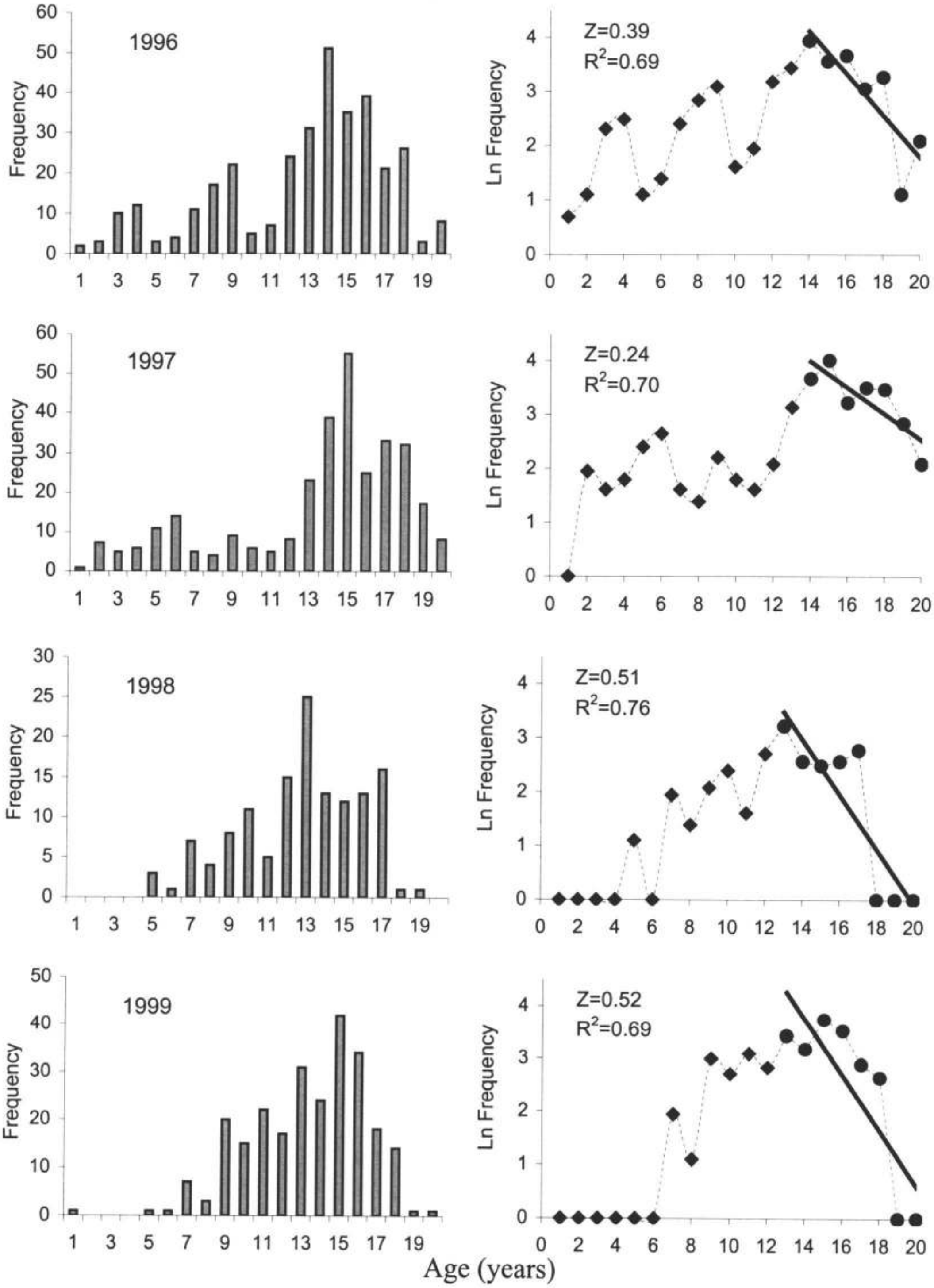


Figure 3.11. Red urchins age distribution for Whale Cove marine reserve between 1996 and 1999. Catch curve analyses for each year are indicated on the right panel. The slope of the descending part of the curve corresponds to the natural mortality rate (M). In a reserve, total mortality (Z) is equal to natural mortality (M).

Discussion

Age distributions clearly differed between the old reserve (Whale Cove) and the area that has been exposed to higher fishing pressure (Depoe Bay). The proportion of older and larger individuals in Whale Cove suggests that urchins are recovering. In contrast, high proportions of young and small urchins in Depoe Bay and the lack of older individuals suggest that the population in this area may be experiencing problems with fertilization success due to low reproductive potential. Sporadic recruitment, low growth rates, and the time it will take a cohort to reach harvestable sizes (10 years), indicate that exploited populations will recover very slowly. After a cohort has been fished out, there will not be resources left to maintain a fishery for several years.

Differences in growth rates among sites are important to compare the time it will take a specific cohort to recruit to the fishery and the recovery rate after exploitation. Rotating spatial management may be important if significant differences in growth and time to reach harvestable sizes are found among sites. Differences between years in these parameters as well as sporadic recruitment might also call for rotational harvest as has been suggested for red urchins (Botsford, et al. 1993, Quinn et al. 1993, Pfister and Bradbury 1996).

We were expecting to find higher growth rates in both fished areas due to less red urchin densities and hence a decrease in food competition. Our results suggest that several factors in addition to abundance may play a role in the growth schedules of populations from different locations. Differences among sites in food availability, partitioning of resources, competition for food as well as interspecific competition with purple urchins can affect red urchins growth rates.

Food availability in Gregory Point is high compared to all other study areas. In Gregory Point red urchins consume mainly perennial kelp while purple urchins eat only annual kelp (Chapter 5). Although the abundance of purple urchins is high in this area, the partitioning of resources diminishes the competition for food between the two species. Abundant perennial kelp in this area contributed to the observed higher growth rates. The presence of purple urchins might also enhance red urchins growth as suggested by Schroeter (1978). Abundances of purple urchins in Gregory Point were higher than in any other area. In Depoe Bay, both annual and perennial kelp abundances are lower than in Gregory Point. In this area competition for food and space between purple and red urchins is present (Chapter 5), suggesting that less food is available and hence lower growth rates can be expected. Although abundances of annual and perennial kelp were similar in Depoe Bay and Simpson Reef, growth rates were lower in Simpson Reef. In this area red urchins relay on annual kelp only (Chapter 5). Therefore, the actual amounts of kelp that have been utilized for growth are less than in Depoe Bay. Food abundance was similar in Whale Cove compared to Depoe Bay and Simpson Reef. In spite of this, lower growth rates were found in this area that might be explained by higher abundances of red urchins above 12 cm that consume large quantities of algae. Food limitation in addition to density dependence may be important factors controlling growth in this area as well as competition for food with purple urchins (Chapter 5). Levitan (1988) found that growth rates of the urchin *Diadema antillarium* decreased as urchin densities increased.

Although higher abundances of predators (*Pycnopodia*) were found in Simpson Reef, annual mortality rates in this area were about the same as in Gregory Point where predators were not as abundant. *Pycnopodia* preys mainly on purple urchins in Simpson Reef and less on juvenile red urchins. The starfish does not consume adult red urchins in this area compare to Gregory Point, where they prey on both juvenile and adult red urchins (Chapter 5). Lower mortality rates in Depoe Bay may be explained by low predator abundances in this area. Mortality estimates from Whale Cove correspond to old urchins above 13 years of age. Due to the abundances of urchins above 13 years old and perhaps older than 20 years, as has been suggested by Ebert et al. (1999), high natural mortality rates in Whale Cove might be due to senescence and high densities as the population reach the carrying capacity of the system. Biomass of adult urchins in this area do not increase or decrease over time but oscillate around a threshold that suggest being close to carrying capacity levels (Chapter 2). Ricker (1945) found that mortality rates can increase with age in bluegill sunfish populations. Mortality can be size specific in urchins where older individuals may have higher mortality rates than younger ones (Ebert, 1993).

Differences in mortality rates among sites may be influenced by the mean size of urchins in each area. Mean urchin sizes in Depoe Bay were low (52.6 mm) compared to Simpson Reef (83.7 mm) and Gregory Point (76 mm); by the contrary, Whale Cove is mostly represented by large urchins (mean size = 122.8 mm). This trend in mean sizes is similar to the trend in mortality found among sites.

Mortality results suggest that when recruitment is not constant, estimates can be affected by predominant cohorts in the length frequency data. Sporadic recruitment creates unimodal or bimodal distributions (Bostford et al. 1994) that can strongly influence annual mortality estimations. Morgan (2000) found that when recruitment occurs every five years, mortality estimates can vary broadly because individual cohorts reach harvestable sizes. An overestimation of mortality occurs when the cohort enters the fishery the first year. The overestimation declines, as the cohort gets older and distribute crossways the fished age or size classes. In this study, frequency data suggest that recruitment has been low or absent since 1992 in all areas studied. This sporadic recruitment may be the cause of the observed higher total mortality rates in the marine reserves that are subject to natural mortality (M) only, compare to the fished areas where total mortality is composed of natural and fishing mortality (F + M). This recruitment effect is clear in Gregory Point and Simpson Reef. In Gregory Point, the 10 year old cohort from 1996 gives a mortality estimate of 0.33 yr^{-1}. The same cohort distributes across older ages in 1997 giving a lower mortality estimate (0.29 yr^{-1}) this year. The growing cohort that was 5 years old in 1996 finally reaches the minimum legal size in 1999 at 9 years of age, creating an overestimation of the mortality rate (0.50 yr^{-1}) due to a steep slope in the age distribution (Fig. 3.10). This recruitment pattern makes mortality estimates to vary among years and among sites. To obtain and unbiased mortality estimate, several years should be analyzed starting with a year where a strong cohort enters the fishery. The cohort can be followed for several years and mortality estimates calculated each year until the mortality rate reaches a plateau and becomes constant.

Laboratory information was useful as a baseline to insure reasonable results from MULTIFAN. Similar growth rates were found between urchins that were constantly well fed in laboratory conditions and wild urchins in Gregory Point. Length frequency analysis is useful to determine growth rates when modes in smaller sizes are apparent in length frequency data; however, age determination for urchins above 20 years was not accurate. MULTIFAN has a limit of 20 years when it assigns years to modes in the length frequency data. Urchins above 15 cm in Whale Cove, the maximum length found in other studied areas, may be older than 20 years, since this area has been protected for 30 years. Ebert et al. (1999) have suggested from growth increment of tagged red urchins that 14 cm individuals might be around 50 years old. This error made growth increments for this area to be constant and higher than increments for all other sites.

Maximum length values ($L\infty$) for Whale Cove were overestimated ($L\infty=$ 764.2). Although $L\infty$ was high in this area, we are confident that the growth coefficient (K) estimate was reliable, since our calibration runs indicated that K was more sensitive to changes in initial S.D. values than to the estimated $L\infty$. Other studies in fishes have shown that $L\infty$ will be overestimated when age of larger fish is not precise (Buxton and Clarke 1986, Buxton 1993); however, K was not affected in these studies.

Mean increments based on growth estimations and laboratory data were lower than the estimates from Ebert et al. (1999) and Morgan (2000) for California, especially for young urchins (4-6 cm). These authors suggest that in California it will take 6-8 years for a cohort to recruit to the fishery. Higher temperatures in California might explain higher growth rates; nevertheless, Ebert et al. (1999) did not find a latitudinal gradient in growth due to temperature differences. They found more differences among closer populations that might be attributed to genetic variation, although no further information exists to support this conclusion.

The importance of reserves to provide information about parameters from populations that are not affected by harvest has not been emphasized when stressing the value of protected areas. Natural mortality estimates are difficult to obtain from fished populations, and several stock assessment techniques require this information as part of parameter input to the model. In most cases natural mortality is guessed at or obtained indirectly. Marine reserves are useful to estimate natural mortality and assess the variation in mortality through time. Per example, the sea urchin population in Gregory Point can be followed until the 9 year old cohort disappears due to natural causes. This is not possible in Simpson Reef (fished area) where the 9 year old cohort that we observed in 1999 will be fished out as soon as it gets fully recruited to the fishery.

A spatial management approach has been suggested for populations that show differences in population parameters (Quinn et al. 1993, Bostford et al. 1993, Polacheck 1990, De Martini 1993, Man et al. 1995). Populations will recover and will recruit to the fishery in a different pace if growth and mortality rates differ among sites. By rotating areas that have been harvested for several years, exploited populations can maintain density levels to assure fertilization success. Areas where slow growth and high mortality are observed will require more time to recover and hence will remain close for longer periods before being reopened for harvest.

CHAPTER 4

ALTERNATIVE COMMUNITY INTERACTIONS: A QUALITATIVE MODELING APPROACH

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Abstract

Shifts in interaction patterns within a community, alternative community patterns, may result from periodic disturbances and climatic variability. The question arises as to the nature of these shifting patterns. Using qualitative mathematical models and field data, we reconstructed community networks from a kelp forest off the Oregon Coast. From qualitative simulations we examined all ecologically plausible interactions among community members, selected the models that match field observations, and summarized highly frequent links to characterize the community network from a particular site. The subset of possible community networks was generated by comparing changes in species abundance with model predictions over two consecutive years. We tested all possible biologically reasonable community networks through qualitative simulations, winnowed out those that matched patterns observed in the field, and further reduced the set of possibilities by retaining those that were stable. We found that a community can be represented by a set of alternative scenarios that were ecologically supported by the literature. From 11,943,936 simulated models, 0.23% matched the field observations; moreover, only 0.006% (748 models) were highly reliable in their predictions and met conditions for stability. Predator-prey interactions as well as non-predatory relationships were consistently found in a high percentage of the 748 models. These highly frequent connections were useful to characterize the community network in the study site. Each alternative model might correspond to a successional stage in the ecological continuum of a kelp forest community. We suggest that alternative networks provide the community with a buffer to disturbance, allowing it to continuously reorganize to adapt to a variable environment and move from one equilibrium state to another. This plasticity to change to different scenarios may contribute to the persistence of these communities. We propose that qualitative simulations represent a powerful technique to raise new hypotheses conserning community dynamics and to reconstruct guidelines that may govern community patterns.

Introduction

The structure of a community at a particular site is determined by the physical environment, biological interactions, episodic disturbances and successional sequences (Power et al. 1996; Winemiller 1996). Communities from the same location can go through different successional stages that are driven by local temporal dynamics. Successional patterns can be the result of different disturbance regimes, changes in species abundances, different life history strategies, and interactions among community members (Winemiller 1996). The responses by a community can be manifold. Community membership can change or interactions among community members can switch, presumably as a result of functional responses. Capturing these responses makes ecosystem modeling a formidable task. The observed response may be the reaction of an unstable community, a community in transition from one configuration to the next or a functional response from one stable configuration to an alternative one. How does one segregate these responses? Determining community stability from empirical observations is problematic for several reasons. Scaling-up predictions from small-scale experiments to large-scale ecological systems are fraught with difficulty because of lack of context (Cooper et al. 1999). It is difficult to parameterize the strength of all important interactions within a community. Measuring community stability from field information is not practical because of generation time constraints among community members and of spatial and temporal scale of observations. Generation times must be measured on the ecologically dominant species, which may be exceedingly long lived (Connell and Sousa 1983), and different life history strategies can have a particular influence in food web structure, determining the fate of community succession (Winemiller 1996). Therefore, only an incomplete understanding of community dynamics is possible.

When modeling ecosystems and communities, the goal is typically to find a single model that will fit the system under study. Defining models that best characterize a specific area is a difficult research question due to the lack of mathematical tools that systematically consider all the possible alternative models that might represent a particular community. Determining alternative communities requires rigorous description of all possible interactions among its members. The task is formidable if interactions among species are not known or need to be quantitatively specified. To our knowledge, the complete quantification and validation of a complex community has only been done once (Schmitz 1997).

In this study we introduce a technique, which we call qualitative simulation, to reconstruct different community interactions and derive the multiple potential community scenarios that can occur in a given system. We developed an algorithm to perform qualitative simulations that test all plausible models that can be generated by a community network. The primary feature of this approach is a comparison of field observations with an array of simulated community models to identify a model or set of models that best represent the community structure in a particular study site. We compared the results of qualitative predictions (the inverse of the negative of the community matrix) (Bender et al. 1984) from a universe of community matrix models, with observed changes in species abundance from year to year.

We apply this approach to members of the kelp forest community off the Oregon Coast. The direct interactions between the kelp forest community species have been documented (Dayton 1985; Foster and Schiel 1985; Duggins 1980). Alternate stable states in relative abundance of species may exist within kelp communities (Simenstad et al. 1978; Duggins 1980), but the existence of shifts in interaction patterns within the same site has not been investigated. Different disturbances and local constraints may lead to alternative communities that depict differences in the community network.

Using qualitative simulations we address the following questions: 1) Given the same species pool, can a community be represented by a unique network? 2) If permutations of all ecologically plausible interactions were exhausted, what percentage of simulated models would match field observations, and what percentage would be stable? 3) Are results ecologically reasonable and in agreement with natural history information?

We propose that a community be represented by a set of related models rather than a single model. The set of models that actually represents a specific area can be identified by looking at existent changes in species abundance over time. The models proposed can serve as templates to predict future direct and indirect effects of disturbances to the system.

Methods

When the community network of a particular geographic area is known or specified, responses of the system to environmental change can be predicted. However, it is often the case that the actual community network is not defined. In this study we conducted the reverse procedure and reconstructed the community network from field observations. We created a base model (community matrix) from the information available in the literature. We used the base model as a framework to perform qualitative simulations. Each step on the simulation procedure reshapes the community matrix with a new combination of species interactions, creating a new matrix. Predictions for the new generated model are compared with field observations and selected if they match the field data. All possible combinations between variables were exhausted, creating millions of models to compare with field information.

Base Model

We constructed a base model that includes the species that have the most influence on the structure of the kelp forest community (Breen and Mann 1976; Duggins 1980,1981a and b; Estes and Palmisano 1974; Mann 1977; Paine and Vadas 1969). The Oregon kelp community is composed of the sunflower star (*Pycnopodia helianthoides*), two species of herbivores, red sea urchins (*Strongylocentrotus franciscanus*) and purple sea urchins (*S. purpuratus*), and three species of macroalgae or kelp, perennials (*Pterygophora californica* and *Laminaria sp.*) and an annual (*Nereocystis luetkeana*) (Fig. 4.1). After the disappearance of sea otters (*Enhydra lutris*) in the Pacific North West, the sunflower star has been the most important sea urchin predator in Washington (Paine and Vadas 1969, Duggins 1983) and Oregon (Montaño-Moctezuma personal observations). Both sea urchin species are important kelp grazers whose change in feeding patterns and diet are significant in structuring the kelp community (Duggins 1981a). Both annual and perennial kelp are highly preferred by both species of urchins (Leighton 1966; Leighton et al. 1966; Lawrence 1975), and are significant subtidal contributors to the benthic algal biomass (Duggins 1981a). Both urchin species have a preference for juvenile annual kelp over older individuals because smaller algae are easier to handle (Leighton 1966; Leighton et al. 1966). We split the annual kelp population into juveniles and adults to account for this preference. Juvenile and adult populations are connected by arrows that indicate the reciprocal contribution from one life stage to the other.

Negative self-effects (links that start and end on the same variable) represent the relationship of the variable to an outside resource not specified in the community network (Puccia and Levins 1985). The negative self-effects on all kelp species represent their dependence on nutrients, light and water supplies. The negative self-effect on juvenile red urchins relates to the contribution of larvae from other locations (Fig. 4.1).

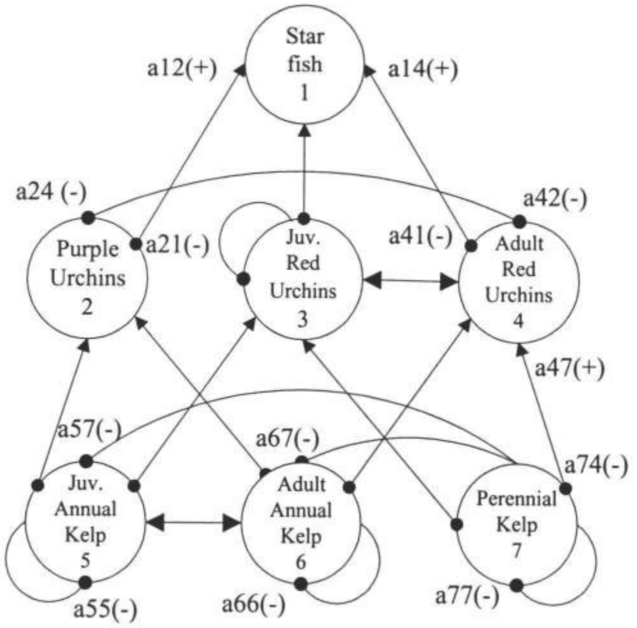
Qualitative Simulations

Qualitative analysis incorporates direct interactions between community species. This interactions are tabulated in the community matrix and illustrated in signed digraphs (Lane and Levins 1977; Puccia and Pederson 1983; Puccia and Levins 1985). Details of the technique and theory have been described by Levins (1974, 1975), Logofet (1993), Li et al. (1999), Castillo et al. (2000), Dambacher et al. (*in press*). General applications to aquatic systems can be found in Puccia and Levins

(1985). A signed digraph consists of a network diagram of a community in which the vertices are variables that are joined by a directed line (link) indicating an interaction. A positive effect is represented by an arrow (→) and a negative effect by a circle (—●). The direct pathway between predators and prey indicated by arrows and circles signifies the benefit received by the consumer and the simultaneous loss suffered by the resource (Fig. 4.1).

