CHAPTER 4

ALTERNATIVE COMMUNITY INTERACTIONS: A QUALITATIVE MODELING APPROACH

Gabriela Montaño Moctezuma, Hiram W. Li, and Philippe A. Rossignol
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 concerning 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. 1998). 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
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.
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.
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.
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).

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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 (80m²). Six transects were systematically allocated to cover the entire area. Each transect was divided in 16 sampling units of 5m² (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.

1. N x N core matrix (A), observations (o), and unknown sub-matrices to be simulated are defined by the user.

2. Model generates all possible unknown combinations (+, −, 0) between variables in a N x N matrix (3\(^n\times n\)).

3. Core matrix (A) is reshaped with each new generated combination and a new model is created.

4. A weighted predictions matrix is calculated for each model generated.

5. Each column from the weighted predictions matrix is compared with field observations.

   - If model predictions match observations, the model is selected.
   - If model predictions do not match observations, the model is discarded.

6. Models with weighted prediction values > 0.5 are further selected and both stability criteria tested.

7. Highly reliable, stable models are saved into an output file for further analysis.
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 \textbf{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.

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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 al. 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 (r² = 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 (r² = 0.56, P < 0.001, n = 80 and r² = 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 (r² = -0.33, P = 0.01, n = 59; r² = -0.41, P = 0.001, n = 59; r² = -0.63, P < 0.001, n = 59, respectively) and positively correlated with adult red urchins (r² = 0.34, P = 0.009, n = 59; r² = 0.32, P = 0.01, n = 59; r² = 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
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.

<table>
<thead>
<tr>
<th></th>
<th>Adult red urchins</th>
<th>Juvenile annual kelp</th>
<th>Perennial kelp</th>
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</thead>
<tbody>
<tr>
<td>Adult annual kelp</td>
<td>.26 (.0234)</td>
<td>.56 (.0000)</td>
<td>.41 (.0003)</td>
</tr>
<tr>
<td></td>
<td>77</td>
<td>80</td>
<td>80</td>
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<table>
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<tr>
<th></th>
<th>Juvenile red urchins</th>
<th>Adult red urchins</th>
<th>Juvenile annual kelp</th>
<th>Adult annual kelp</th>
</tr>
</thead>
<tbody>
<tr>
<td>Juvenile annual kelp</td>
<td>−.33 (.0119)</td>
<td>.34 (.0088)</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td></td>
<td>59</td>
<td>59</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Adult annual kelp</td>
<td>−.41 (.0016)</td>
<td>.32 (.0139)</td>
<td>.44 (.0005)</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>59</td>
<td>59</td>
<td>64</td>
<td></td>
</tr>
<tr>
<td>Perennial kelp</td>
<td>−.63 (.0000)</td>
<td>.61 (.0000)</td>
<td>.61 (.0000)</td>
<td>.60 (.0000)</td>
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<tr>
<td></td>
<td>59</td>
<td>59</td>
<td>64</td>
<td>64</td>
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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.

<table>
<thead>
<tr>
<th>Species</th>
<th>Reserves</th>
<th></th>
<th>Exploited Areas</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Whale Cove</td>
<td>Gregory Point</td>
<td>Simpson Reef</td>
</tr>
<tr>
<td>Starfish</td>
<td>+</td>
<td>−</td>
<td>0</td>
</tr>
<tr>
<td>Purple urchins</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Juvenile red urchins</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Adult red urchins</td>
<td>+</td>
<td>−</td>
<td>+</td>
</tr>
<tr>
<td>Juvenile annual kelp</td>
<td>0</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Adult annual kelp</td>
<td>0</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Perennial kelp</td>
<td>+</td>
<td>0</td>
<td>+</td>
</tr>
</tbody>
</table>

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
While urchin landings peaked in 1991 (322 thousand pounds), the amount decreased to 19 thousand pounds in 1995 (Richmond et al. 1997). 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).

<table>
<thead>
<tr>
<th>Study Site</th>
<th>a) Tested Models</th>
<th>b) Models that matched the data</th>
<th>c) Highly reliable models</th>
</tr>
</thead>
<tbody>
<tr>
<td>Whale Cove</td>
<td>11,943,936</td>
<td>26,955 (0.23%)</td>
<td>748 (.006 %)</td>
</tr>
<tr>
<td>Gregory Point</td>
<td>11,943,936</td>
<td>109,273 (0.91%)</td>
<td>951 (.008 %)</td>
</tr>
<tr>
<td>Simpson Reef (quota ≤ MSY)</td>
<td>11,943,936</td>
<td>13,501 (0.11%)</td>
<td>90 (.0008%)</td>
</tr>
<tr>
<td>Depoe Bay (quota ≤ MSY)</td>
<td>11,943,936</td>
<td>498,758 (4.18%)</td>
<td>78 (.0007%)</td>
</tr>
<tr>
<td>Depoe Bay (quota &gt; MSY)</td>
<td>11,943,936</td>
<td>462,576 (3.87%)</td>
<td>55 (.0005%)</td>
</tr>
</tbody>
</table>
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 purple 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.

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<table>
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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.