The power of qualitative analysis relies on the lack of need to measure exact quantitative interactions between species. Measuring the strength of all connections in a community greater than 3 variables is a difficult assignment. Qualitative simulations are particularly useful when the interactions in a system are not well known but changes in the abundance of each variable in the system are available. In each study site changes in the environment (perturbations or inputs to the system) can cause parameter changes (growth, mortality, survival) in one or more species. Each member of the community will react to this input either by increasing, decreasing or not changing in abundance.

We compared changes in species densities from 1996 to 1997 with the changes predicted by each plausible model that could be generated from a community with seven variables. The total number of possible interactions and combinations (+, –, 0) in a system with seven variables is $3^{(7x7)}$. We developed an algorithm (Appendix A) that generates all the possible models with all the combinations between variables (qualitative simulations). We set constraints to avoid non-biological systems, such as macroalgae eating herbivores and carnivores or herbivores eating their predators (Fig. 4.2). The program calculates an inverse matrix (prediction matrix) (Bender et al. 1984; Levins 1974, 1975; Dambacher *in press*) for each generated model and compares each column of the prediction matrix with the observed changes in density of all species (Fig. 4.3). Changes in species abundance from year to year are assumed to be in response to a disturbance to the system; therefore, correspond to predictions from the inverse matrix. The program selects the models that match field data and identifies the variable or species where the disturbance entered the system. Output from the simulations gives the set of community matrices that match field observations.



Community Matrix

Species	1	2	3	4	5	6	7
1	a_{11}	**a_{12}**	a_{13}	**a_{14}**	a_{15}	a_{16}	a_{17}
2	**a_{21}**	a_{22}	a_{23}	**a_{24}**	a_{25}	a_{26}	a_{27}
3	a_{31}	a_{32}	a_{33}	a_{34}	a_{35}	a_{36}	a_{37}
4	**a_{41}**	**a_{42}**	a_{43}	a_{44}	a_{45}	a_{46}	**a_{47}**
5	a_{51}	a_{52}	a_{53}	a_{54}	**a_{55}**	a_{56}	**a_{57}**
6	a_{61}	a_{62}	a_{63}	a_{64}	a_{65}	**a_{66}**	**a_{67}**
7	a_{71}	a_{72}	a_{73}	**a_{74}**	a_{75}	a_{76}	**a_{77}**

≡

1	2	3	4	5	6	7
0	**1**	1	**1**	0	0	0
-1	0	0	**-1**	1	1	0
-1	0	-1	1	1	0	1
-1	**-1**	1	0	0	1	**1**
0	-1	-1	0	**-1**	1	**-1**
0	-1	0	-1	1	**-1**	**-1**
0	0	-1	**-1**	0	0	**-1**

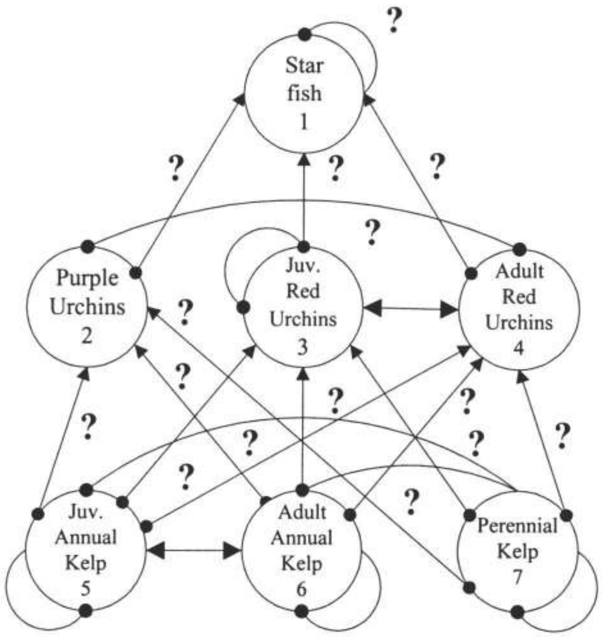
Figure 4.1. Representation of the kelp forest community off the Oregon coast. The signed digraph indicates different relationships: commensalism (→), amensalism (—•), interference competition (•—•), and predator prey (•⟶). A variable can have a negative effect on itself or being self-damped (links that start and end on the same variable), when it receives continuous supply from outside the specified system. The respective community matrix is shown. As an example, shaded areas correspond to interactions highlighted in the signed digraph.

From the community matrices we constructed each system's signed digraph (Fig 4.3).

Predictions from the inverse matrix can be subject to a high degree of indeterminacy, as reported by Schmitz (1997) and Yodzis (1988). Dambacher (*in press*) found that model predictions did not weigh the relative amount of negative feedback cycles in relation to total feedback. Therefore, weak and equivocal outcomes were mistaken for significant model predictions. Dambacher (*in press*) developed the concept of 'weighted predictions matrix' to assess the effect of disturbance on all community members with a 'weighted' value that measures the reliability of each prediction. Weighted prediction values > 0.5 are reliable while values < 0.5 will have high indeterminacy. A mathematical explanation of the weighted table of predictions is in Dambacher (*in press*). Our analysis discerns between models with highly reliable predictions and models with unreliable predictions (Table 4.1). We were able to discriminate models with high weighted prediction values from a pool of millions of simulated models.

Only models that met the following criteria were selected: 1) models that matched the observed field patterns in all variables, 2) potentially stable models, and 3) models with weighted prediction values > 0.5. We considered a model to be stable if: a) all characteristic polynomial coefficients had the same sign, and b) the Hurwitz determinants were > 0 (Puccia and Levins 1985, Logofet 1993). Table 4.2 illustrates a flow diagram of the simulation procedure. 11,943,936 models generated by qualitative simulations were compared with field observations.

The simulation program was written for MATLAB 5.3.1.29215a (The Mathworks Inc., Saddle River, New Jersey) and was run for 15 days under a SUN Ultra 10 computer.



Community Matrix

$$\begin{vmatrix} ? & ? & ? & ? & 0 & 0 & 0 \\ ? & ? & 0 & ? & ? & ? & ? \\ ? & 0 & -1 & 1 & ? & ? & ? \\ ? & ? & 1 & ? & ? & ? & ? \\ 0 & ? & ? & ? & -1 & 1 & ? \\ 0 & ? & ? & ? & 1 & -1 & ? \\ 0 & ? & ? & ? & ? & ? & -1 \end{vmatrix}$$

Figure 4.2. Community matrix of the Oregon kelp forest. Question marks depict the different relationships between species that were tested with qualitative simulations. Fixed values (shaded) indicate constraints to avoid non-biological models.

Simulated Model

Field Observations

Species	Change in Density
1	+
2	0
3	0
4	+
5	0
6	0
7	+

Compare Each Column ⟶ to find a match

Inverse Matrix

Species	1	2	3	4	5	6	7
1	+	–	+	+	0	+	+
2	+	+	0	–	+	0	0
3	–	0	0	0	0	0	0
4	–	–	0	+	0	+	+
5	0	–	0	0	+	0	0
6	+	0	0	–	0	0	0
7	+	0	0	0	0	0	+

Set of Community Matrices

$$\begin{vmatrix} 0 & 0 & 1 & 0 & 0 & 0 & 0 \\ 0 & -1 & 0 & 0 & 1 & 1 & 0 \\ -1 & 0 & -1 & 1 & 1 & 1 & 1 \\ 0 & 0 & 1 & 0 & 0 & 1 & 0 \\ 0 & -1 & -1 & 0 & -1 & 1 & 0 \\ 0 & -1 & -1 & -1 & 1 & -1 & 1 \\ 0 & 0 & -1 & 0 & -1 & -1 & -1 \end{vmatrix} \quad \begin{vmatrix} 0 & 0 & 1 & 0 & 0 & 0 & 0 \\ 0 & -1 & 0 & 0 & 1 & 1 & 0 \\ -1 & 0 & -1 & 1 & 1 & 1 & 1 \\ 0 & 0 & 1 & 0 & 1 & 0 & 0 \\ 0 & -1 & -1 & -1 & -1 & 1 & 1 \\ 0 & -1 & -1 & 0 & 1 & -1 & 0 \\ 0 & 0 & -1 & 0 & -1 & -1 & -1 \end{vmatrix} \quad \begin{vmatrix} 0 & 0 & 1 & 0 & 0 & 0 & 0 \\ 0 & -1 & 0 & 0 & 1 & 1 & 0 \\ -1 & 0 & -1 & 1 & 1 & 1 & 0 \\ 0 & 0 & 1 & 0 & 0 & 1 & 0 \\ 0 & -1 & -1 & 0 & -1 & 1 & 0 \\ 0 & -1 & -1 & -1 & 1 & -1 & 1 \\ 0 & 0 & 0 & 0 & -1 & -1 & -1 \end{vmatrix}$$

Alternative Signed Digraphs

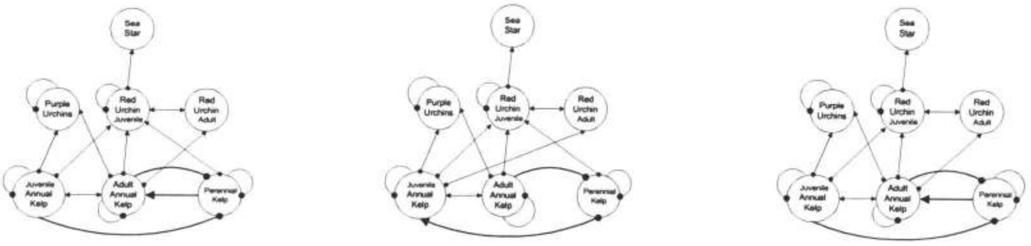


Figure 4.3. Qualitative simulation procedure to obtain the models that best represent the community structure from Whale Cove. Shaded areas indicate the column that matched the observations, which is the variable (species 7) where the disturbance entered the system. The inverse matrix (prediction matrix) shows the predictions about the effect (+, –, 0) on equilibrium abundances for each species when a disturbance causes a parameter change in all variables. Changes in species abundance from year to year are assumed to be in response to a disturbance to the system. Therefore, they correspond to predictions from the inverse matrix.

Table 4.1. Weighted predictions matrix from two models (A and B) that matched Whale Cove data. Disturbance at each species is read down the columns of the matrix, and responses of each species is read along the rows. Species: 1. Sunflower stars, 2. Purple urchins, 3. Juvenile red urchins, 4. Adult red urchins, 5. Juvenile annual kelp, 6. Adult annual kelp, and 7. Perennial kelp. Predictions that matched the data (shaded area) are highly reliable (weighted predictions > 0.5) in model A compared to model B (weighted predictions < 0.5). The perturbation enters the system through variable 7 (perennial kelp).

Model A

Species	1	2	3	4	5	6	7
1	.032	−.20	1	.33	−.20	1	1
2	1	1	0	−1	1	0	0
3	−1	0	0	0	0	0	0
4	−.18	−.33	0	.60	−.33	1	1
5	.33	−1	0	0	1	0	0
6	1	0	0	−1	0	0	0
7	−.14	1	0	.50	−1	0	1

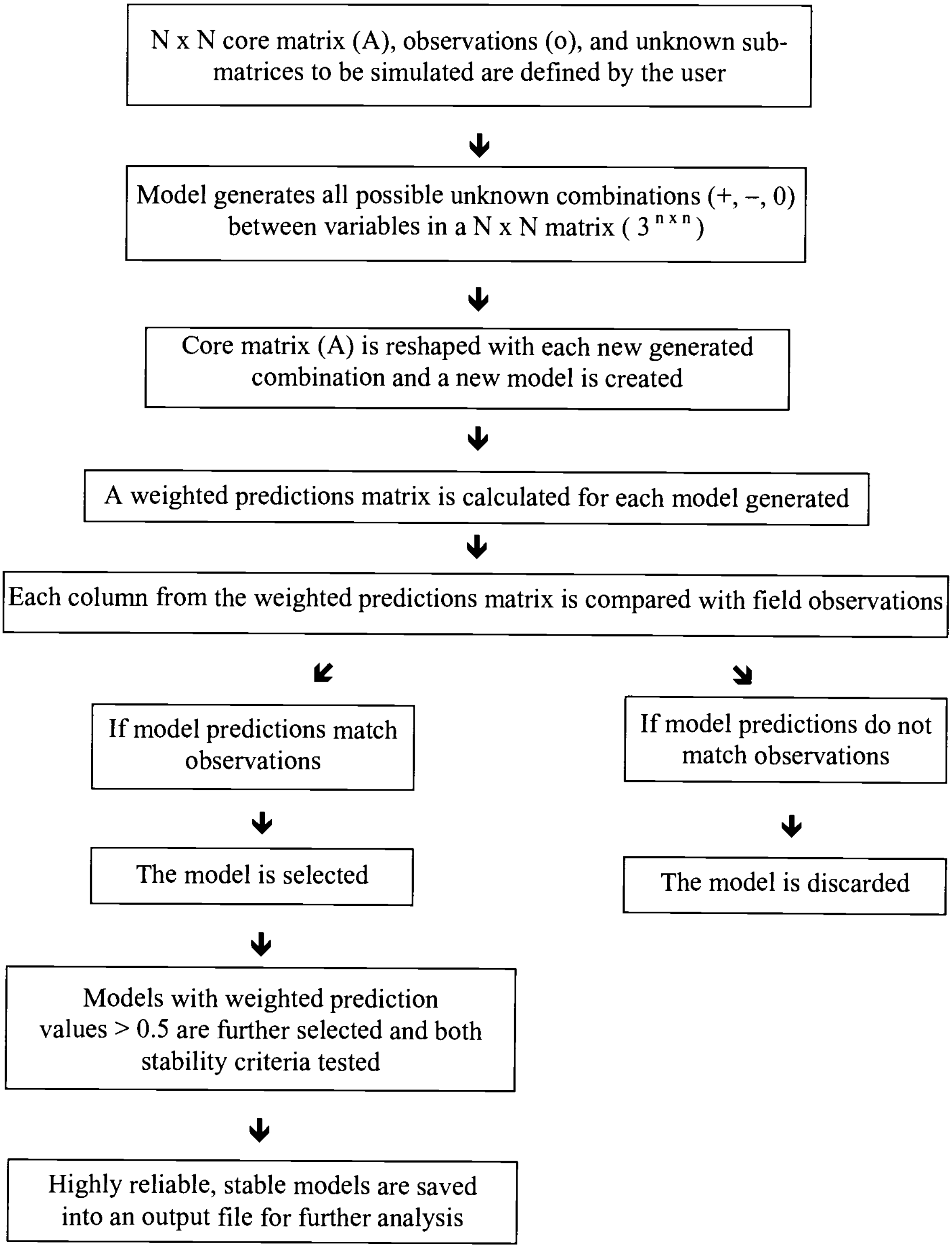
Model B

Species	1	2	3	4	5	6	7
1	.60	−.40	1	.50	.67	1	.20
2	−.14	1	−1	0	−.33	−1	0
3	0	−1	1	0	.33	1	0
4	.43	−.56	.56	.33	.71	1	.20
5	−.33	1	−1	−.33	−.11	−1	0
6	−.33	1	−1	−.33	−.33	−1	0
7	.60	−1	1	.50	.67	1	.20

Field Data

We collected information about changes in each species density during the summer and fall of 1996 and 1997 in Whale Cove, a marine reserve off the Oregon Coast. The data were collected by SCUBA divers along 40 X 2 m transects ($80m^2$). Six transects were systematically allocated to cover the entire area. Each transect was divided in 16 sampling units of $5m^2$ (swath). In each swath, divers recorded the

Table 4.2. Flow diagram for the Matlab algorithm (Appendix A) utilized to perform qualitative simulations. 11,943,936 models generated by qualitative simulations were compared with field observations.



number of red and purple urchins and sunflower stars. The number of macroalgae was obtained by the analysis of video transects that were recorded at the same time and site (swath) as the other species.

Results

Species Densities

From 1996 to 1997, sunflower stars, adult red urchins and perennial kelp mean densities significantly increased (t test; P = 0.08, df = 184; P = 0.07, df = 183 and P = 0.02, df = 152, respectively), and there were no significant changes in purple urchins, juvenile red urchins, juvenile and adult annual kelp (P = 0.38, df = 184; P = 0.38, df = 183; P = 0.31, df = 152 and P = 0.13, df = 152, respectively) (Fig. 4.4). We compared changes in densities with model predictions, as previously described (Fig. 4.3).

Community Interactions

Results from simulations indicate that the kelp forest community from Whale Cove can be represented by a set of alternative models that have consistent species interactions. We found that in a relatively simple (7 variables) community, where millions of potential models can be generated, only 26,955 stable simulated communities, comprising 0.23% of all possible 11,943,936 simulations, had model outputs conforming to the field data. From the models that matched the field observations, 748 (0.006%) were highly reliable in their predictions (weighted predictions > 0.5) and were selected to represent the community from Whale Cove.

The following predator-prey interactions were consistently found in a high percentage of the 748 models (Table 4.3): a) sunflower stars prey on juvenile red urchins (100%), b) purple urchins graze on juvenile and adult annual kelp

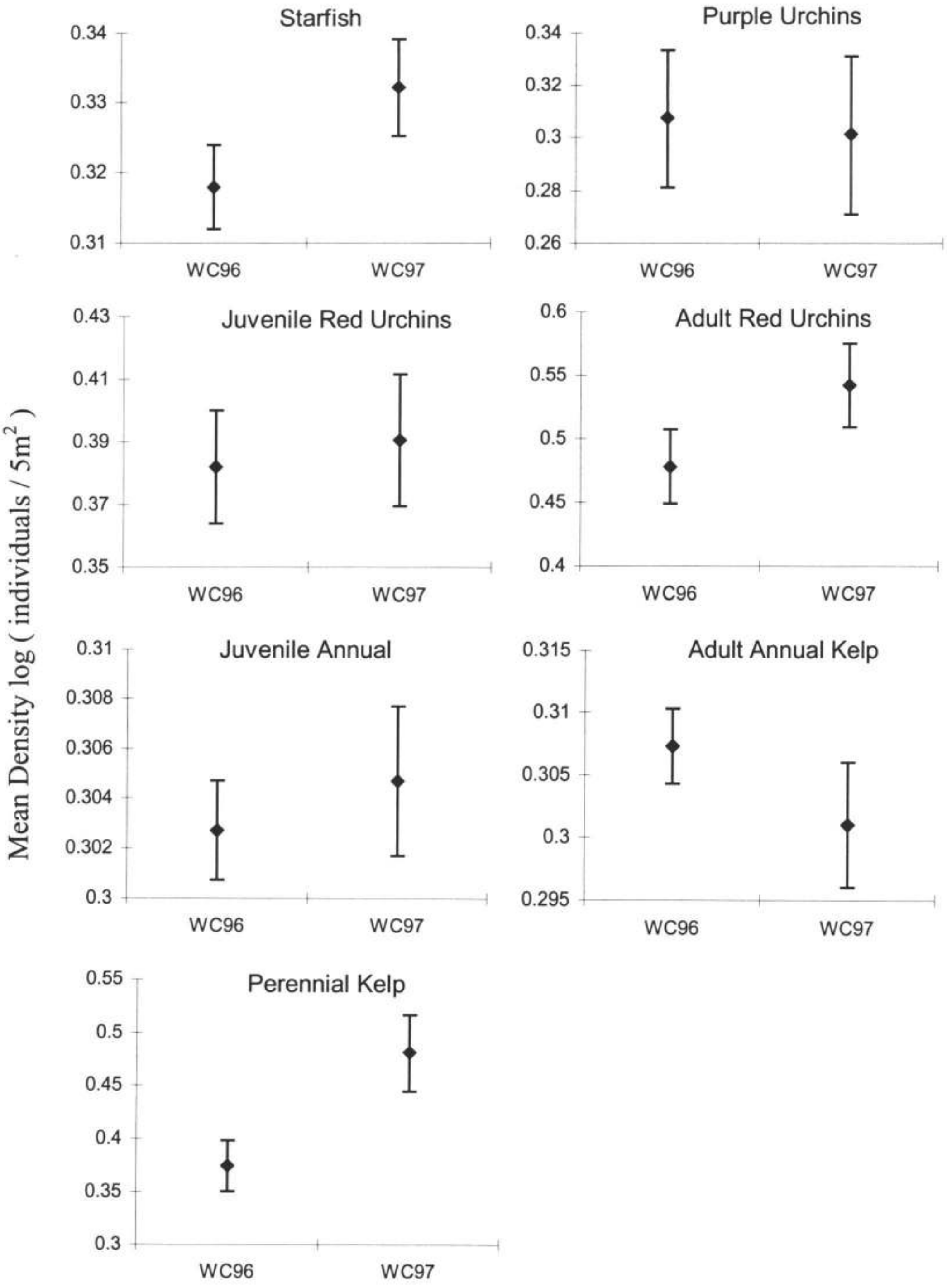


Figure 4.4. Changes in mean density of each species over two consecutive years (1996-1997). WC96 = Whale Cove 1996, WC97 = Whale Cove 1997. Statistically significant increases or decreases in density were considered as + or –, respectively, and non-significant changes as 0 for the qualitative analysis.

simultaneously (32%), c) adult red urchins graze on either juvenile (46%) or adult annual kelp (46%), and d) juvenile red urchins graze on juvenile and adult annual kelp and perennial kelp simultaneously (17%). The models describe non predator-prey direct interactions between variables: a) perennial kelp have a positive effect (commensalism) on juvenile and adult annual kelp (54%), b) juvenile and adult annual kelp have a negative effect (amensalism) on perennial kelp (61%), and c) no relationship was found between purple urchins and adult red urchins (64% and 90%, respectively). By considering the species interactions that were highly consistent among models (Table 4.3), we narrowed the community network to characterize Whale Cove (Fig. 4.5). These sets of alternative structures reveal that certain constraints in the array of links are necessary to match the field observations and achieve stability. Particular species interactions cannot be present at the same time. For instance, none of the models indicated that sunflower stars consume both urchin species and urchins do not graze on all kelp species simultaneously (Fig. 4.5). There are also specific combinations that are strongly associated, such as adult red urchins, annual kelp and perennial kelp. When adult red urchins graze on adult annual kelp, the positive link from perennial kelp to adult annual kelp is always present (Fig. 4.5a, d, e, and f); if adult red urchins shift to graze on juvenile annual kelp, the positive effect from perennial kelp shifts to juvenile annual kelp (Fig. 4.5b, and c). Because of this association, the positive effect from perennial kelp to either juvenile or adult annual kelp should be present all the time (Fig. 4.5). The negative effect from annual to perennial kelp can disappear only if purple and adult red urchins graze on the same resource (Fig. 4.5c, and d). If they graze on different algae, the negative effect from annual to perennial kelp should be present (Fig. 4.5e). In 8% of the models, adult red urchins graze on both juvenile and adult annual kelp simultaneously. If this is the case, both a positive effect from perennial to annual kelp and a negative effect from annual to perennial kelp should be present (Fig. 4.5f).

Particular interactions were common in all models such as the relation between sunflower stars and juvenile red urchins (100% of the models), and no interaction from red urchins to purple urchins (90%) (Table 4.3). This suggests that perhaps

Table 4.3. Percentage of times a specific relation between variables was found in models from Whale Cove. Bold numbers indicate a possible combination between variables; for example, for the predator prey effects, the combination **0 1 0** means that sunflower stars (*Pycnopodia*) only eat juvenile red urchins (JR). This combination appeared in 100 % of the models. JA=juvenile annual kelp; AA=adult annual kelp; P=perennial kelp; PU=purple urchins; JR=juvenile red urchins; AR=adult red urchins. Higher percentages are bolded. N = 748 models.

	Predator Prey Effects (Stars-urchins)							
	PU JR AR	PU JR AR	PU JR AR	PU JR AR	PU JR AR	PU JR AR	PU JR AR	PU JR AR
	0 0 0	**0 0 1**	**1 0 0**	**0 1 1**	**0 1 0**	**1 0 1**	**1 1 0**	**1 1 1**
Sunflower Stars	0	0	0	0	**100**	0	0	0

	Grazing Effects (Urchins-Kelp)							
	JA AA P	JA AA P	JA AA P	JA AA P	JA AA P	JA AA P	JA AA P	JA AA P
	0 0 0	**0 0 1**	**1 0 0**	**0 1 1**	**0 1 0**	**1 0 1**	**1 1 0**	**1 1 1**
Purple urchins	18	10	20	0	20	0	**32**	0
Juvenile red urchins	11	10	10	13	11	13	15	**17**
Adult red urchins	0	0	**46**	0	**46**	0	8	0

	Kelp Relationships					
	P-AA			AA-P		
	-1	**0**	**1**	**-1**	**0**	**1**
Perennial kelp adult annual kelp	0	46	**54**	**61**	28	11
	P-JA			JA-P		
	-1	**0**	**1**	**-1**	**0**	**1**
Perennial kelp juvenile annual kelp	0	46	**54**	**61**	28	11

	Urchin Relationships					
	PU-AR			AR-PU		
	-1	**0**	**1**	**-1**	**0**	**1**
Purple urchins adult red urchins	6	**64**	30	10	**90**	0
	PU-JR			JR-PU		
	-1	**0**	**1**	**-1**	**0**	**1**
Purple urchins juvenile red urchins	0	**100**	0	0	**100**	0

	Self Effects				
	Present (**-1**)	Absent (**0**)		Present (**-1**)	Absent (**0**)
Sunflower stars	0	**100**	Juvenile red urchins	**100**	0
Purple urchins	**80**	20	Adult red urchins	0	**100**

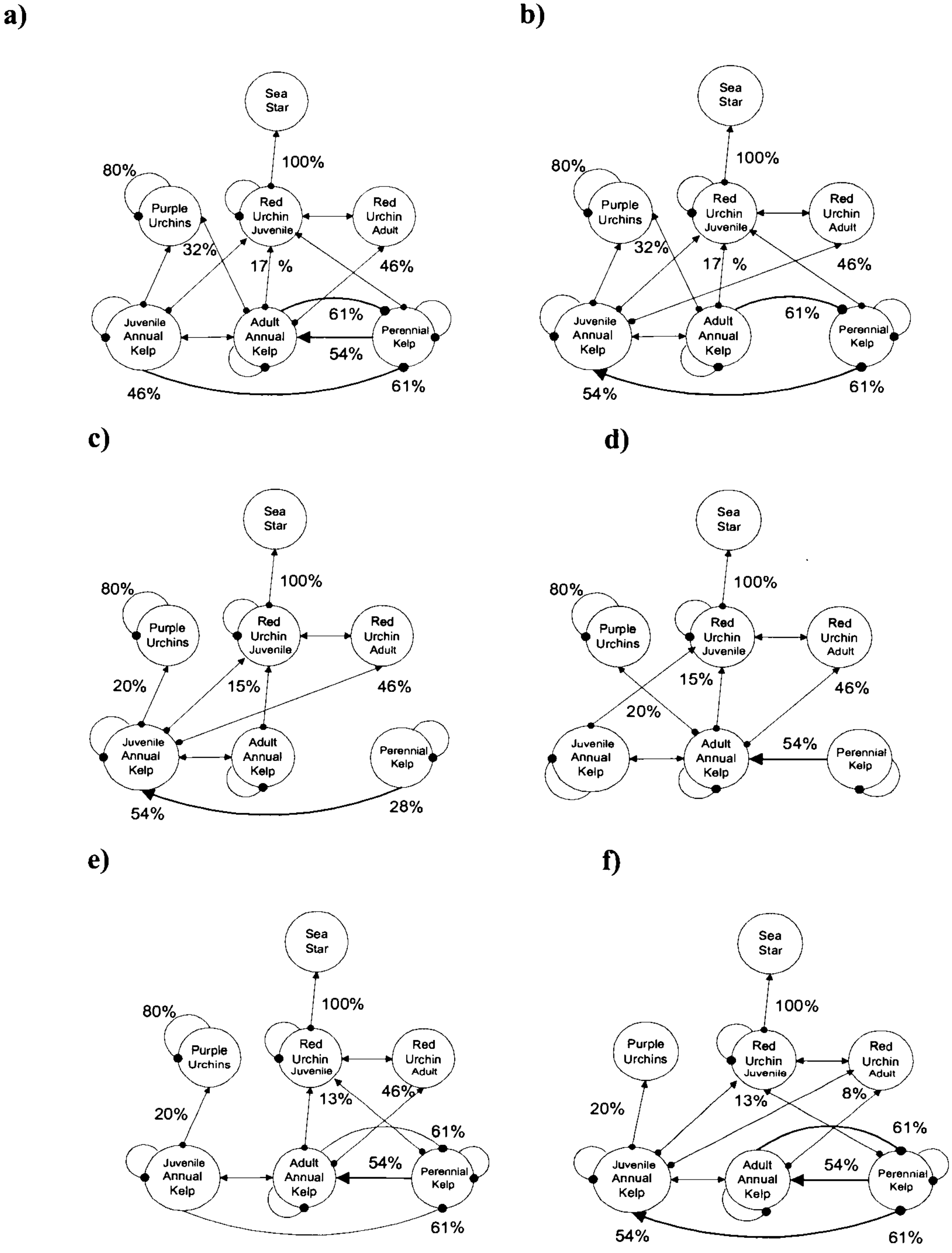


Figure 4.5. Summary of alternative models suggested by qualitative simulations for Whale Cove old marine reserve. Digraphs were summarized from Table 4.3 (N = 748 models). The percentages of models that suggested a relationship between species are indicated. For example, in 32% of the models, purple urchins graze on juvenile and adult annual kelp (a and b). More details in Table 4.3.

connections that appeared with high frequency can prevail through time while other links are more likely to shift.

Some interactions between species were more variable than others. If we compare predator-prey interactions of sunflower stars to grazing of urchins, we notice that in the first there is no variability since all models (100%) suggested that sunflower stars prey on juvenile red urchins. Variability increases for the grazing of purple urchins, as the percentage of models that suggested a specific combination goes from 10% to 32%. It is even greater for the grazing of juvenile red urchins with percentages going from 10% to 17%, with no combination being highly dominant (Table 4.3). These can be interpreted as a measure of variability of the whole system. In all 748 models, disturbance through the perennial kelp population generated the predictions that matched the field data. A change in the environment caused a direct change in the perennial kelp birth or death rates, causing other members of the community to change as well.

Discussion

We suggest that communities are best represented as sets of alternative stable models with a core of consistent species interactions. Local and regional variation in community patterns and organization and the important role of environmental variability in ecosystem structure has been lately recognized in ecological studies (Winemiller 1996).

We propose representing a community from the same location as a set of highly similar stable systems instead of a unique model. This conclusion conforms with Puccia and Levins (1985) and Lane (1986), who argued that the quest for a unique model should be substituted with the concept of numerous models. From millions of plausible models, we were able to summarize the set of trophic interactions that best characterize the community from Whale Cove. We suggest that the 748 alternative models represent the variability of the system and measure the deviation of the actual community from the core system. If we assume that the core system is represented by all the possible biologically reasonable interactions between species (fully connected), systems that are less connected denote a variant from the core community. The community from Whale Cove can take the form of any of the suggested networks, giving a dynamic attribute to the system.

We hypothesize that each alternative model corresponds to a successional stage that can shift from one structure to another each time the system is perturbed. The set of alternative models denotes a continuum in the ecological succession of a particular community. We suggest that the intuition, that the same assemblage of species can have different network structures representing successional patterns, has a theoretical basis.

Each model represents an alternative hypothesis of community organization and structure that was consistent with field observations. Our modeling approach introduces qualitative simulations as a means to reconstruct different community interactions. It may be applied when information about changes in species densities from year to year are available. Insights from the natural history of the system are useful to interpret observed patterns (Power et al. 1996) and build models that mimic reality. Comparison with data can reveal actual connections among community members that are hard to detect from observational studies.

Lane (1986) found 85 to 97 % agreement between model predictions and observations. Nevertheless, she expressed concern about the uncertainty of knowing if alternative systems could give a better agreement. With qualitative simulations, we obtained 100 % agreement between model predictions and observations because all the possible biological combinations are analyzed. There is no concern about missing any possible network. Our approach strengthens the concept of alternative community structure because of its universal nature. So far, there is not a general model that explains community variability. Moreover, due to the observed variation in space and time, it seems to be unjustified to think about a unique food web to represent a community even within the same region and at different temporal scales (Winemiller 1996).

Rules of assembly in a community dictate that there are constraints in the number of network combinations that can represent a specific system (Diamond 1975). Our data show that from millions of tested models, a very low percentage (0.23%) matched the observed data, and an even smaller percentage (0.006%) was highly reliable. None of the highly determined models suggested that all the possible links between species could be present at the same time. For example, the models wherein sunflower stars consume all urchin groups and urchins graze on all available kelp species were either unstable or unreliable (weighted prediction values < 0.3). This supports the idea that only certain combinations between variables can exist simultaneously in order to achieve stability, and that natural selection could have operated at the system level to create such constraints (DeAngelis and Waterhouse 1987). Constraints in food web connectance can be determined by the synergistic effects of factors such as the stability properties of the system, morphology (size limitations), and perhaps species linked randomly (Warren 1994).

Stable systems can behave near an equilibrium point or move from one equilibrium state to another (DeAngelis and Waterhouse 1987). We propose that each community network represents a different equilibrium that is constantly changing to adapt to a variable environment (physical changes, food availability, fluctuations in species abundance), and when disturbed it will move from one structure to another.

There are controversial views about the evidence of multiple equilibrium points and the existence of stable communities with different structures (Lewontin 1969; Sutherland 1974, 1990; Connell and Sousa 1983). The set of models presented in this study can be used as an alternative hypothesis to test experimentally the temporal and spatial patterns of trophic structure that can arise when different perturbations affect a system. The same disturbance to alternative communities may result in different responses by the species of interest due to different direct and indirect interactions among community members.

Foster and Schiel (1988) argue that the concept of alternate stable states cannot be applied to kelp forest communities because its dual property confuses the idea of the system natural variation. We agree and demonstrate that the alternate view (one or the other) should be replaced by the idea of alternative states (more than two scenarios) that confers a dynamic property of the system and describes its variability.

Holling (1973) presents the idea that the persistence of a system is more relevant than its constancy, particularly when external unexpected changes prevail. Perhaps this persistence is more likely to occur if communities have the plasticity to change to different structures when they are disturbed. Each system could be locally stable, having several "domains of attraction" (Holling 1973), and when perturbed will move from one domain to another. We suggest that different domains of attraction can be set by changes in patterns of trophic interactions that are the consequence of external perturbations. Shifts from one domain to another are fundamental to maintain persistence of a system. This process reinforces the idea that a community can best be represented by a set of models instead of a single one, and confers to the system a more dynamic balance.

We emphasize that the suggested models are simplifications of the entire system. Nevertheless, they include the species with a significant impact in the kelp community. Simplification is important to understand properties of systems and interpret predictions (Puccia and Levins 1985). In addition, secondary and tertiary species might have little influence on the dynamics of the core elements of a community, since their relative abundance and biomass is low compare to core species (Winemiller 1996).

Qualitative analysis assumes that the sampled communities are in a moving equilibrium, a fair assumption if we consider that systems can experience changes after a perturbation and maintain an equilibrium as a community even though individual species abundances fluctuate (Lane and Levins 1977). Proposed models can be verified and assumed equilibrium relaxed by repeating the analysis over consecutive years to assess if the suggested set of models remains constant. Perhaps the variable where the disturbance enters the system changes from time to time, but the suggested community structures and interactions prevail. Possibly, only the percentages that suggest a specific relationship between species will increase or decrease giving more or less emphasis to the same suggested interactions. This test could give a measure of the variability of the system.

Qualitative modeling helped to reveal specific links among members of the kelp forest community that have not been described by observations or experimentation. Although negative relationships (interference competition and amensalism) among kelp species have been described, our models reveal that additionally beneficial interactions (mutualism and commensalism) among algae might be playing an important role in structuring the kelp forest community.

Although the structure and composition of a community can often be described, its dynamic properties are rarely considered or addressed. Our work gives an insight into the existence of alternative community configurations that can potentially represent a particular community under different environmental constraints and disturbances. This alternative set of models can be useful to understand the dynamic properties of kelp communities and to assess how each specific network will respond to changes in the environment. Indirect interactions can have surprising results on system behavior (Carpenter and Kitchell 1988), difficult to understand without knowing the pattern of direct interactions among community members (Bodini 1998). The presence and strength of indirect effects has proven difficult, however, to assess due to methodological and logistical constraints (Wootton 1994). The models suggested in this study can provide insights about the importance of indirect effects in understanding community organization and dynamics.

Some questions arise from these findings that may lead to future research. It may be worthwhile to identify what triggers a shift from one trophic structure to another, how frequent these changes occur, and what physical and biological mechanisms are related to structural changes in the system.

CHAPTER 5

VARIABILITY OF COMMUNITY INTERACTION NETWORKS IN KELP FOREST RESERVES AND ADJACENT EXPLOITED AREAS

Gabriela Montaño Moctezuma, Hiram W. Li, and Philippe A. Rossignol

Abstract

One purpose of the ecology of community networks is to understand how community assemblages are affected by environmental dynamics. Regional and small-scale local oceanographic conditions can lead to high variability in community structure even among similar habitats. Communities with identical species composition can depict distinct networks due to different levels of disturbance as well as physical and biological processes. In this study we apply qualitative simulations to reconstruct community networks in four different areas off the Oregon coast, and describe spatial variation between set aside areas with different protection times from harvest and areas that have been exposed to different harvest regimes. We found that different community networks can represent each study site. Differences were found in predator-prey interactions as well as non-predatory interactions between community members. In addition, each site is represented by a set of models that shifts from one community network to another creating alternative stages among sites. The set of alternative models that characterize each study area depicts a sequence of functional responses where each specific model or interaction structure creates different species composition patterns. Actual links between community members are useful to understand the patterns observed in the field. Different management practices that have been used in the past or are currently established may lead to alternative communities that require distinct management approaches. Our findings suggest that management strategies should be analyzed at a community level that considers the possible consequences of shifting from one community scenario to another. We think that this analysis provides an effective approach to characterize community interactions where experimental manipulations of all species is difficult and that it provides a conceptual framework to understand community organization and dynamics.

Introduction

The notion that alternative communities can occur in similar habitats but at different locations and at different times still deserves attention (MacArthur 1972; Diamond 1975; Sutherland 1974,1990). Although communities from different locations can be represented by the same number of species, the trophic network of the system might completely differ due to changes in the physical environment, to succession or to changes in species abundances.

The structure of a community relates to competition and harvesting of resources and adjustments of species abundance, resulting in unique combinations that vary in space and time. Comparing community variants in various locations may help to understand the extent to which observed differences in structure are set by the physical environment, and the extent of successional events or the biological interactions among species.

Although community analysis is critical to management, there are many uncertainties that make its description and analysis difficult. High environmental variation is common in marine systems and small-scale episodic events are important contributors to systems variability. Community structure and its dynamics can be strongly affected by climatic variability and deviations from long-term daily or monthly averages (anomalies) may be considered ecosystem disturbances (McGowan, et at. 1998). Communities encompass many populations with different life histories that are affected by oceanographic events. Local environmental variations have a strong influence in recruitment patterns, larval development, growth, mortality and species abundances that lead to small scale food web variation (Winemiller 1996).

Past research indicates that kelp forest species composition varies considerably in time and space (Mann 1977; Foster and Schiel 1985). Disturbances, such as, spatial and temporal changes in physical factors, fluctuations in recruitment success, and numerous harvest regimes, can have significant effects on the structure and dynamics of the subtidal kelp forest communities in the Pacific Northwest (Harrold and Pearse 1987; Duggins 1980; VanBlaricom and Estes 1988; Foster and Schiel 1988). Different sites may vary in species composition due in part to vagaries of recruitment (currents, dispersal, entrainment, and settlement of propagules), and history of human use. Communities that have been exposed to different physical, biological or anthropogenic disturbances may trigger successional patterns within the same site and also among communities from different geographic areas.

In this study we use qualitative simulations to reconstruct and compare the community network in four different areas off the Oregon Pacific coast. These communities have been exposed to different harvest regimes: 1) a heavily fished area, and 2) a moderately fished area. Two other sites have been protected from the fishery for different time periods: 3) a newly designated marine reserve (protected for 8 years), and 4) an established old marine reserve (protected for 35 years). This technique compares field observations with a collection of simulated community models to identify a model or set of models that best characterize the community in each particular study site. Using qualitative simulations we were able to select, from millions of simulated models, those that matched the field observations from each study site.

Marine reserves have been proposed as management tools to protect and preserve population integrity and biodiversity. Several studies analyze the potential benefits of marine reserves at the population level but few examples (Cole et al. 1990; Russ 1985; Russ and Alcala 1989; Duran and Castilla 1989; McClanahan and Muthiga 1988; Bell 1983; Castilla & Moreno 1982) examine the spatial variation and community dynamics between protected areas and exploited areas. Differences and similarities in thropic networks can arise when communities have been exposed to different exploitation regimes and distinct management practices. Trophic interactions of a pristine community can reveal insights about the natural condition of a system and can provide a baseline to use as a reference when assessing the effect of harvest on exploited communities (Dayton et al. 1998). Understanding spatial and temporal variation in community structure is important to assess the success of reserves as management tools.

Although some species interactions within the kelp forest have been described experimentally, no information exists about how the interactions can function together to represent the community network from a specific area. We used the suggested models (community network) to understand different kelp forest community patterns observed in each study site.

Study Areas

We studied the kelp forest community structure in four sites along the Oregon Coast. A marine reserve (Gregory Point) and its adjacent exploited area (Simpson Reef) are located in the South. Whale Cove marine reserve and its contiguous fished area (Depoe Bay) are located in the North. Both reserves are inlets close to the shoreline and the exploited areas are located farther offshore. Wave action is strong during the winter and moderate during the summer. The substratum in all areas is predominantly bedrock (70%) and boulders (15%) with small patches of sand (11%) and shell (4%). The average depth ranged from 7-10 m in Whale Cove and Gregory Point, respectively to 15 m in Depoe Bay and Simpson Reef. Adult red urchins are the only species commercially harvested in all areas in the past. In 1993, Gregory Point was set aside and established as a subtidal reserve. Whale Cove is an old reserve established 35 years ago as a habitat restoration site where harvest has never taken place. In both protected areas, the sport and commercial harvest of subtidal invertebrates is not allowed. The main management practices that have been used in Depoe Bay and Simpson Reef are based on a limited entry system and a minimum size limit of 8.9 cm. The abundance of harvestable urchins in the fished areas as well as their average size have declined (Richmond et al. 1997). The four studied areas represent a gradient going from a strong disturbance (Depoe Bay), intermediate disturbance (Simpson Reef), short recovery period (Gregory Point) and no disturbance (Whale Cove).