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<td>(Urchins-Kelp)</td>
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<td>PU-AR</td>
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<tr>
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<td></td>
</tr>
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<td>PU-AR</td>
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<td>AR-PU</td>
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<td>Absent ( 0 )</td>
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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)

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<th>PU JR AR</th>
<th>PU JR AR</th>
<th>PU JR AR</th>
<th>PU JR AR</th>
<th>PU JR AR</th>
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<td>0 1 0</td>
<td>1 0 1</td>
<td>1 1 0</td>
<td>1 1 1</td>
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</tbody>
</table>

| Sunflower stars | 0 | 0 | 60 | 0 | 13 | 0 | 27 | 0 |

### Grazing Effects (Urchins-Kelp)

<table>
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<td>0 1 0</td>
<td>1 0 1</td>
<td>1 1 0</td>
<td>1 1 1</td>
</tr>
</tbody>
</table>

| 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

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<td>48</td>
<td>52</td>
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<table>
<thead>
<tr>
<th>Perennial kelp</th>
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</thead>
<tbody>
<tr>
<td>adult annual kelp</td>
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### Urchin Relationships

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<th>AR-PU</th>
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### Self Effects

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<table>
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<tr>
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<td>100</td>
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<tr>
<td>Adult red urchins</td>
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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.

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Sunflower stars

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Purple urchins

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Juvenile red urchins

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Adult red urchins

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<tr>
<td>Purple urchins</td>
</tr>
<tr>
<td>Juvenile red urchins</td>
</tr>
<tr>
<td>Adult red urchins</td>
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</tbody>
</table>
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.

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<td>Adult red urchins</td>
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</table>
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.
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 Palmsano 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 pristine conditions 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 no 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 urchin’s 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 role as protection agents is 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 status 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 pristine areas (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.
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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 = n x n 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;rr=2;rz=2;ur=1;yr=1;xc=1;xr=1;
A=[[-1 1 1 0 0 0 1;
    -1 0 0 0 0 1 1;
    -1 0 1 1 1 1 0;
    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
',A');
    fprintf(fid,'%2d %2d %2d %2d %2d %2d %2d
',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 j4=0:1
                                                        for j5=0:1
                                                            for j6=0:1
                                                                for j7=0:1
                                                                    for j8=0:1
                                                                        for j9=0:1
                                                                            for sl=-1:0
                                                                                for pu=-1:0
                                                                                    for ml=-1:0
                                                                                        for xl=-1:0
                                                                                            a=reshape([i1 i2 i3 i4 i5 i6 i7 i8 i9],n,n);
                                                                                            P=reshape([j1 j2 j3],nr,nc);
                                                                                            S=reshape([sl],sr,sc);
                                                                                            Pu=reshape([pu],pur,puc);
                                                                                            M=reshape([ml m2],rz,zc);
                                                                                            X=reshape([xl x2],xr,xc);
                                                                                            U=reshape([ul],ur,uc);
                                                                                            end
                                                                                        end
                                                                                    end
                                                                                end
                                                                            end
                                                                        end
                                                                    end
                                                                end
                                                            end
                                                        end
                                                    end
                                                end
                                            end
                                        end
                                    end
                                end
                            end
                        end
                    end
                end
            end
        end
    end

end
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
  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
',a');
  fprintf(fid,'%2d
',m)
  fprintf(fid,'%2d %2d %2d
',P');
  fprintf(fid,'%2d
',m)
  fprintf(fid,'%2d
',S');
  fprintf(fid,'%2d
',m)
  fprintf(fid,'%2d
',Pu');
  fprintf(fid,'%2d
',m)
  fprintf(fid,'%2d
',M');
  fprintf(fid,'%2d
',m)
  fprintf(fid,'%2d
',X');
  fprintf(fid,'%2d
',m)
  fprintf(fid,'%2d
',U');
  fprintf(fid,'%2d
',m);
% 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;
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));
    rep(l)=length(find(ren>=0.5&ren>0.0));
    sig(l)=a(N+3)/abs(a(N+3));
    cuenta(l)=b;
end
fprintf(fid,'%2d\n',1/N)
fclose(fid)
fclose(fidb)
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 filenamelhigh cuenta -ascii

%To find stable models

load filenamelhigh
nr=7; nc=7;
load filenamelall
for l=1:length(filenamelhigh)
    A((l-1)*nr+1:l*nr,:)=filenamelall((filenamelhigh(l)-
    1)*nr+1:filenamelhigh(l)*nr,:));
end
a=A;
clear filenamelall
[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:-1:1)';
c2(:,3)=p(6:-1:3)';
    %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;
% 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 il=mn:mx
co=co+1;
perm(co,:)= [il];
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
% b) Submatrix = 1x3
load est2filename1
nr=7;nc=7;
load filenameall
for l=1:length(est2filename1)
    A((l-1)*nr+1:l*nr,:) = filenameall((est2filename1(l)-1)*nr+1:
est2filename1(l)*nr,:);
end
clear filenameall
[n1,nc]=size(A);
nm=n1/nr;
mn=-1;mx=1;
co=0;
for il=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)**

```matlab
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
    end
end

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

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

```matlab
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
end

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