Methods

We built a 'core model' based on the existing kelp forest information in the literature. The community comprises the sunflower star (*Pycnopodia helianthoides*), two species of herbivores: red sea urchins (*Strongylocentrotus franciscanus*) and purple sea urchins (*S. purpuratus*), and three species of macroalgae or kelp: perennials (*Pterygophora californica* and *Laminaria sp.*) and the annual *Nereocystis luetkeana* (Fig. 5.1).

We considered the sunflower stars as the most important sea urchin predators in Oregon (Montaño-Moctezuma personal observations), and both urchin species and kelp as the species with the most impact on kelp forest community dynamics (Foster and Schiel 1988; Breen and Mann 1976; Duggins 1980,1981a and b; Estes and Palmisano 1974; Mann 1977; Paine and Vadas 1969). *Nereocystis luetkeana* forms a surface canopy that varies in thickness depending on their abundance and perennial kelp constitutes a subsurface canopy. The red sea urchin population was divided in two variables (juveniles and adults) to denote the effect of the fishery on adults > 8.9 cm in length (test diameter). We split the annual kelp population in juveniles and adults to account for the preference that both urchin species have for juvenile *Nereocystis* over older individuals (Leighton 1966; Leighton et al. 1966). The core model has 7 variables and the exploited areas include the fishery as an additional variable (Fig. 5.1).

Members of the community are capable of consuming all prey presented in the core models (Fig 5.1); for instance, sunflower stars can prey on both urchin species and urchins can graze on all algae. Due to food availability constraints and species interactions, the actual links between species may likely differ among sites. To find the actual structure in each study area, we compared changes in species abundances from 1996 to 1997 to an array of model predictions generated by qualitative simulations (Chapter 4). Qualitative simulations are based in the qualitative analysis theory that uses signed digraphs to represent a system, and analyzes a community through a community matrix (Lane and Levins 1977; Puccia and Pederson 1983;

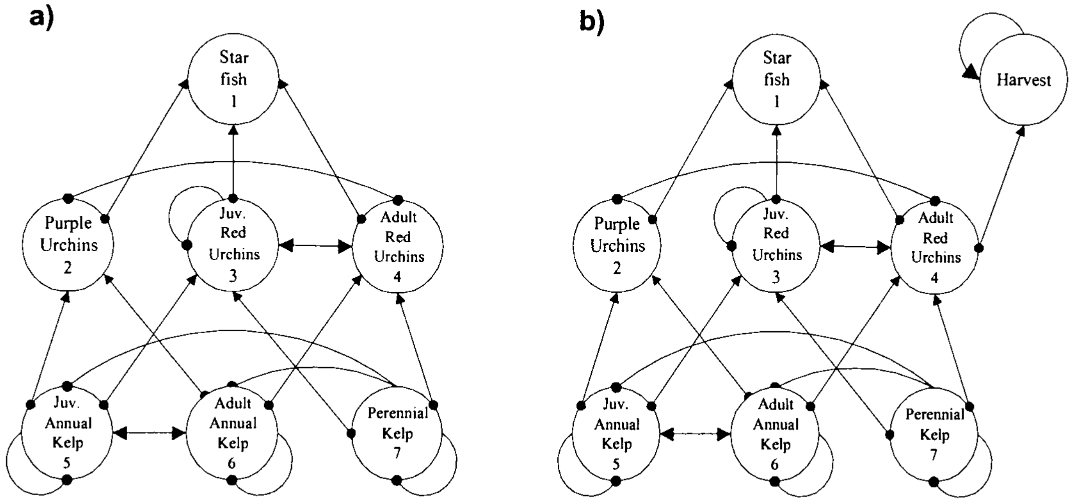


Figure 5.1. Signed digraphs of the kelp forest core communities off the Oregon coast: a) marine reserves and b) exploited areas. Different species interactions are indicated: positive effect (→), negative effect (—•), interspecific competition (•—•), and predator prey (•——→). Juvenile and adult populations are connected by arrows (←——→) that indicate the reciprocal contribution from one life stage to the other. Self-effects (links that connect a variable to itself) represent the relation of the variable to an outside resource not specified in the community network. The negative self-effects on all kelp species represent their dependence on nutrients, light and water supplies and the negative self-effect on juvenile red urchins relates to the contribution of larvae from other locations. The positive self-effect denotes a harvest with fixed quota (constant number of individuals removed per unit time).

Puccia and Levins 1985; Levins 1974, 1975; Li et al. 1999; Castillo et al. 2000; Dambacher et al. 2001). Unlike traditional community analyses, which require detailed information about the strength of direct and indirect interactions, loop analysis relies on a simple qualitative matrix of positive interactions (→), negative interactions (—•), and no interactions (0). Qualitative simulations are particularly useful when changes in species abundances are available and the interactions between community members are not known. Our technique generates all the models that can be produced with all species combinations (+, –, 0) in a 7 x 7 community matrix. The simulation program calculates a prediction matrix (inverse of the negative of the community matrix) for all the generated models. The prediction matrix gives information about the changes of each species abundances, either an increase (+), decrease (–) or no change (0), after the community has perturbations or presses in the environment (input to the system). We assumed that the changes in species abundances observed in the field are a response to the environmental input and therefore correspond to the changes predicted by the models.

Each prediction matrix was compared to changes in each species density and only models that match the field data were selected. The selected models were then tested for stability and reliability in their predictions (Dambacher et al. *in press*) and only stable and highly reliable models were subsequently chosen. More details of the technique and the algorithm can be found in Chapter 4. The same procedure was performed in each of the four study areas.

We collected information about changes in each species density during each of the summer and fall of both 1996 and 1997 in the four study sites. Six (40 x 2 m) transects were located in each study site. The data were collected by two divers who counted the organisms within 1 m right and left of the transect line at 5 m intervals, creating 5 x 1 m quadrants. In each quadrant divers wrote down information about the number of sunflower stars, red urchins, and purple urchins. In the marine reserves (Whale Cove and Gregory Point), we videotaped each transect to estimate the number of annual kelp and perennial kelp. Changes in densities of annual and perennial kelp in both exploited areas (Simpson Reef and Depoe Bay) were indirectly estimated through Spearman's rank correlation patterns between kelp variables and the variables that showed significant changes in each exploited area.

Four fishery scenarios described by Dambacher (personal communication) were tested to represent the systems from the exploited areas: 1) artisanal harvest (fishers as obligate predators), 2) a well managed fishery with a quota ≤ Maximum Sustainable Yield (MSY), 3) a modern fishery, where quota is in equilibrium with community (at MSY), and 4) a fishery with fixed quota > MSY. Four simulations per exploited area (Simpson Reef and Depoe Bay) were conducted to select the fishery scenario that best represents each fished area (Fig. 5.2).

The simulation program was written for MATLAB 5.3.0.10183 (Mathworks Inc., Saddle River, New Jersey) and each simulation was run for 15-18 days under a Sun Ultra 10 computer. We ran ten simulations total, one for each marine reserve, and four for each exploited area.

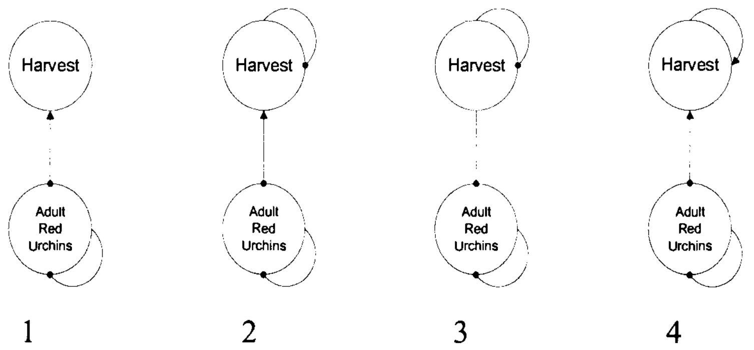


Figure 5.2. Fishery scenarios described by Dambacher (*personal communication*) tested to identify the models from the harvested areas: 1) artisanal harvest (obligate predator), 2) well managed fishery (quota ≤ MSY), 3) modern fishery where perfect quota is in equilibrium with community (right at MSY), and 4) fishery with fixed quota > MSY.

Results

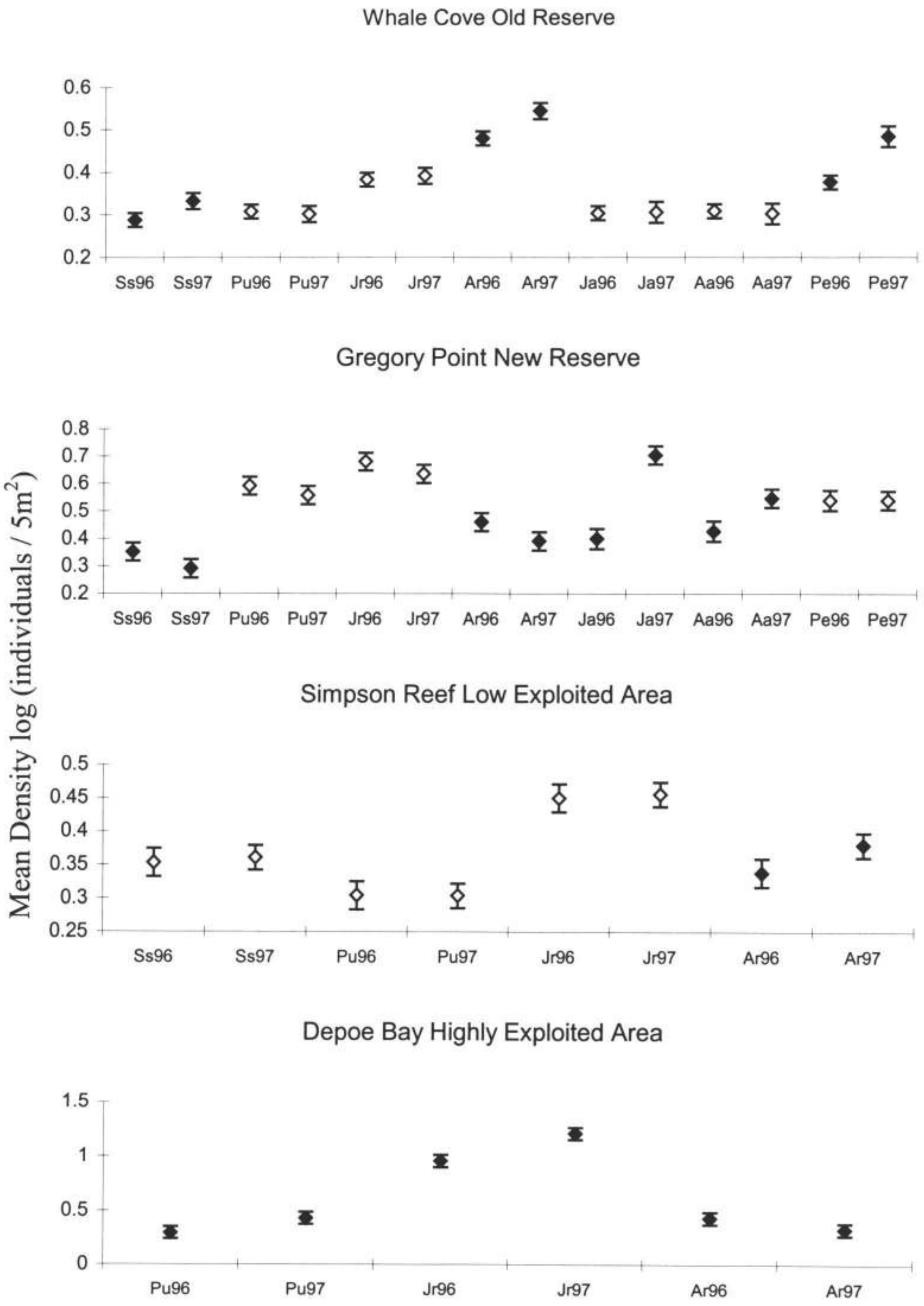
Changes in Species Densities

In Whale Cove sunflower stars, adult red urchins and perennial kelp mean densities increased from 1996 to 1997 (t test; $P = 0.08$, df= 184; $P = 0.07$, df= 183 and $P = 0.02$, df= 152, respectively), and there were no changes in purple urchins, juvenile red urchins, juvenile and adult annual kelp ($P = 0.38$, df= 184; $P = 0.38$, df= 183; $P = 0.31$, df= 152 and $P = 0.13$, df= 152, respectively) (Fig. 5.3). In Gregory

Point sunflower stars and adult red urchins decreased ($P = 0.03$, df = 195 and $P = 0.09$, df = 194, respectively). Juvenile and adult annual kelp increased ($P < 0.001$, df = 176 and $P = 0.01$, df = 176, respectively) and there were no significant changes in purple urchins, juvenile red urchins and perennial kelp ($P = 0.30$, df = 194; $P = 0.21$, df = 194 and $P = 0.50$, df = 176, respectively) (Fig. 5.3). In Simpson Reef adult red urchins increased ($P = 0.04$, df = 141) and there were no changes in sunflower stars, purple urchins and juvenile red urchins ($P = 0.33$, df = 141; $P = 0.53$, df = 115 and $P = 0.45$, df = 141, respectively) (Fig. 5.3). Since adult red urchins was the only species that significantly increased, they were used to indirectly estimate changes in annual and perennial kelp abundances using correlations. Adult annual kelp had a positive correlation with adult red urchins ($r^2 = 0.26$, $P = 0.02$, $n = 77$); therefore, they were judged to have increased. Juvenile annual kelp and perennial kelp had a positive correlation with adult annual kelp ($r^2 = 0.56$, $P < 0.001$, $n = 80$ and $r^2 = 0.41$, $P < 0.001$, $n = 80$, respectively); hence they increased (Table 5.1a). In Depoe Bay purple and juvenile red urchins increased ($P < 0.001$, df = 189 and $P < 0.001$, df = 189, respectively) and adult red urchins decreased ($P = 0.08$, df = 189). Juvenile and adult annual kelp and perennial kelp were negatively correlated with juvenile red urchins ($r^2 = -0.33$, $P = 0.01$, $n = 59$; $r^2 = -0.41$, $P = 0.001$, $n = 59$; $r^2 = -0.63$, $P < 0.001$, $n = 59$, respectively) and positively correlated with adult red urchins ($r^2 = 0.34$, $P = 0.009$, $n = 59$; $r^2 = 0.32$, $P = 0.01$, $n = 59$; $r^2 = 0.61$, $P < 0.001$, $n = 59$, respectively); therefore, all three kelp variables decreased and were positively correlated among them (Table 5.1b). To compare model predictions with field observations, statistically significant ($P < 0.09$) increases were considered as (+), significant decreases as (–), and no significant changes as (0) (Table 5.3).

Interaction Patterns

We found that kelp community interaction patterns differed among sites. Differences occur in predator-prey interactions as well as non-predatory interactions (competition, mutualism, commensalisms, and amensalism) between herbivores and


Whale Cove Old Reserve

Gregory Point New Reserve

Simpson Reef Low Exploited Area

Depoe Bay Highly Exploited Area

Figure 5.3. Changes in mean density of each species over two consecutive years (1996-1997) in two reserves and adjacent exploited areas. Significant changes are indicated as black triangles and non-significant changes as white triangles. Ss = sunflower stars, Pu = purple urchins, Jr = juvenile red urchins, Ar = adult red urchins, Ja = juvenile annual kelp, Aa = adult annual kelp, and Pe = perennial kelp. Standard error bars are indicated.

among kelp species. Interactions that differed among sites appeared in high percentages of the suggested set of models and were used to characterize and highlight differences and similarities among study areas. Although the overall community is composed of the same species, each community is connected differently in each particular site, likely due to particular physical and biological processes and disturbances that affect each system.

Table 5.1. Correlations among variables that were used to indirectly estimate changes in annual and perennial kelp abundances. a) Simpson Reef and b) Depoe Bay exploited areas. Only variables that showed a significant change from 1996-97 were used for the correlations. r values are bolded, P-values are in parenthesis, and sample sizes are indicated at the bottom.

a)

	Adult red urchins	Juvenile annual kelp	Perennial kelp
Adult annual kelp	**.26** (.0234) 77	**.56** (.0000) 80	**.41** (.0003) 80

b)

	Juvenile red urchins	Adult red urchins	Juvenile annual kelp	Adult annual kelp
Juvenile annual kelp	**–.33** (.0119) 59	**.34** (.0088) 59	1	
Adult annual kelp	**–.41** (.0016) 59	**.32** (.0139) 59	**.44** (.0005) 64	1
Perennial kelp	**–.63** (.0000) 59	**.61** (.0000) 59	**.61** (.0000) 64	**.60** (.0000) 64

Table 5.2. Changes in each variable density from 1996 to 1997. Significant increases in densities are indicated as (+), decreases as (–), and non-significant changes as (0). * No data in two consecutive years for comparison; yet, all models predict a decrease in starfish.

	Reserves		Exploited Areas	
Species	Whale Cove	Gregory Point	Simpson Reef	Depoe Bay
Starfish	+	–	0	*
Purple urchins	0	0	0	+
Juvenile red urchins	0	0	0	+
Adult red urchins	+	–	+	–
Juvenile annual kelp	0	+	+	–
Adult annual kelp	0	+	+	–
Perennial kelp	+	0	+	–

A set of alternative models characterized the kelp interaction structure in each study area (Table 5.4). In Whale Cove and Gregory Point marine reserves, from 11,943,936 simulated models, 748 (0.006%) and 951 (0.008%) models that matched the field observations were highly reliable and were stable, respectively. In Simpson Reef and Depoe Bay, 90 (0.0008%) and 78 (0.0007%) models, respectively represented the exploited areas. Under a heavy fished scenario (Depoe Bay), 55 (0.005%) models matched the field observations; however, all models were unstable (Table 5.3).

The harvest at Simpson Reef can be described as a managed fishery with a quota ≤ MSY (Fig. 5.4). Although this fishery is not regulated by quotas, the average harvest pressure in this area is low (116.8 thousand pounds) compared to Depoe Bay

(337.4 thousand pounds). While urchin landings peaked in 1991 (322 thousand pounds), the amount decreased to 19 thousand pounds in 1995 (Richmond et al. 1977). This information is consistent with models that suggest a low harvest scenario where quantities taken from the system seem to be in equilibrium with the community.

The models suggest that Depoe Bay could be in transition from a well managed fishery (quota ≤ MSY) to a fishery with a fixed quota > MSY (Fig. 5.5). Results indicate that the amount of urchins that have been removed from the system oscillates between a sustainable amount and quantities exceeding the capacity of the system. Fishery records show large fluctuations in landings (mean = 337.4; S.D. = 404.7 thousand pounds) that peaked in 1990 (1,373 thousand pounds) and declined to 157 thousand pounds in 1995 (Richmond, et al. 1997). Although all proposed models with a fixed quota > MSY matched field observations, they were unstable suggesting that under this fishery scenario harvest is no longer sustainable.

Table 5.3. a) Number of tested models generated by qualitative simulations, b) number and percentage of models that matched the field observations, and c) models that were highly reliable (weighted predictions > 0.5).

Study Site	a) Tested Models	b) Models that matched the data	c) Highly reliable models
Whale Cove	11,943,936	26,955 **(.23%)**	748 **(.006 %)**
Gregory Point	11,943,936	109,273 **(.91%)**	951 **(.008%)**
Simpson Reef (quota ≤ MSY)	11,943,936	13,501 **(.11%)**	90 **(.0008%)**
Depoe Bay (quota ≤ MSY)	11,943,936	498,758 **(4.18%)**	78 **(.0007%)**
Depoe Bay (quota > MSY)	11,943,936	462,576 **(3.87%)**	55 **(.0005%)**

Specific interactions between species appeared in high percentages of models (Tables 5.4-5.7). We selected interactions with higher percentages of appearance to create the signed digraphs that best characterize the interaction patterns from each particular area (Fig. 5.4). Similar patterns of sunflower stars predation were found in both marine reserves (Whale Cove and Gregory Point) where sunflower stars prey on juvenile red urchins (100%, 51% of the models, respectively). They consume purple urchins (60%) in Simpson Reef and eat both juvenile and adult red urchins (100%) in Depoe Bay (Tables 5.4-5.7 and Fig. 5.4). In a lower percentage of models from Gregory Point (27%) and Simpson Reef (27%), sunflower stars prey on juvenile red urchins. Tegner and Dayton (1977) found that small urchins can get protection from predators under the spine canopy of adult red urchins. Apparently, protection is not present in most areas since sunflower stars are mainly consuming juvenile red urchins. The size of juvenile urchins at all sites (47-70 mm) is above the average (32 mm) that has been observed hiding under adult red urchin spines. Sunflower stars did not prey on purples urchins probably because their densities are very low in all areas (Fig. 5.6). However, although the abundance of purple urchins in Gregory Point is high (Fig. 5.6), sunflower stars are not consuming them either. Maximum size of purple urchins prevents them from attaining a refuge size from sunflower stars predation; their strategy then consists of creating large aggregations that serve as refuges from attacks. Adult red urchins distribution is more random (Moitoza and Phillips 1979; Duggins 1980).

In both marine reserves, purple urchins graze on juvenile and adult annual kelp (32%, 33%, respectively), and they rely on perennial kelp in Depoe Bay (36%). Models suggest that in Simpson Reef and Depoe Bay, purple urchins depend on other resources outside the system as denoted by the negative self-effect (41% and 38%, respectively). Self-effects are links that connect a variable to itself and represent the relation of the variable to an outside resource not specified in the community network (Puccia and Levins 1985). Juvenile red urchins grazing effects were different in all sites. They consume all algae groups in Whale Cove, although the percentage of models that suggested this combination is low (17%), and other combinations presented similar percentages (Table 5.4). These indicate a high variability of juveniles' consumption habits. In Gregory Point, juvenile red urchins graze on perennial kelp (42%); they consume juvenile and adult annual kelp in Simpson Reef (32%), and rely on other available food outside the specified system (negative self-effect) in Depoe Bay (60%) (Tables 5.4-5.7 and Fig. 5.4).

In Whale Cove and Simpson Reef, adult red urchins graze on juvenile and adult annual kelp (46% and 48%, respectively). They consume perennial kelp in Gregory Point (66%), and eat all kelp groups in Depoe Bay ((Tables 5.4-5.7 and Fig. 5.4).

Besides predator prey interactions we found particular differences among sites in the relation between urchins and kelp species. There is no interaction from purple urchins to adult red urchins in all the areas except Simpson Reef where the relationship is positive (44%). Adult red urchins have no relation with purple urchins in Whale Cove (90%). The interaction from adult red urchins to purple urchins is positive in Gregory Point (83%) and the link is negative in Simpson Reef (60%) and Depoe Bay (100%) (Tables 5.4-5.7 and Fig. 5.4). Suggested model structures are consistent with natural history information, which describes facilitation (Gregory Point) afforded to small urchins (juvenile reds and purple urchins) from adult red urchins by capturing drift algae and making it more available for consumption. Adult red urchins are more efficient in capturing drift algae because they have long spines, and under abundant food availability they facilitate algae to small urchins (Tegner & Dayton 1977; Duggins 1981b; Breen et al. 1985). Adult red urchins can have a strong negative impact on purple urchins (Simpson Reef and Depoe Bay) because of their long spines, by increasing competition for space (Schroeter 1978). The trophic consequence of interference competition when red urchins are large in size is exclusion of purple urchins from grazing on the preferred annual kelp. Purple urchins are limited to consume drift algae in Simpson Reef (negative self-effect) or perennial kelp in Depoe Bay (Fig. 5.4). The opposite is true in Gregory Point where the benefit (positive link) from adult red urchins allow purple urchins to graze on both juvenile and adult annual kelp, confining red urchins to eat perennial kelp (Fig. 5.4).

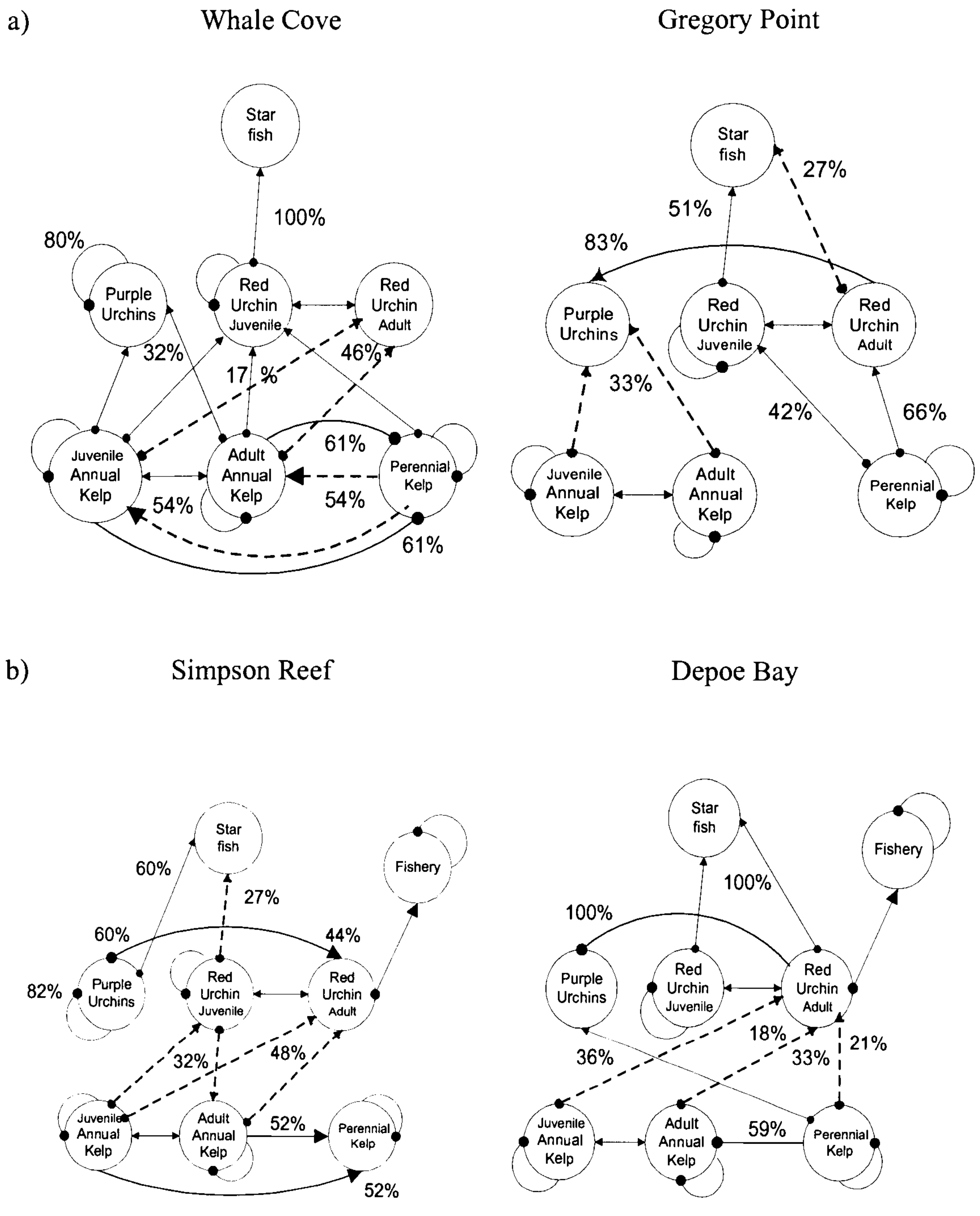


Figure 5.4. Summary of alternative models suggested by qualitative simulations: a) Marine reserves and b) Exploited areas. Digraphs were summarized from Tables 5.4-5.7. The percentages of models that suggested a specific interaction between species are indicated. For example, in 32% of the models from Whale Cove, purple urchins graze on juvenile and adult annual kelp simultaneously. Dashed lines indicate that links from the same species cannot be present simultaneously.

Table 5.4. Percentage of times a specific relation between variables was found in models from Whale Cove Old Marine Reserve. Bold numbers indicate a possible combination between variables; for example, for the predator prey effects, the combination **0 1 0** means that sunflower stars (*Pycnopodia*) only eat juvenile red urchins (JR). This combination appeared in 100 % of the models. JA=juvenile annual kelp; AA=adult annual kelp; P=perennial kelp; PU=purple urchins; JR=juvenile red urchins; AR=adult red urchins. Higher percentages are bolded. N = 748 models.

	Predator Prey Effects (Stars-urchins)							
	PU JR AR	PU JR AR	PU JR AR	PU JR AR	PU JR AR	PU JR AR	PU JR AR	PU JR AR
	0 0 0	**0 0 1**	**1 0 0**	**0 1 1**	**0 1 0**	**1 0 1**	**1 1 0**	**1 1 1**
Sunflower stars	0	0	0	0	**100**	0	0	0

	Grazing Effects (Urchins-Kelp)							
	JA AA P	JA AA P	JA AA P	JA AA P	JA AA P	JA AA P	JA AA P	JA AA P
	0 0 0	**0 0 1**	**1 0 0**	**0 1 1**	**0 1 0**	**1 0 1**	**1 1 0**	**1 1 1**
Purple urchins	18	10	20	0	20	0	**32**	0
Juvenile red urchins	11	10	10	13	11	13	15	**17**
Adult red urchins	0	0	**46**	0	**46**	0	8	0

	Kelp Relationships					
	P-AA			AA-P		
	-1	**0**	**1**	**-1**	**0**	**1**
Perennial kelp adult annual kelp	0	46	**54**	**61**	28	11
	P-JA			JA-P		
	-1	**0**	**1**	**-1**	**0**	**1**
Perennial kelp juvenile annual kelp	0	46	**54**	**61**	28	11

	Urchin Relationships					
	PU-AR			AR-PU		
	-1	**0**	**1**	**-1**	**0**	**1**
Purple urchins adult red urchins	6	**64**	30	10	**90**	0
	PU-JR			JR-PU		
	-1	**0**	**1**	**-1**	**0**	**1**
Purple urchins juvenile red urchins	0	**100**	0	0	**100**	0

	Self Effects				
	Present (-1)	Absent (0)		Present (-1)	Absent (0)
Sunflower stars	0	**100**	Juvenile red urchins	**100**	0
Purple urchins	**80**	20	Adult red urchins	0	**100**

Table 5.5. Percentage of times a specific relation between variables was found in models from Gregory Point New Marine Reserve. Bold numbers indicate a possible combination between variables; for example, for the predator prey effects, the combination **0 1 0** means that sunflower stars (*Pycnopodia*) only eat juvenile red urchins (JR). This combination appeared in 51 % of the models. JA=juvenile annual kelp; AA=adult annual kelp; P=perennial kelp; PU=purple urchins; JR=juvenile red urchins; AR=adult red urchins. Higher percentages are bolded. N = 951 models.

	Predator Prey Effects (Stars-urchins)							
	PU JR AR	PU JR AR	PU JR AR	PU JR AR	PU JR AR	PU JR AR	PU JR AR	PU JR AR
	0 0 0	**0 0 1**	**1 0 0**	**0 1 1**	**0 1 0**	**1 0 1**	**1 1 0**	**1 1 1**
Sunflower stars	0	27	3	19	**51**	0	0	0

	Grazing Effects (Urchins-Kelp)							
	JA AA P	JA AA P	JA AA P	JA AA P	JA AA P	JA AA P	JA AA P	JA AA P
	0 0 0	**0 0 1**	**1 0 0**	**0 1 1**	**0 1 0**	**1 0 1**	**1 1 0**	**1 1 1**
Purple urchins	2	1	**33**	5	**33**	5	17	4
Juvenile red urchins	28	**42**	8	5	8	5	4	0
Adult red urchins	34	**66**	0	0	0	0	0	0

	Kelp Relationships					
	P-AA			AA-P		
	-1	**0**	**1**	**-1**	**0**	**1**
Perennial kelp adult annual kelp	25	**40**	35	38	**47**	15
	P-JA			JA-P		
	-1	**0**	**1**	**-1**	**0**	**1**
Perennial kelp Juvenile annual kelp	25	**40**	35	38	**47**	15

	Urchin Relationships					
	PU-AR			AR-PU		
	-1	**0**	**1**	**-1**	**0**	**1**
Purple urchins adult red urchins	42	**56**	2	5	12	**83**
	PU-JR			JR-PU		
	-1	**0**	**1**	**-1**	**0**	**1**
Purple urchins juvenile red urchins	0	**100**	0	0	**100**	0

	Self Effects				
	Present (**-1**)	Absent (**0**)		Present (**-1**)	Absent (**0**)
Sunflower stars	46	**54**	Juvenile red urchins	**100**	0
Purple urchins	27	**73**	Adult red urchins	0	**100**

Table 5.6. Percentage of times a specific relation between variables was found in models from Simpson Reef with a well managed fishery (quota ≤ MSY). Bold numbers indicate a possible combination between variables; for example, for the predator prey effects, the combination **1 0 0** means that sunflower stars (*Pycnopodia*) eat purple urchins (PU). This combination appeared in 60 % of the models. JA=juvenile annual kelp; AA=adult annual kelp; P=perennial kelp; PU=purple urchins; JR=juvenile red urchins; AR=adult red urchins. Higher percentages are bolded. N = 90 models.

	Predator Prey Effects (Stars-urchins)							
	PU JR AR	PU JR AR	PU JR AR	PU JR AR	PU JR AR	PU JR AR	PU JR AR	PU JR AR
	0 0 0	**0 0 1**	**1 0 0**	**0 1 1**	**0 1 0**	**1 0 1**	**1 1 0**	**1 1 1**
Sunflower stars	0	0	**60**	0	13	0	27	0

	Grazing Effects (Urchins-Kelp)							
	JA AA P	JA AA P	JA AA P	JA AA P	JA AA P	JA AA P	JA AA P	JA AA P
	0 0 0	**0 0 1**	**1 0 0**	**0 1 1**	**0 1 0**	**1 0 1**	**1 1 0**	**1 1 1**
Purple urchins	**41**	13	**23**	0	**23**	0	0	0
Juvenile red urchins	0	0	**32**	1	**32**	1	27	7
Adult red urchins	0	4	**48**	0	**48**	0	0	0

	Kelp Relationships					
	P-AA			AA-P		
	-1	**0**	**1**	**-1**	**0**	**1**
Perennial kelp adult annual kelp	0	**52**	**48**	0	**48**	**52**
	P-JA			JA-P		
	-1	**0**	**1**	**-1**	**0**	**1**
Perennial kelp juvenile annual kelp	0	**52**	**48**	0	**48**	**52**

	Urchin Relationships					
	PU-AR			AR-PU		
	-1	**0**	**1**	**-1**	**0**	**1**
Purple urchins adult red urchins	16	**40**	**44**	**60**	40	0
	PU-JR			JR-PU		
	-1	**0**	**1**	**-1**	**0**	**1**
Purple urchins juvenile red urchins	0	**100**	0	0	**100**	0

	Self Effects				
	Present (**-1**)	Absent (**0**)		Present (**-1**)	Absent (**0**)
Sunflower stars	27	**73**	Juvenile red urchins	**100**	0
Purple urchins	**82**	18	Adult red urchins	0	**100**

Table 5.7. Percentage of times a specific relation between variables was found in models from Depoe Bay with a well managed fishery (quota ≤ MSY). Bold numbers indicate a possible combination between variables; for example, for the predator prey effects, the combination **0 1 1** means that sunflower stars (*Pycnopodia*) eat juvenile red urchins (JR) and adult red urchins (AR). This combination appeared in 100 % of the models. JA=juvenile annual kelp; AA=adult annual kelp; P=perennial kelp; PU=purple urchins; JR=juvenile red urchins; AR=adult red urchins. Higher percentages are bolded. N = 78 models.

	Predator Prey Effects (Stars-urchins)							
	PU JR AR	PU JR AR	PU JR AR	PU JR AR	PU JR AR	PU JR AR	PU JR AR	PU JR AR
	0 0 0	**0 0 1**	**1 0 0**	**0 1 1**	**0 1 0**	**1 0 1**	**1 1 0**	**1 1 1**
Sunflower stars	0	0	0	**100**	0	0	0	0

	Grazing Effects (Urchins-Kelp)							
	JA AA P	JA AA P	JA AA P	JA AA P	JA AA P	JA AA P	JA AA P	JA AA P
	0 0 0	**0 0 1**	**1 0 0**	**0 1 1**	**0 1 0**	**1 0 1**	**1 1 0**	**1 1 1**
Purple urchins	**38**	**36**	0	0	26	0	0	0
Juvenile red urchins	**60**	31	1	0	8	0	0	0
Adult red urchins	0	21	18	14	**33**	14	0	0

	Kelp Relationships					
	P-AA			AA-P		
	-1	**0**	**1**	**-1**	**0**	**1**
Perennial kelp adult annual kelp	**59**	33	8	17	**46**	37
	P-JA			JA-P		
	-1	**0**	**1**	**-1**	**0**	**1**
Perennial kelp juvenile annual kelp	36	**56**	8	20	**45**	35

	Urchin Relationships					
	PU-AR			AR-PU		
	-1	**0**	**1**	**-1**	**0**	**1**
Purple urchins adult red urchins	3	**54**	44	**100**	0	0
	PU-JR			JR-PU		
	-1	**0**	**1**	**-1**	**0**	**1**
Purple urchins juvenile red urchins	0	**100**	0	0	**100**	0

Self Effects

	Present (-1)	Absent (0)
Sunflower stars	0	**100**
Purple urchins	**49**	**51**

	Present (-1)	Absent (0)
Juvenile red urchins	**100**	0
Adult red urchins	0	**100**

Table 5.8. Percentage of times a specific relation between variables was found in models from Depoe Bay with a fishery with fixed quota > MSY. Bold numbers indicate a possible combination between variables; for example, for the predator prey effects, the combination **0 1 0** means that sunflower stars (*Pycnopodia*) eat juvenile red urchins (JR). This combination appeared in 76 % of the models. JA=juvenile annual kelp; AA=adult annual kelp; P=perennial kelp; PU=purple urchins; JR=juvenile red urchins; AR=adult red urchins. Higher percentages are bolded. N = 55 models.

	Predator Prey Effects (Stars-urchins)							
	PU JR AR	PU JR AR	PU JR AR	PU JR AR	PU JR AR	PU JR AR	PU JR AR	PU JR AR
	0 0 0	**0 0 1**	**1 0 0**	**0 1 1**	**0 1 0**	**1 0 1**	**1 1 0**	**1 1 1**
Sunflower stars	0	0	0	9	**76**	0	15	0

	Grazing Effects (Urchins-Kelp)							
	JA AA P	JA AA P	JA AA P	JA AA P	JA AA P	JA AA P	JA AA P	JA AA P
	0 0 0	**0 0 1**	**1 0 0**	**0 1 1**	**0 1 0**	**1 0 1**	**1 1 0**	**1 1 1**
Purple urchins	0	0	0	0	**100**	0	0	0
Juvenile red urchins	**62**	38	0	0	0	0	0	0
Adult red urchins	42	0	0	0	**58**	0	0	0

	Kelp Relationships					
	P-AA			AA-P		
	-1	**0**	**1**	**-1**	**0**	**1**
Perennial kelp adult annual kelp	**93**	7	0	0	**51**	49
	P-JA			JA-P		
	-1	**0**	**1**	**-1**	**0**	**1**
Perennial kelp Juvenile annual kelp	27	**73**	0	0	24	**76**

	Urchin Relationships					
	PU-AR			AR-PU		
	-1	**0**	**1**	**-1**	**0**	**1**
Purple urchins adult red urchins	9	**91**	0	**93**	7	0
	PU-JR			JR-PU		
	-1	**0**	**1**	**-1**	**0**	**1**
Purple urchins juvenile red urchins	0	**100**	0	0	**100**	0

	Self Effects				
	Present (-1)	Absent (0)		Present (-1)	Absent (0)
Sunflower stars	**58**	42	Juvenile red urchins	**100**	0
Purple urchins	0	**100**	Adult red urchins	0	**100**

Perennial kelp connection to adult annual kelp is positive in Whale Cove (54%), negative in Depoe Bay (59%), and no link is present in Gregory Point (40%) and Simpson Reef (52%). The link from perennial to juvenile annual kelp is positive in Whale Cove (54%), and there is no relationship in any other area. Juvenile and adult annual kelp have a negative interaction on perennial kelp in Whale Cove (61%), the interaction is positive in Simpson Reef (52%), and there is no relationship in Gregory Point (47%) and Depoe Bay (46%) (Tables 5.4-5.7 and Fig. 5.4).

Annual kelp can negatively affect under story kelp (perennials) by reducing the light that reaches the bottom and thus inhibiting the growth of under story plants. This shading effect is stronger if the abundance of annual kelp increases. Perennial kelp are better competitors when space is limited and can inhibit recruitment and reduce survival of annual kelp (Foster 1975b; Duggins 1980; Dayton 1985). The suggested positive interaction between annual and perennial kelp has not been reported in the literature and was surprisingly present in all models (Tables 5.4-5.8). Further experimentation is suggested to determine what this positive relationship among kelp might be and what consequences it might have in structuring kelp communities.

A strong harvest pressure (Fig. 5.5b) can create different interaction patterns compared to a moderate harvest (Fig. 5.5a). The fishery affects adult red urchins by decreasing the abundance of adult urchins above the minimum size limit (8.9 cm). In Depoe Bay, under a low harvest pressure scenario, sunflower stars are capable of eating adult red urchins (Fig. 5.5a). When the harvest pressure increases, sunflower stars switch to prey solely on juvenile red urchins (Fig. 5.5b) because the abundance of adult red urchins have been depleted by the fishery. A competition for adult red urchins between the fishery and sunflower stars may exist under these conditions. Adult red urchins maximum size can be reduced when the harvest pressure increases (quota > MSY). Smaller adult red urchins are weaker competitors because they have smaller spines. Under these conditions, their negative effect on purple urchins might be weak, enabling purple urchins to graze on annual kelp (100%) instead of the less preferred perennial kelp (Fig. 5.5b).

The community interactions suggested for each site can be useful to explain the species composition differences observed among sites (Fig. 5.6). In Whale Cove, the grazing effect of both species of urchins on annual kelp keeps their abundances very low (2%). Low annual kelp abundances reduce the negative shading effect on perennial kelp suggested in the models and promotes perennial kelp dominance (42%). In addition, juvenile red urchins maintain a low grazing pressure on perennial kelp due to their low abundance (12%) (Fig. 5.6).

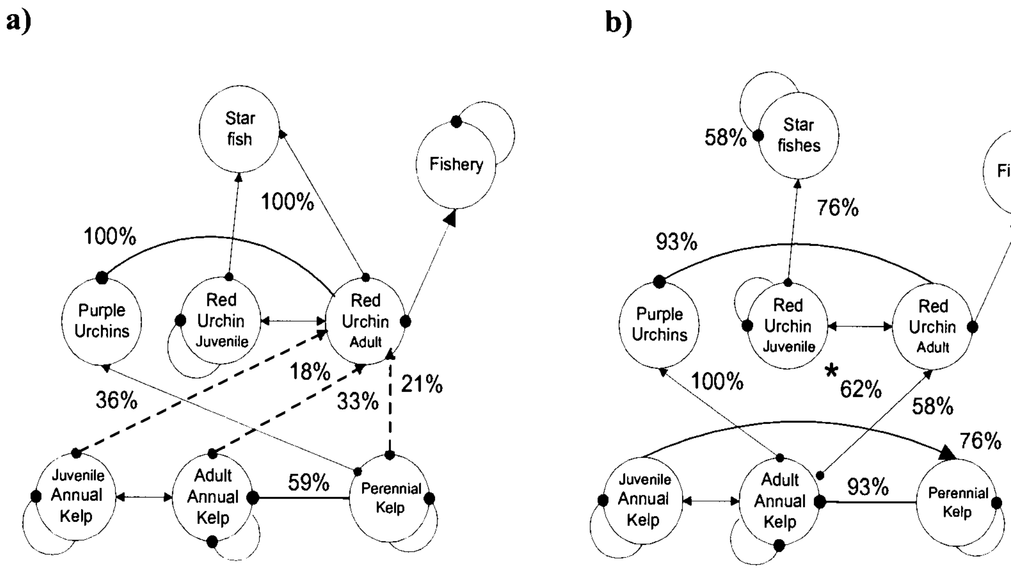
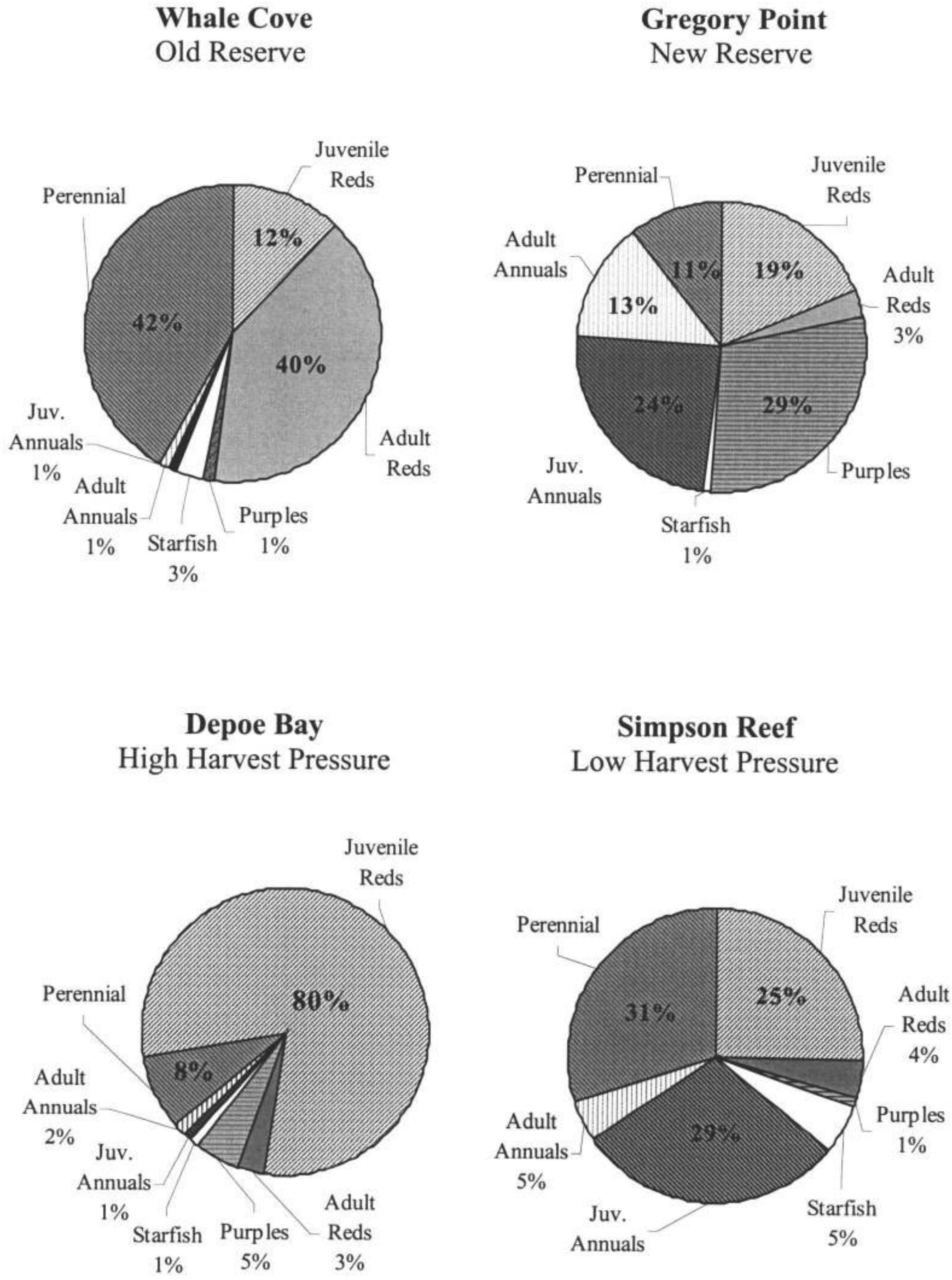


Figure 5.5. Summary of alternative models suggested by qualitative simulations for Depoe Bay. a) well managed fishery scenario (quota ≤ MSY), and b) fishery that is not in equilibrium with the system (fixed quota > MSY). Digraphs were summarized from Tables 5.7 (a) and 5.8 (b). The percentages of models that suggested a relationship between species are indicated. For example, in 100% of the models starfish consume both juvenile and adult red urchins (a). In 76% of the models sunflower stars prey on juvenile red urchins (b). * 62% of the models suggested that juvenile red urchins do not graze on any algae.



Whale Cove Old Reserve

Gregory Point New Reserve

Depoe Bay High Harvest Pressure

Simpson Reef Low Harvest Pressure

Figure 5.6. Percent composition (densities) of the kelp forest community species in two marine reserves and adjacent exploited areas off the Oregon coast.

In Gregory Point, both juvenile and adult red urchins keep perennial kelp abundances low (11%). Purple urchins control either juvenile or adult annual kelp, enabling them to maintain a moderate abundance (13% and 24%, respectively). Compared to Whale Cove, where grazing pressure decimates annual kelp, the partitioning of resource in Gregory Point allow for a better representation of all kelp species. Due to the positive connection from adult red urchins to purple urchins that provides protection from predators, the abundance of purple urchins (29%) is greater than in any other site. The presence of a dense annual kelp canopy reduces available light and inhibits perennial kelp dominance (11%) (Duggins 1980; Reed and Foster 1984).

The species composition in Simpson Reef is more even, indicating a more diverse scenario that arises from both low grazing pressure and the interaction among kelp. The fishery maintains low adult red urchin densities (4%) and sunflower star predation maintains moderately low juvenile red urchins abundances (25%). Perennial kelp abundance (31%) is controlled by the shading effect of abundant annual kelp (34%) (Fig.5.6). When both annual and perennial kelp are similarly abundant, perennial kelp are less effective in out-competing annual kelp and under a dense surface canopy scenario, annual kelp can prevent perennial kelp recruitment (Duggins 1980; Reed and Foster 1984).

The low perennial and annual kelp densities (8% and 3%, respectively) in Depoe Bay, are difficult to explain based on urchin grazing since models suggest that juvenile red urchins, which are very abundant (80%), rely on resources outside the specified system or graze on perennial kelp. Only 9% of the models indicate that they consume either juvenile or annual kelp (Table 5.7). Perhaps the absence of kelp has been a common pattern for this site in the past few years, causing grazers to depend on more available alternative food (coralline algae, diatoms, drift algae, detritus). The relative abundance of adult red urchins is very low (3%) due to the combined effect of predation and harvest. Likely, they are the ones that control annual kelp. Recruitment of annual kelp is inhibited by the negative effect from perennial kelp that perhaps prevents their recovery, reducing the kelp diversity in this area (Fig. 5.6).

Discussion

A community can be represented as a set of alternative models with consistent species interactions useful to characterize the community network of a particular site (Chapter 4). This study suggests that in addition to multiple structures, conspicuous differences in community interactions among sites exist. Exposure to distinct physical and biological disturbances likely created specific patterns of interactions among community members at each site. Although several alternative models can represent each area, we found that specific interactions between community members do not overlap; contrary, these interactions that appeared in high percentages of the models, clearly differed among sites and were key to differentiate the community network that represents each area.

We found, as suggested by Foster and Schiel (1988), that kelp forest systems are stable but very dynamic. Small-scale perturbations can trigger short-time changes in species composition and abundance, while large-scale disturbances create entirely different types of community structures (Foster and Schiel 1988).

Our results agree with Winemiller's (1996) findings that geographical and seasonal variations within interaction patterns are more common than previously thought and call for a dynamic approach when characterizing local and regional ecosystems. As in the variations he found in food web structure of rivers and floodplains, we found particular differences in species interactions among kelp forest communities at different sites. In our example, sunflower stars (*Pycnopodia*) prey only on juvenile red urchins in both Whale Cove and Gregory Point marine reserves. The stars are not able to consume adult red urchins because many have reached a size that is a refuge from predation. Whale Cove is a marine reserve that has been protected for 35 years and the average size of adult red urchins in this area (12.3 cm) is greater than in any other place we studied (Chapter 2). In Whale Cove, adult red urchins have grown too large on average to be consumed by *Pycnopodia*. Duggins (1981b) and Moitoza and Phillips (1979) found by experimentation that *Pycnopodia* would not eat red urchins larger than 8 cm test diameter. Adult red urchins, after being protected for eight years in Gregory Point, have also reached a large size (7.6 cm). The average size of adult red urchins in Depoe Bay is significantly smaller (5.3 cm) (Chapter 2) and within the size range that *Pycnopodia* can consume.

The models representing the protected areas suggest that a problem might already exist in controlling the adult red urchin population since *Pycnopodia* is no longer consuming them. Larger predators may help to control adult urchins. In New Zealand, fishes that are protected from being harvest attain sizes large enough to prey on large urchins, but they need a sufficient home range within the protected area (Ballantine 1991). Both Whale Cove and Gregory Point are small (0.13 km2 and 0.22 km2, respectively), and perhaps significant populations of resident fish predators such as wolf-eels (*Anarrhichthys ocellatus*) or cabezon (*Scorpaenichthys marmoratus*) will require a larger area.

Types of interactions among species can change within a community because of facultative responses to local conditions. Although sea urchins can consume both perennial and annual kelp, and they have preferences for annual kelp in experimental situations (Leighton 1966, Lawrence 1975), our results suggest that the direct relationship between urchins (interference competition or commensalism) combined with *Pycnopodia* predation is important in the partitioning of resources. When the preferred food (annual kelp) is scarce and adult red urchins have a negative relationship with purple urchins (Depoe Bay), purple urchins will be limited to graze on the less preferable perennial kelp. When food is abundant and adult red urchins have a positive relationship with purple urchins (Gregory Point), the later graze on annual kelp, the only situation under which adult reds consume perennials. These differences in consumption (partitioning of resources) and inter guild relationships shape the structure of the community. Besides the relationships between community members, other factors that affect species abundance can have a strong influence on community dynamics, with switching responses from less available resources to the most abundant species (Winemiller 1996). Duggins (1981a) found that sporadic shifts in urchin diets from macroalgae to non-common salps and diatoms had an important effect on community organization. We found that even changes in the species of macroalgae that urchins regularly consume can create different community patterns.

Studies on kelp forest community succession have shown that multiple factors combined with local processes can create distinctive species composition patterns in different areas (Foster and Schiel 1985, 1988; Laur et al. 1988; Estes and Palmisano 1974; Estes et al. 1978). We suggest that these observed patterns may also result from shifts in the community network within and between sites. The set of alternative models that characterize each study area depicts a sequence of functional responses where each specific model or interaction structure creates a different species composition pattern. When the system is disturbed, a new network configuration arises, shifting the community to a new alternative stage. Each particular stage results from the combination of different patterns of *Pycnopodia* predation, the direct interaction between sea urchins, differences between urchin species in their utilization of resources, and the direct interaction between algae.

Our models present a comparison of four sites that have been disturbed in different levels, going from a strong disturbance in Depoe Bay, intermediate disturbance in Simpson Reef, short recovery period in Gregory Point, and long recuperation time in Whale Cove. These disturbances have created different community networks with specific species interactions that triggered the development of particular species composition patterns among sites. The species composition from each site represents a stage in a sequential spectrum where areas that experience intense disturbances (Depoe Bay) and long term recovery from harvest (Whale Cove) seem to be at the extremes of the spectrum, where dominance of perennial kelp and high abundance of urchins shape each community, creating a two species scenario in Whale Cove and one species dominance (red urchins) in Depoe Bay. In Whale Cove, low grazing pressure on perennial kelp resulted in fewer algal species due to dominance of resources and competition from perennial kelp. On the other extreme, heavy grazing in Depoe Bay precludes algal species from colonizing, surviving and reproducing. Intermediate stages were found in Gregory Point and Simpson Reef, where predators, herbivores and kelp species are in similar abundances. Both areas have been exposed to intermediate disturbances: moderate harvest (Simpson Reef) and partial recovery from harvest (Gregory Point), that has maintained moderate urchin abundances. Intermediate grazing intensity can enhance diversity by precluding monopolization by stronger competitors (Vadas 1968; Ayling 1981).

The fate of low diversity areas such as Depoe Bay will depend on herbivores grazing effects. If urchins remain abundant and the same grazing pressure continues, the same low diversity scenario can persist for several years. If urchins abundance decreases due to an increase in predation, low recruitment or diseases, kelp will recruit in the available substrate creating a more algal dominated community with an evenly representation of perennial and annual kelp (Foster 1975a; Duggins 1980; Harrold and Pearse 1987). The future of the community in Whale Cove will depend on a storm regime strong enough to detach perennial kelp, leaving available space for annual kelp to recolonize. The strong grazing intensity on annual kelp in this area may preclude young annual kelp to become establish after recruitment. As models suggests, the problem resides on controlling adult red urchins; however, recruitment of small urchins into the adult population may be limited by the intense predation on juvenile red urchins in this area. When annual kelp abundance is low, the over story component of the community is lost and in turn, can lead to lose an important habitat for pelagic species and epiphytic flora and fauna (Dayton 1998). Gregory Point might shift to a community with low diversity when juvenile red urchins grow big enough to completely escape *Pycnopodia* predation. High abundance of big adult red urchins might out compete purple urchins reversing their positive effect on purple urchins, suggested by models, to a negative effect. This new configuration can break the partitioning of resources that we suggest as favorable for a more diverse scenario.

One of the most important factors that have been attributed to control the structure of the kelp forest community is urchins grazing. Nevertheless, studies are not conclusive due to the enormous variation among geographic areas and within local sites (Foster 1975a and b; Foster and Schiel 1985 and 1988). Competition among algae has been suggested to be more important than grazing in the intertidal (Dayton 1975; Foster 1982) and subtidal (Reed and Foster 1984). Furthermore, kelp succession in the subtidal can be controlled by algal interactions (Paine and Vadas 1969). In Chile, storms and algal competitive hierarchies have a greater importance in structuring the kelp communities than urchin grazing (Castilla & Moreno 1982). The importance of positive interactions among kelp species has not been examined. Mulder et al. (2001) found that in bryophyte communities, interspecific facilitation is an important mechanism to control diversity and productivity under stressful conditions. Our models suggest that besides negative relationships (interference competition and amensalism) among kelp species, benefic interactions (mutualism and commensalisms) might be playing an important role.

Results from Depoe Bay reveal that when the harvest pressure is no longer in equilibrium with the community (quota > MSY) different community patterns arise. These findings suggest that management strategies should be analyzed at the community level and must consider the possible consequences of shifting from one community scenario to another. This concept of dynamic structure is important to better design specific management strategies that consider a different approach to each particular community. The impacts of climate shifts and fisheries on marine communities and their constituent populations are linked to the structure of the community web. Disturbances that act as “presses” to increase or decrease the population growth rate of a particular species may manifest themselves differently according to the stability and structure of the local system. Our suggested models can provide a theoretical background on which to interpret field results, and offer a useful additional tool to assess the consequences of different management options before a decision is taken.

Our modeling approach suggests that marine reserves limited to just the protection of invertebrates should be avoided to maintain the integrity of the community. If predators such as fishes remain being harvest within the reserve, their effect on controlling herbivores is reduced causing a cascading effect through the food web. Protecting target species such as invertebrates without their predators may lead to communities with low diversity that do not represent the natural state of a system but a pattern more similar to a disturbed area that fails to achieve the desired recovered community scenario.

Current patterns of community organization may greatly differ from patterns that existed decades ago due to the disappearance of several species from the community (Dayton et al. 1998). Although communities persist and the role of existing species have changed (Dayton et al. 1998), set aside undisturbed areas, that allow the recovery of lost species and the re-establishment of original communities, is crucial to understand community dynamics. Marine reserves can serve as reference sites to discern between the effects of climatic variation and the impacts of anthropogenic disturbances on community organization.

CHAPTER 6

CONCLUSIONS

Although two marine reserves have been set-aside in the Oregon Coast there is no information about the status of the populations inside these reserves. An assessment of their recovery, therefore was not available. This study analyses the red sea urchin as indicator of population recovery inside Oregon marine reserves. The effect of exploitation was assessed by comparing populations inside reserves to those of adjacent exploited areas.

The response of the red urchin population in Whale Cove and Gregory Point marine reserves suggests that populations inside the reserve will recover. However, for a long lived species the recuperation time will be long compared to short lived species. The population in Gregory Point, which has been protected for eight years, finally showed increases in biomass, mean densities, and maximum size after six years of protection. The role of source populations within protected areas can be evaluated in terms of the emigration of adults into exploited areas or the production of larvae. Ocean circulation patterns studied by satellite-tracked surface drifters were useful to evaluate the fate of larvae released inside reserves. Time of spawning determines larvae trajectories and how far they will travel. Urchins that spawn in early spring in Whale Cove may provide larvae to southern Oregon, suggesting a connection between both Oregon reserves. They also can provide larvae to northern California when spawning is delayed. Larvae from Gregory Point provide recruits to California. Winter spawning will be influenced by currents that travel north, transporting larvae from Whale Cove to Washington and Vancouver and larvae produced in Gregory Point to Whale Cove and surrounding areas. These findings suggest that reserves may be inadequate for sustaining local populations and adjacent exploited areas for species with long larval stages; however, they will be important source of recruits for reserves and exploited areas located within the dispersal range of larvae. This metapopulation array suggests a network of reserves along the Pacific Northwest is needed to assure the maintenance of source populations.

The possible differences in life history and population dynamics that have been suggested in red urchin populations located within the same region call for a spatial management approach (Quinn et al. 1993, Bostford et al. 1993, Polacheck 1990, De Martini 1993, Man et al. 1995) and rotational harvest (Pfister and Bradbury 1996) in some areas. Spatial and temporal variation in growth rates makes populations reach harvestable sizes at different times and recover at different rates after being harvest. Exploited populations can maintain a source status if densities remain above levels that allow fertilization success. This can be assured by rotating areas that have been harvested for several years and that start showing a decline in population levels. Areas where slow growth and high mortality are observed will require more time to recover and hence will remain closed for longer periods before being reopened for harvest. The value of marine reserves to provide parameter estimations from unharvested populations should be emphasized. Natural mortality is often difficult to acquire from fished areas; yet, it is commonly required in stock assessment models.

The importance of red urchins in structuring the kelp forest community has been emphasized in several studies (Estes and Palmisano 1974, Estes et al. 1978, Duggins 1980, 1981, Dayton 1985, Foster and Schiel 1985, Schiel and Foster 1986, Laur et al. 1988). Spatial and temporal variability in kelp community patterns and organization has been suggested by Foster and Schield (1985, 1988). We demonstrate by qualitative simulations that kelp forest communities are very dynamic. In this study, we suggest that communities are best represented as sets of similar alternative stable systems instead of a single model. From millions of plausible models, a set of trophic interactions can be summarized to characterize the community network from a specific area. Predator-prey interactions as well as non-predatory relationships (competition, mutualism, amensalism) differed among sites. Each set of models denotes an alternative hypothesis of community organization and structure that was consistent with field observations.

Particular differences in species interactions among kelp forest communities can also exist among sites due to physical and biological disturbances. Local conditions can create changes in predation, consumption (partitioning of resources), competition, commensalisms, and functional responses among species. This shifts in the community network generates a different species composition pattern that represents a stage in a sequential spectrum. Areas that experience intense disturbances (Depoe Bay) and long term recovery from harvest (Whale Cove) seem to be at the extremes of the spectrum. Dominance of perennial kelp and high abundance of urchins shape each community, creating a two species scenario in Whale Cove and one species dominance (red urchins) in Depoe Bay. Intermediate stages were found in Gregory Point and Simpson Reef, where predators, herbivores and kelp species are in similar abundances. Both areas have been exposed to intermediate disturbances: 1) moderate harvest (Simpson Reef) and 2) partial recovery from harvest (Gregory Point), that has maintained moderate urchin abundances. Models suggest that marine reserves where only target species are protected but their predators remain being harvest may become low diversity areas more similar to a heavy fished area.

Community interactions changed when harvest was no longer in equilibrium with the system. Our findings suggest that a fishery scenario where the quota is greater than the maximum sustainable yield (MSY) will destabilize the system. The consequences of shifting from one community scenario to another can be useful in current management designs to incorporate a more dynamic approach.

The Oregon kelp forest community has not been described due to difficult ocean conditions that prevent from doing experimental work. The incorporation of field observations and modeling techniques in this study provide a hypothesis of the plausible similarities and differences of four kelp forest communities in Oregon.

BIBLIOGRAPHY

Alcala, A.C. 1988. Effects of marine reserves on coral fish abundances and yields of Philippine coral reefs. Ambio **17**:194-199.

Allison, G.W., J. Lubchenco, and M.H. Carr. 1998. Marine reserves are necesary but not sufficient for marine conservation. Ecological Applications **8** Supplement:S79-S92.

Ayling, A.M. 1981. The role of biological disturbance in temperate subtidal encrusting communities. Ecology **62**:830-847.

Baelde, P. 1994. Growth, mortality and yield per-recruit of deep-water royal prawns (*Haliporoides sibogae*) off eastern Australia, using the length-based MULTIFAN method. Marine Biology **118**:617-625.

Ballantine, W. J. 1991. Marine reserves for New Zealand. University of Auckland, Leigh Laboratory Bulletin 25. University of Auckland, New Zealand.

Barry, J.P and M.J. Tegner. 1990. Inferring demographic processes from size-frequency distributions: simple models indicate specific patterns of growth and mortality. Fishery Bulletin **88:**13-19

Barth, J. A. 2001. Ocean surface drifters released off the Oregon Coast. College of Oceanic and Atmospheric Sciences. Coastal Oceanography webpage. htpp://www

Barth, J. A. and Smith, R.L. 1998. Separation of a coastal upwelling jet at Cape Blanco, Oregon, USA. *In*: Pillar, S.C., Moloney, C.L., Payne, A.I.L., Shillington, F.A., *editors*. Benguela Dynamics: Impacts of variability on shelf-sea environments and their living resources. South African Journal of Marine Science **19**:5-14.

Barth, J. A., S.D. Pierce, and R.L. Smith. 2000. A separating coastal upwelling jet at Cape Blanco, Oregon and its connection to the California current system. Deep-Sea Research II **47**: 783-810.

Bell, J.D. 1983. Effects of depth and marine reserve fishing restrictions on the structure of a rocky reef fish assemblage in the northwestern Mediterranean Sea. Journal of Applied Ecology **20**: 357-369

Bender, E.A., T.J. Case and M.E. Gilpin. 1984. Perturbation experiments in community ecology: theory and practice. Ecology **65**: 1-13.

Berger, E.M. 1973. Gene-enzyme variation in three sympatric species of *Littorina*. Biological Bulletin **145**:83-90.

Bjorndal, K.A., A.B. Bolten, A. L. Coan Jr., and P. Kleiber. Estimation of Green Turtle (*Chelonia mydas*) Growth Rates from Length-Frequency Analysis. Copeia **1**: 71-77.

Black, K.P., P.J. Moran, and L.S. Hammond. 1991. Numerical models show coral reef can be self seeding. Marine Ecology Progress Series **74**:1-11.

Bodini, A. 1998. Representing ecosystem structure through signed digraphs. Model reconstruction, qualitative predictions and management: the case of a freshwater ecosystem. OIKOS **83**:93-106.

Bostford, L.W., J.F. Quinn, S.R. Wing and J.G. Brittnacher. 1993. Rotating spatial harvest of a benthic invertebrate, the red sea urchin, *Strongylocentrotus franciscanus*. Pages 409-428 *in* Proceedings of the International Symposium on Management Strategies for Exploited Fish Populations, Alaska 1992. Sea Grant College Program. USA.

Botsford, L.W., C.L. Moloney, A. Hastings, J.L. Largier, T.M. Powell, K. Higgins, and J.F. Quinn. 1994. The influence of spatially and temporally varying oceanographic conditions on meroplanktonic metapopulations Deep-Sea Research Part II Topical Studies in Oceanography **41**:107 145.

Breen, P.A. and K.H. Mann. 1976. Destructive grazing of kelp by sea urchins in Eastern Canada. Journal of the Fisheries Research Board of Canada **33**:1278-1283.

Breen, P.A., W. Carolsfield, K.L. Yamanaka. 1985. Social behavior of juvenile red sea urchins, *Strongylocentrotus franciscanus* (Agassiz). Journal of Experimental Marine Biology and Ecology **92**:45-61.

Burton, R.S. and M.W. Feldman. 1982. Population genetics of coastal and estuarine invertebrates: does larval behavior influence population structure? Pages: 537-551 *in* Kennedy, V.S., editor. Estuarine Comparisons. Academic Press, New York.

Buxton, C.D. and J. Clarke. 1986. Age, growth and feeding of the blue hottentot *Pachymetopon aèneum* (Pisces:Sparidae) with notes on reproductive biology. South African Journal of Zoology **21:**33-38.

Buxton, C.D. and M.J. Smale. 1989. Abundance and distribution patterns of three temperate marine reef fish (Teleostei: Sparidae) in exploited and unexploited areas off the Southern Cape Coast. Journal of Applied Ecology **26**: 441-451.

Buxton, C.D.1993. Life history changes in exploited reef fishes on the east coast of South Africa. Environmental Biology of Fishes **36**:47-63.

Carpenter, S.R. and J.F. Kitchell. 1988. Introduction. Pages 1-8. *In* S.R. Carpenter, *editor*. Complex interactions in lake communities. Springer-Verlag, New York.

Carr, M.H.; and D.C. Reed. 1993: Conceptual issues relevant to marine harvest refuges:examples from temperate reef fishes. Canadian Journal of Fisheries and Aquatic Sciences **50**:2019-2028.

Castilla, J.C., and C.A. Moreno. 1982. Sea urchins and *Macrocystis pyrifera*: Experimental test of their ecological relations in southern Chile. Pages 257-263 *in*: J.M. Lawrence, editor. International Echinoderms Conference, Tampa Bay. A.A. Balkema, Rotterdam.

Castillo, G.C., H.W. Li, and P.A. Rossignol. 2000. Absence of overall feedback in a benthic estuarine community: a system potentially buffered from impacts of biological invasions. Estuaries **23**:275-291.

Cole, R.G.; T.M Ayling, and R.G. Greese. 1990: Effects of marine reserve protection at Goat Island, northern New Zealand. New Zealand Journal of Marine and Freshwater Research **24**:197-210.

Conell, J.H., and W.P. Sousa. 1983. On the evidence needed to judge ecological stability or persistence. American Naturalist **121**:789-824.

Cooper, S.D., S. Diehl, K. Kratz and O. Sarnelle. 1998. Implications of scale for patterns and processes in stream ecology. Australian Journal of Ecology **23**:27-40.

Dambacher, J.M., H.W. Li, and P.A. Rossignol. 2001. (*in press*). Relevance of community structure in assessing indeterminacy of ecological predictions. Ecology.

Davis, G.E. 1977. Effects of recreational harvest on a spiny lobster, *Panulirus argus*, population. Bulletin of Marine Science **27**:223-236.

Dayton, P.K. 1975. Experimental evaluation of ecological dominance in a rocky intertidal algal community. Ecological Monographs. **45**:137-59.

Dayton, P.K. 1985. Ecology of kelp communities. Annual Review of Ecology and Systematics **16**:215-245.

Dayton, P.K., M.J. Tegner, P.B. Edwards, and K.L. Riser. 1998. Sliding baselines, ghosts, and reduced expectations in kelp forest communities. Ecological Applications **8**:309-322.

DeAngelis, D.L. and J.C. Waterhouse. 1987. Equilibrium and nonequilibrium concepts in ecological models. Ecological Monographs **57**:1-21.

DeMartini, E.E. 1993. Modeling the potential of fishery reserves for managing Pacific coral reef fishes. Fishery Bulletin. **91**:414-427.

Denny, M.W. and M.F. Shibata. 1989. Consequences of surf-zone turbulence for settlement and external fertilization. American Naturalist **134**:859-889.

Diamond, J.M. 1975. Assembly of species communities. Pages 342-444. *In* M.L. Cody and J.M. Diamond, editors. Ecology and evolution of communities. Harvard University Press, Cambridge, USA.

Dias, P.C. 1996. Source and sink in population biology. TREE **11**: 326-333.

Doherty, P.J., S. Planes, and P. Mather. 1995. Gene flow and larval duration in seven species of fish from the Great Barrier Reef. Ecology **76**:2373-2391.

Duggins, D.O. 1980. Kelp dominated communities:experimental studies on the relationships between sea urchins, their predators and their algal resources. Ph.D. Dissertation. University of Washington. 134 pp.

Duggins, D.O. 1981a. Sea urchins and kelp: the effects of short-term changes in urchin diet. Limnology and Oceanography **26**:391-394.

Duggins, D.O. 1981b. Interspecific facilitation in a guild of benthic marine herbivores. Oecologia **48**:157-163.

Duggins, D.O. 1983. Starfish predation and the creation of mosaic patterns in a kelp dominated community. Ecology **64**:1610-1619.

Duran, L.R., and J.C. Castilla 1989. Variation and persistence of the middle rocky intertidal community of central Chile, with and without human harvesting. Marine Biology **103**:555-562.

Ebert, T.A., J.D. Dixon, S.C. Schroeter, P. Kalvas, N.T. Richmond, W.A. Bradbury, and D.A. Woodby. 1999. Growth and mortality of red sea urchins (*Strongylocentrotus franciscanus*) across a latitudinal gradient. Marine Ecology Progress Series **190**:189-211.

Ebert, T.A., S.C. Schroeter, J.D. Dixon, and P. Kalvas. 1994. Settlement patterns of red and purple sea urchins (*Strongylocentrotus franciscanus* and *S. purpuratus*) in California, USA. Marine Ecology Progress Series **111**:41-52.

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

Ebert, T.A.; M.P. Russell. 1992. Growth and mortality estimates for red sea urchin, (*Strongylocentrotus franciscanus*), from San Nicolas Island, California. Marine Ecology Progress Series **81**:31-41.

Ebert, T.A.; M.P. Russell. 1993. Growth and mortality of subtidal red sea urchins (*Strongylocentrotus franciscanus*) at San Nicolas Islands, California, USA: Problems with models. Marine Biology **117**:79-89.

Estes, J.A. and J.F. Palmisano. 1974. Sea otters: their role in structuring nearshore communities. Science **185**:1058-1060.

Estes, J.A., N.S. Smith, J.F. Palmisano. 1978. Sea otter predation and community organization in the western Aleutian Islands, Alaska. Ecology **59**:822-833.

Foster, M.S. 1975a. Algal succession in a *Macrocystis pyrifera* forest. Marine Biology **32**:313-329.

Foster, M.S. 1975b. Regulation of algal community development in a *Macrocystis pyrifera* forest. Marine Biology **32**:331-342.

Foster, M.S. 1982. Factors controlling the intertidal zonation of *Iridaea flaccida* (Rhodophyta). Journal of Phycology **18**:285-94.

Foster, M.S. and D.R. Schiel. 1985. The ecology of giant kelp forest in California: a community profile. US Fish and Wildlife Service Biological Report **85**:1-152.

Foster, M.S. and D.R. Schiel. 1988. Kelp communities and sea otters: keystone species or just another brick in the wall? Pages 92-115 *in*: G. R. VanBlaricom, and J.A. Estes, editors. The community ecology of sea otters. Ecological Studies 65. Springer-Verlag, Berlin.

Fournier, D.A. and P.A. Breen. 1983. Estimation of abalone mortality rates with growth analysis. Transactions of the American Fisheries Society. **112**:403-411.

Fournier, D.A., J.R. Sibert, and M. Terceiro. 1991. Analysis of length frequency samples with relative abundance data for the Gulf of Maine northern shrimp (*Pandalus borealis*) by MULTIFAN method. Canadian Journal of Fisheries and Aquatic Sciences **48**:591-598.

Fournier, D.A., J.R. Sibert, J. Majkowski, and J. Hampton. 1990. MULTIFAN a likelihood-based method for estimating growth parameters and age composition from multiple length frequency data sets illustrated using data for southern bluefin tuna (Thunnus maccoyii). Canadian Journal of Fisheries and Aquatic Sciences **47**:301-317.

García-Rubies, A., and M. Zabala. 1990. Effects of total fishing prohibition on the rocky fish assemblages of Mendes Islands marine reserve (NW Mediterranean). Sciensia Marina **54**:317-328.

Harrison, S. 1991. Local extintion in a metapopulation context: an empirical evaluation. Pages: 73-88, *in* Gilpin, M.E. and I. Hanski, editors. Metapopulation Dynamics: Empirical and Theoretical Investigations. Academic Press, London.

Harrold, C. and J.S. Pearse. 1987. The ecological role of echinoderms in kelp forest. Pages 137-233 *in*: M. Jangoux and J.M. Lawrence, editors. Echinoderm Studies, volume 2. Balkema, Rotterdam. Netherlands.

Hasselblad, V. 1966. Estimation of parameters for a mixture of normal distributions. Technometrics **8**:431-222.

Holling, C.S. 1973. Resilience and Stability of Ecological Systems. Annual Review of Ecological Systems **4**:1-23.

Huyer, A. 1977. Seasonal variation in temperature, salinity, and density over the continental shelf off Oregon. Limnology and Oceanography **22**:442-453.

Huyer, A., R.D. Pillsbury, and R.L. Smith. 1974. Observations in a coastal upwelling region during a period of variable winds (Oregon coast, July 1972). Tethys **6**:391-404.

Huyer, A., Smith, R.L., and J.C. Sobey. 1979. The spring transition in currents over the Oregon continental shelf. Journal of Geophysical Research **84**:6995-7011.

Johnson, D.F. and K.W. Hess. 1990. Numerical simulations of blue crab larvae dispersal and recruitment. Bulletin of Marine Science **46**:195-213.

Lane, A.P. 1986. Symmetry, change, perturbation, and observing mode in natural communities. Ecology **67**:223-239.

Lane, A.P. and R. Levins. 1977. Dynamics of aquatic systems. II. The effects of nutrient enrichment on model plankton communities. Limnology and Oceanography **22**:454-471.

Larson, R.J. 1980. Territorial behavior of the black and yellow rockfish and gopher rockfish (Scorpaenidae, *Sebastes*). Marine Biology **58**:111-122.

Laur, D.R., A.W. Ebeling, and D.A. Coon. 1988. Effects of sea otter foraging on subtidal reef communities off Central California. Pages 151-167 *in*: G.R. VanBlaricom, and J.A. Estes, editors. The community ecology of sea otters. Ecological Studies 65. Springer-Verlag, Berlin.

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

Leighton, D.L. 1966. Studies of food preferences in algivorous invertebrates of southern California kelp beds. Pacific Scientists **20**:104-13.

Leighton, D.L. 1967. Ecological investigations of sea urchin populations along the Palos Verdes peninsula. In: North, W.J. Kelp habitat improvement project. Annual Report 1966-1967. California Institute of Technology, Pasadena. P. 41-54

Leighton, D. L., L. G. Jones, and W. J. North. 1966. Ecological relationships between giant kelp and sea urchins in Southern California. Pages 141-153 *in*: E. G. Young, and J.L. McLachlan, editors. Proceedings of the fifth international seaweed symposium. Pergamon Press, England.

Levin, L. A. 1990. A review of methods for labeling and tracking marine invertebrate larvae. Ophelia **32**:115-144.

Levins, R. 1970. Extinction. Lectures of Mathematics in the Life Science **2**:75-107.

Levins, R. 1974. The qualitative analysis of partially specified systems. Annals of the New York Academy of Sciences **231**:123-138.

Levins, R. 1975. Evolution in communities near equilibrium. Pages 16-50 *in*: M. Cody and J.M. Diamond, editors. Ecology and evolution of communities. Harvard University Press, Cambridge, USA.

Levitan, D.R. 1988. Density dependent size regulation and negative growth in the sea urchin *Diadema antillarum* Phillippi. Oecologia 76:627-639.

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

Lewontin, R.C. 1969. The meaning of stability. Brookhaven Symposia in Biology **22**:13-24.

Li, H.W., P.A. Rossignol, and G. Castillo. 1999. Risk analysis of species introductions: Insights from qualitative modeling. Pages 431-447 *in*: R.Claudi and J. H. Leach, editors. Nonindigenous fresh water organisms. Vectors, biology, and impacts. CRC Press, Boca Raton, Florida, USA.

Logofet, D.O. 1993. Matrices and graphs: stability problems in mathematical ecology. CRC Press, Boca Raton, Fl. 308 pp.

MacArthur, R.H. 1972. Geographical ecology. Harper and Row, New York, USA.

Macdonald, P.D., and T.J. Pitcher. 1979. Age-group from size-frequency data: a versatil and efficient method of analyzing distribution mixtures. Journal of the Fisheries Research Board of Canada 36: 987-1001.

Man, A., R. Law, and N. V. C. Polunin. 1995. Role of marine reserves in recruitment to reef fisheries: a metapopulation model. Biological Conservation **71**: 197-204.

Mann, K.H. 1977. Destruction of kelp beds by sea urchins: a cyclical phenomenon or irreversible degradation? Helgoländer wiss. Meeresunters **30**:455-467.

McClanahan, T.R., and N.A. Muthiga. 1988. Changes in Kenyan coral reef community structure and function due to exploitation. Hydrobiologia **166**: 269-276.

McClanahan, T.R., and S.H. Shafir. 1990. Causes and consequences of sea urchin abundance and diversity in Kenyan coral reef lagoons. Oecologia **83**:362-370.

McGowan, J.A., D.R. Cayan, and L.M. Dorman. 1998. Climate-ocean variability and ecosystem response in the Northeast Pacific. Science **281**: 210-217.

Miller, B.A., and R.B. Emlet. 1997. Influence of nearshore hydrodynamics on larval abundance and settlement of sea urchins Strongylocentrotus franciscanus and S. purpuratus in the Oregon upwelling zone. Marine Ecology Progress Series **148**:83-94.

Miller, B.A., and R.B. Emlet. 1999. Development of newly metamorphosed juvenile sea urchins (*Strongylocentrotus franciscanus and S. purpuratus*): morphology, the effects of temperature and larval food ration, and a method for determining age. Journal of Experimental Marine Biology and Ecology, **235**: 67-90.

Moitoza, D.J. and D.W. Phillips. 1979. Prey defense, predator preference, and nonrandom diet: The interactions between *Pycnopodia helianthoides* and two species of sea urchins. Marine Biology **53**:299-304.

Morgan, L.E., L.W. Botsford, S.R. Wing, and B.D. Smith. 2000. Spatial variability in growth and mortality of the red sea urchin, *Strongylocentrotus franciscanus,* in northtern California. Canadian Journal of Fisheries and Aquatic Sciences **57**:980-992.

Mulder, C.P.H., D.D. Uliassi, and D.F. Doak. 2001. Physical stress and diversity-productivity relationships: the role of positive interactions. PNAS **98**:6704-6708.

Neill, J.B. 1987. A novel technique for tagging sea urchins. Bulletin of Marine Science **41**:92-94.

Paddack, M.J. and J.A. Estes. 2000. Kelp forest fish populations in marine reserves and adjacent exploited areas of central California. Ecological Applications **10**:855-870.

Paine, R.T. and R.L. Vadas 1969. The effects of grazing by sea urchins, Strongylocentrotus spp., on benthic algal populations. Limnology and Oceanography **14**:710-719.

Palmer, M. A. 1988. Dispersal of marine meiofauna: a review and conceptual model explaining passive transport and active emergence with implications for recruitment. Marine Ecology Progress Series **48:**81-91.

Palmer, M.A., J.D. Allan and C.A. Butman. 1996. Dispersal as a regional process affecting the local dynamics of marine and stream benthic invertebrates. TREE **11**: 322-326.

Palumbi, S. R. 1995. Using genetics as an indirect estimator of larval dispersal. Pages 369-387 *in* L. McEdward, editor. Ecology of marine invertebrate larvae. CRC Press, Boca Raton, Florida, USA.

Pennington, J.T. 1985. The ecology of fertilzation of echinoid eggs: the consequences of sperm dilution, adult aggregation, and synchronous spawning. Biological Bulletin (Woods Hole) **169**:417-430.

Pfister, C.A. and A. Bradbury. 1996. Harvesting red sea urchins: recent effects and future predictions. Ecological Applications **6**:298-310.

Polacheck, T. 1990: Year around closed areas as a management tool. Natural Resource Modeling **4**:327-353.

Polunin, N.V.C., and C.M. Roberts. 1993. Greater biomass and value of target coral-reef fishes in two small Caribbean marine reserves. Marine Ecology Progress Series **100**:167-176.

Possingham, H.P. and J. Roughgarden. 1990. Spatial population dynamics of a marine organism with a complex life cycle. Ecology **71**:973-985.

Power, M.E., M.S. Parker, and J.T. Wootton. 1996. Distrubance and food chain length in rivers. Pages 286-297. *In* G.A. Polis and K. O. Winemiller, *editors*. Food webs. Integration of patterns and dynamics. Chapman & Hall Press, New York, USA.

Powers, D. A., F. W. Allendorf, and T. Chen. 1990. Application of molecular techniques to the study of marine recruitment problems. Pages 104-121 *in* K. Sherman, L. M. Alexander, and B. D. Gold, editors. Large marine ecosystems: patterns, processes, and yields. American Association for the Advancement of Science, Washington, D.C. USA.

Puccia, C.J. and J. Pederson. 1983. Models and field data of New England tide pools. Pages 709-718. *In* W.K. Lauenroth, G.V. Skogerboe and M. Flug, *editors*. Analysis of ecological systems: state-of-the-art in ecological modeling. Development in environmental modeling: 5. Elsevier New York, USA.

Puccia, C.J. and R. Levins. 1985. Qualitative modeling of complex systems: an introduction to loop analysis and time averaging. Harvard University Press, Cambridge, USA.

Quinn, J.F., S.R. Wing and L.W. Bostford. 1993. Harvest refugia in marine invertebrate fisheries: models and applications to the red sea urchin, *Strongylocentrotus franciscanus*. American Zoologist **33**:537-550.

Rao, C.R. 1973. Linear statistical inference and its applications, 2nd edition. John Wiley and Sons. New York, N.Y., USA.

Reed, D.C. and M.S. Foster. 1984. The effects of canopy shading on algal recruitment and growth in a giant kelp forest. Ecology **65**:937-948.

Richmond, N., J. Schaefer, C. Wood, and J. McCrae. 1997. History and status of the Oregon sea urchin fishery, 1986-1996. Oregon Department of Fish and Wildlife. Marine Resource Program. Newport, Oregon, USA. Unpublished report.

Ricker, W.E. 1945. Natural mortality among Indiana bluegill sunfish. Ecology **26**:111-121.

Roberts, C.M. 1995. Rapid build-up of fish biomass in a Caribbean Marine Reserve. Conservation Biology **9**:815-826.

Russ, G.R. 1985. Effects of protective management on coral reef fishes in the Central Philippines. Pages 219-224, *in* Proceedings of the 5th International Coral Reef Congress, Tahiti. Vol.4.

Russ, G.R. and A.C. Alcala. 1989. Effects of intense fishing pressure on an assemblage of coral reef fish. Marine Ecology Progress Series **56**:13-27.

Saavedra, C., A. Zapata, A. Guerra, and G. Alvarez. 1993. Allozyme variation in European populations of the oyster *Ostrea edulis*. Marine Biology **115**:85-95.

Sale, P.F. 1978. Coexistence of coral reef fishes – a lottery for living space. Environmental Biology of Fishes **3**:85-102.

Sale, P.F. 1990. Recruitment of marine species: is the bandwagon rolling in the right direction? Trends in Ecology and Evolution **5**:25-27.

Sammarco, P.W. and J.C. Andrews. 1988. Localized dispersal and recruitment in Great Barrier Reef corals: the helix experiment. Science **239**:1422-1424

Schmitz, O.J. 1997. Press perturbations and the predictability of ecological interactions in a food web. Ecology **78**:55-69.

Schnute, J.T. and D. Fournier. 1980. A new approach to length-frequency analysis: growth structure. Canadian Journal of Fisheries and Aquatic Sciences **37**:1337-1351.

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. dissertation, University of California at Santa Barbara, USA.

Shepherd, S.A. 1990. Studies on Southern Australian abalone (genus *Haliotis*). XII. Long term recruitment and mortality dynamics of an unfished population. Australian Journal of Marine and Freshwater Resources **41**:475-492.

Siddall, S.E., R.E. Malouf, M.E.C. Vieira, and E. Gomez-Reyes. 1986. Use of dispersion models for prediction of bivalve larval recruitment. Journal of Shellfish Research **7**:133.

Simenstad, C.A., J.A. Estes, and K.W. Kenyon. 1978. Aleuts, sea otters, and alternate stable-state communities. Science **200**:403-411.

Sloan, N.A. 1985. Echinoderm fisheries of the world: a review. Pages 109-124 *In* B. F. Keegan and B. D. S. O'Connor, editors. Proceedings of the Fifth International

Echinoderm Conference, Galway, 24-29 September 1984. Balkema, Rotterdam.

Smith, B.D., L.W.Bostford and S.R. Wing. 1998. Estimation of growth and mortality parameters from size frequency distributions lacking age patterns: the red sea urchin (*Strongylocentrotus franciscanus*) as an example. Canadian Journal of Fisheries and Aquatic Sciences **55**:1236-1247.

Smith, R.L. 1981. A comparison of the sructure and variability of the flow field in three upwelling regions: Oregon, Northwest Africa and Peru. Pages 51-53, *in* Richards, F.A. editor. Coastal upwelling. American Geophysical Union, Washington.

Strathmann, R. 1978. Length of pelagic period in echinoderms with feeding larvae from the Northeast Pacific. Journal of Experimental Marine Biology and Ecology **34**:23-27.

Strub, P.T., J.S. Allen, A. Huyer, and R.L. Smith. 1987. Seasonal cycles of currents, temperature, winds, and sea level over the northeast Pacific continental shelf: 35°N to 48°N. Journal of Geophysical Research **92**:1507-1526.

Sutherland, J.P. 1974. Multiple stable points in natural communities. American Naturalist **108**:859-873.

Sutherland, J.P. 1990. Perturbations, resistance, and alternative views of the existence of multiple stable points in nature. American Naturalist **136**:270-275.

Swan, E.F. 1961. Some observations on the growth rate of sea urchins in the genus *Strongylocentrotus*. Biological Bulletin **120**:420-427.

Tegner, M.J. and Dayton, P.K. 1977. Sea urchin recruitment patterns and implications of commercial fishing. Science **196**:324-326.

Tegner, M.J and P.K., Dayton. 1981. Population structure, recruitment and mortality of two sea urchins (*Strongylocentrotus franciscanus and S. purpuratus*) in a kelp forest. Marine Ecology Progress Series **5**:255-268.

Tegner, M.J. 1989. The feasibility of enhancing red sea urchin, *Strongylocentrotus franciscanus*, stocks in California: An analysis of the options. Marine Fisheries Review **51**:1-22.

Vadas, R.L. 1968. The ecology of Agarum and the kelp bed. Ph.D. dissertation, University of Washington, Seattle, USA.

VanBlaricom, G.R. and J.A. Estes. 1988. The community ecology of sea otters. Ecological Studies 65. Springer-Verlang Berlin Heidelberg.

Waldford, L.A. 1946. A new graphical method of describing the growth of animals. Biological Bulletin, (Woods Hole) **90**:141-147.

Waples, R. S. and R. H. Rosenblatt. 1987. Patterns of larval drift in southern California marine shore fishes inferred from allozyme data. Fishery Bulletin **85**:1-11.

Warren, P.H. 1994. Making connections in food webs. TREE **9**:136-141.

Weil, M.E. and R.G. Laughlin. 1984. Biology, population dynamics and reproduction of the queen conch Strombus gigas Linne in the Archipelago de los Roques National Park. Journal of Shellfish Research **4**:45-62.

Winemiller, K.O. 1996. Factors driving temporal and spatial variation in aquatic floodplain food webs. Pages 298-312. *In* G.A. Polis and K.O. Winemiller, *editors*. Food webs. Integration of patterns and dynamics. Chapman & Hall Press, New York, USA.

Wing, S.R., J.L. Largier, L.W. Bostford and J.F. Quinn. 1995. Settlement and transport of benthic invertebrates in an intermittent upwelling region. Limnology and Oceanography **40**:316-329.

Wing, S.R., L.W. Bostford, J.L. Largier, and S. Ralston. 1998. Meroplankton distribution and circulation associated with a coastal retention zone in the northern California upwelling zone. Limnology and Oceanography **43**:1710-1721.

Wootton, J.T. 1994. The nature and consequences of indirect effects in ecological communities. Annual Review of Ecology and Systematics **25**:443-466.

Yodzis, P. 1988. The indeterminacy of ecological interactions as perceived through perturbation experiments. Ecology **69**:508-515.

APPENDIX

APPENDIX. Algorithm for Qualitative Simulations.

Written for MATLAB 5.3.1.29215 (The Mathworks Inc.) by Gabriela Montaño Moctezuma (montanog@ucs.orst.edu) and Antonio Martínez (amartine@oce.orst.edu), June, 1999.

%A = community matrix
%o = field observations
%a = **nxn** sub-matrix
%N = community matrix order

```
fid=fopen('filename1','wt');
fidb=fopen('filename1all','wt');
N=7;EPS=1e-50;
n=3;nr=1;nc=3;sr=1;sc=1;pur=1;puc=1;zr=2;zc=1;ur=1;uc=1;yr=1;yc=1;xr=
1;xc=2; rr=1;rc=1;
A=[-1 1 1 1 0 0 0;
   -1 0 0 0 0 0 1;
   -1 0 -1 1 1 1 1;
   -1 0 1 0 1 1 1;
    0 0 -1 -1 -1 1 0;
    0 0 -1 -1 1 -1 -1;
    0 -1 -1 -1 0 0 -1];
  o=[1 -1 1 1 1 -1 1];
 for j=1:N
    O(:,j)=o';
 end
fprintf(fid,'%2d %2d %2d %2d %2d %2d %2d\n',A');
fprintf(fid,'%2d %2d %2d %2d %2d %2d %2d\n',o);
l=0;m=0;
 for i1=0:1
    for i2=0:1
       for i3=0:1
          for i4=0:1
             for i5=0:1
                for i6=0:1
                   for i7=0:1
                      for i8=0:1
                         for i9=0:1
                            for j1=0:1
                               for j2=0:1
                                  for j3=0:1
                                     for s1=-1:0
                                        for pu=-1:0
                                           for m1=-1:0
                                              for x1=-1:0
  a=reshape([i1 i2 i3 i4 i5 i6 i7 i8 i9],n,n);
  P=reshape([j1 j2 j3],nr,nc);
  S=reshape([s1],sr,sc);
  Pu=reshape([pu],pur,puc);
  M=reshape([m1 m2],zr,zc);
  X=reshape([x1 x2],xr,xc);
  U=reshape([u1],ur,uc);
```

```
  Y=reshape([y1],yr,yc);
  A(2:4,5:7)=a;
  A(5:7,2:4)=-a';
  A(1:1,2:4)=P;
  A(2:4,1:1)=-P';
  A(1:1,1:1)=S;
  A(2:2,2:2)=Pu;
  A(5:6,7:7)=M;
  A(7:7,5:6)=X;
  A(2:2,4:4)=U;
  A(4:4,2:2)=Y;
  As=adj(-A);
  Ad=round(As)./(abs(round(As))+EPS);
  Rp=(Ad-O);
  Rn=(Ad+O);
  T=0;
  ncon=0;
  for j=1:N
       l=l+1;
     Dp=length(find(Rp(:,j)));
     Dn=length(find(Rn(:,j)));
     if Dp==0|Dn==0
        m=m+1;
        T=1;
        ncon=ncon+1;
if ncon==1
   pe=permanent2(A',pv1,v1);
   r=round(pe./(pe+EPS));
   per=(As./(pe+EPS)).*r;
   over=det(A);
end
   buena=per(:,j);
   tot=sum(abs(buena));
   buena(N+1)=tot;
   buena(N+2)=j;
   buena(N+3)=over;
fprintf(fid,'%2d %2d %2d\n',a');
fprintf(fid,'%2d\n',m)
fprintf(fid,'%2d %2d %2d\n',P');
fprintf(fid,'%2d\n',m)
fprintf(fid,'%2d\n',S');
fprintf(fid,'%2d\n',m)
fprintf(fid,'%2d\n',Pu');
fprintf(fid,'%2d\n',m)
fprintf(fid,'%2d\n',M');
fprintf(fid,'%2d\n',m)
fprintf(fid,'%2d\n',X');
fprintf(fid,'%2d\n',m)
fprintf(fid,'%2d\n',U');
fprintf(fid,'%2d\n',m);
fprintf(fid,'%2d\n',Y');
fprintf(fid,'%2d\n',m);
fprintf(fid,'%6.3f %6.3f %6.3f %6.3f %6.3f %6.3f %6.3f %6.3f %4d
%4d\n',buena);
fprintf(fidb,'%2d %2d %2d %2d %2d %2d %2d\n',A');
```

```
end
end
end
end
end
end
end
end
end
end
end
end
end
end
end
end
end
end
end
end
end
end
fprintf(fid,'%2d\n',l/N)
fclose(fid)
fclose(fidb)

% To find highly reliable models (weighted predictions >0.5)

fid=fopen('filename1','rt');
N=7;EPS=1e-50;
n=3; nr=1;nc=3;sr=1;sc=1;pur=1;puc=1;zr=1;zc=1;xr=1;xc=1;%c
for j=1:N
    a=fscanf(fid,'%2g',N);
A(j,:)=a';
   end
   o=fscanf(fid,'%g',N);
   for l=1:500000
for j=1:n
   [a,c]=fscanf(fid,'%g',n);
end
if c==0
   break
   end
a=fscanf(fid,'%g',1);
a=fscanf(fid,' %g',n);
for j=1:14
   a=fscanf(fid,'%g',1);
end
b=fscanf(fid,'%g',1);
a=fscanf(fid,'%g',N+3);
bueno(l)=a(N+1);
ren=abs(a(1:N));
renp(l)=length(find(ren>=0.5&ren>0.0));
sig(l)=a(N+3)/abs(a(N+3));
cuenta(l)=b;
```

```
end
sigteor=(-1)^N;
indx=find(bueno>=3&bueno<3.5);
bueno=bueno(indx);
renp=renp(indx);
sig=sig(indx);
cuenta=cuenta(indx);
indx2=find(renp==N-3);
bueno=bueno(indx2);
renp=renp(indx2);
sig=sig(indx2);
cuenta=cuenta(indx2);
indx3=find(sig==sigteor);
bueno=bueno(indx3);
renp=renp(indx3);
sig=sig(indx3);
cuenta=cuenta(indx3);
fclose(fid)
save filename1high cuenta -ascii

%To find estable models

load filename1high
nr=7;nc=7;
load filename1all
for l=1:length(filename1high)
A((l-1)*nr+1:l*nr,:)=filename1all((filename1high(l)-
1)*nr+1:filename1high(l)*nr,:);
end
a=A;
clear filename1all
[m,n]=size(a);
nm=m/n;
l=0;
for j=1:nm
   b=a((j-1)*n+1:j*n,:);j
   p=round(poly(b));
%Hurtwitz determinant H2
c1=zeros(2,2);
c1(:,1)=p(2:-1:1)';
c1(:,2)=p(4:-1:3)';
%Hurtwitz determinant H3
c2=zeros(3,3);
c2(1:2,1)=p(2:-1:1)';
c2(:,2)=p(4:-1:2)';
c2(:,3)=p(6:-1:4)';
%Hurtwitz determinant H4
c3=zeros(4,4);
c3(1:2,1)=p(2:-1:1)';
c3(:,2)=p(4:-1:1)';
c3(:,3)=p(6:-1:3)';
c3(:,4)=p(8:-1:5)';
%Hurtwitz determinant H5
c4=zeros(5,5);
c4(1:2,1)=p(2:-1:1)';
```

```
c4(1:4,2)=p(4:-1:1)';
c4(:,3)=p(6:-1:2)';
c4(:,4)=p(8:-1:4)';
c4(2:5,5)=p(9:-1:6)';
%Hurtwitz determinant H6
c5=zeros(6,6);
c5(1:2,1)=p(2:-1:1)';
c5(1:4,2)=p(4:-1:1)';
c5(:,3)=p(6:-1:1)';
c5(:,4)=p(8:-1:3)';
c5(2:6,5)=p(9:-1:5)';
c5(4:6,6)=p(9:-1:7)';
%Hurtwitz determinant H7
c6=zeros(7,7);
c6(1:2,1)=p(2:-1:1)';
c6(1:4,2)=p(4:-1:1)';
c6(1:6,3)=p(6:-1:1)';
c6(:,4)=p(8:-1:2)';
c6(2:7,5)=p(9:-1:4)';
c6(4:7,6)=p(9:-1:6)';
c6(6:7,7)=p(9:-1:8)';
%Hurtwitz determinant H8
c7=zeros(8,8);
c7(1:2,1)=p(2:-1:1)';
c7(1:4,2)=p(4:-1:1)';
c7(1:6,3)=p(6:-1:1)';
c7(:,4)=p(8:-1:1)';
c7(2:8,5)=p(9:-1:3)';
c7(4:8,6)=p(9:-1:5)';
c7(6:8,7)=p(9:-1:7)';
c7(8,8)=p(9)';
dc1=det(c1);
dc2=det(c2);
dc3=det(c3);
dc4=det(c4);
dc5=det(c5);
dc6=det(c6);
dc7=det(c7);

%First stability criteria
   ip=length(find(p(1:n)>0));
   in=length(find(p(1:n)<0));
   cp=0;cn=0;cd=0;
   if ip==n & p(n+1)==0
      cp=1;
   end
   if ip==n & p(n+1)>0
      cp=1;
   end

   if in==n & p(n+1)==0
      cn=1;
   end
   if in==n & p(n+1)<0
      cn=1;
```

```
   end
%Second stability criteria
   if dc1>0 & dc2>0 & dc3>0 & dc4>0 & dc5>0 & dc6>0 & dc7>0
      cd=1;
   end
   if cp==1|cn==1
      if cd==1
         l=l+1;
         numa(l)=sr2(j);
      end
   end
end
numa=numa;
save est2filename1 numa -ascii

%To find the percentage of times a specific interaction between
species is repeated in selected models

% a)Submatrix = 1x1
load est2filename1
nr=7;nc=7;
load filename1all
for l=1:length(est2filename1)
A((l-1)*nr+1:l*nr,:)= filename1all((est2filename1(l)-1)*nr+1:
est2filename1(l)*nr,:);
end
clear filename1all
[n1,nc]=size(A);
nm=n1/nr;
mn=-1;mx=1;
co=0;
for i1=mn:mx
         co=co+1;
         perm(co,:)=[i1];
      end
[nperm,nn]=size(perm);
ir=[1]; %Input:interaction array to be found
ic=[1]; %Input:interaction array to be found
nele=max(length(ir),length(ic));
cmtot=zeros(nperm,1);
for j=1:nm
   ib=(j-1)*nr+1;
   ie=j*nr;
   a=A(ib:ie,:);
   suba=reshape(a(ir,ic),1,1);
   for k=1:nperm
   res=find(perm(k,:)-suba==0);
   if length(res)==nele
      cmtot(k)=cmtot(k)+1;
   end
   end
end
[perm cmtot*100/nm]
smt=sum(cmtot);
if smt==nm
```

```
   input('great')
end

% b)Submatrix = 1x3
load est2filename1
nr=7;nc=7;
load filename1all
for l=1:length(est2filename1)
A((l-1)*nr+1:l*nr,:)= filename1all((est2filename1(l)-1)*nr+1:
est2filename1(l)*nr,:);
end
clear filename1all
[n1,nc]=size(A);
nm=n1/nr;
mn=-1;mx=1;
co=0;
for i1=mn:mx
   for i2=mn:mx
      for i3=mn:mx
         co=co+1;
         perm(co,:)=[i1 i2 i3];
      end
   end
end
[nperm,nn]=size(perm);
ir=[4]; %Input:interaction array to be found
ic=[5 6 7]; %Input:interaction array to be found
nele=max(length(ir),length(ic));
cmtot=zeros(nperm,1);
for j=1:nm
   ib=(j-1)*nr+1;
   ie=j*nr;
   a=A(ib:ie,:);
   suba=reshape(a(ir,ic),1,3);
   for k=1:nperm
   res=find(perm(k,:)-suba==0);
   if length(res)==nele
      cmtot(k)=cmtot(k)+1;
   end
   end
end
[perm cmtot*100/nm]
smt=sum(cmtot);
if smt==nm
   input('great')
end
```

The following functions need to be saved as separate files to be recalled by the main program:

Function: Permanent **(save as: permanent2.m)**

```
function  [per]=permanent(A,pv1,v1);
[n]=length(A);
v1=1:n-1;
pv1=perms(v1);
for l=1:n
for m=1:n
AS=zeros(n-1,n-1);
AS(1:l-1,1:m-1)=A(1:l-1,1:m-1);
AS(1:l-1,m:n-1)=A(1:l-1,m+1:n);
AS(l:n-1,1:m-1)=A(l+1:n,1:m-1);
AS(l:n-1,m:n-1)=A(l+1:n,m+1:n);
for j=1:n-1
P(j,:)=abs(AS(j,pv1(:,j)));
end
per(l,m)=sum(prod(P));
end
end

%Permanent function written by Antonio Martínez, June, 1999
```

Function: Adjoint **(save as: adj.m)**

```
function [B] = adj(A)
%ADJ Matrix adjoint.
%   ADJ(A) is the adjoint matrix of square matrix A.
%   It is computed using the Cayley-Hamilton Theorem.
%   The inverse of A is: INV(A) = ADJ(A)/det(A).
%
%   Matrices that are not invertable still have an adjoint.
%
%   See also INV, PINV, RANK, SLASH.

ce = poly(eig(A));
cesize = max(size(ce));
p = [0 ce(1:(cesize-1))];
s = (-1)^(max(size(A))+1);
B = s*polyvalm(p,A);
return

%Adjoint function written by Paul Godfrey (pjg@mlb.semi.harris.com),
April, 1998.
```