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Implications of Complex Connectivity Patterns, Disturbance, Allee Effects, and Fisheries in the Dynamics of Marine Metapopulations

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by

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Dedication

To God, my mum, dad, brothers, and sister.

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Thank you God for giving me strength in this journey and teaching me on the way that science and faith do not contradict because all knowledge comes from You.

Implications of Complex Connectivity Patterns, Disturbance, Allee effects, and Fisheries in the Dynamics of Marine Metapopulations

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Nearshore populations have been depleted and some have not yet recovered. Therefore, theoretical studies focus on improving fisheries management and designing marine protected areas (MPAs). Depleted populations may be undergoing an Allee effect, i.e. a decrease in fitness at low densities. Here, I constructed a marine metapopulation model that included pre- and post-dispersal Allee effects using a network theory approach. Networks represent metapopulations as groups of nodes connected by dispersal paths. With this model I answered four questions: What is the role of Allee effects on habitat occupancy? Are MPAs effective in recovering exploited populations? What is the importance of larval dispersal patterns in preventing local extinctions due to exploitation and Allee effects? Can exploitation fragment nearshore metapopulations?

When weak Allee effects are included, habitat occupancy drops as larval retention decreases because more larvae are lost to unsuitable habitat. With strong Allee effects habitat occupancy also drops at high larval retention because more larvae are needed to overcome the Allee effect. Post-dispersal Allee effects seem more detrimental for nearshore metapopulations. MPA effectiveness seems also lower in a post-dispersal Allee effect scenario. In overexploited systems, local populations that go extinct are also

less likely to recover even after protecting the whole coastline. In exploited nearshore metapopulations with Allee effects, local occupancy or the recovery of local populations depends not only on larval inflow from neighbor populations, but also on larval inflow for these neighbors. Nearshore metapopulations with intense fishing mortality and Allee effects may also suffer a decrease in dispersal strength and fragmentation. Population fragmentation occurs when large populations are split into smaller groups. A tool for detecting partitioning in a network is modularity. The modularity analysis performed for red abalone in the Southern California Bight showed that exploitation increases partitioning through time before the entire metapopulation collapses.

These findings call for research effort in estimating the strength of potential Allee effects to prevent stock collapse and assess MPA effectiveness, evaluating the predictability of local occupancy by centrality metrics to help identify important sites for conservation, and using modularity analysis to quantify the health of exploited metapopulations to prevent their collapse.

Table of Contents

List of Tables

List of Figures

Chapter 1: Simultaneous drivers of metapopulation persistence modulate the effectiveness of marine protected areas

INTRODUCTION

A major interest in ecology and conservation biology is to understand the factors determining the dynamics and persistence of populations. Given that many nearshore species are distributed in patches and have obligate dispersal stages, marine ecologists have used metapopulation concepts to study the relationship between larval connectivity and spatial structure in maintaining populations (e.g. Iwasa and Roughgarden 1986; Roughgarden and Iwasa 1986; Quinn et al. 1993; Morgan and Botsford 2001). More recent studies have further emphasized this approach when designing and assessing marine protected areas (MPAs; e.g. Kaplan et al. 2009; Costello et al. 2010; White et al. 2010a; Watson et al. 2011). Studies tackling MPA effectiveness have found that fisheries (e.g. Morgan and Botsford 2001; Kaplan et al. 2009), local extinctions (e.g. Man et al. 1995), and larval dispersal patterns (e.g. Costello et al. 2010) are all important in defining persistence and dynamics of nearshore populations. In turn, heavily exploited marine populations can exhibit population decrease at low densities, a phenomenon known as the Allee effect (Stoner and Ray-Culp 2000; Gascoigne and Lipcius 2004; Berec et al. 2007; Micheli et al. 2008). However, it is unknown how multiple biological, environmental, and anthropogenic drivers interact with each other to determine the dynamics of exploited nearshore populations with potential Allee effects. The present study has two objectives, (1) to assess the role of Allee effects, age at maturity, reproductive rate, larval dispersal patterns, environmental disturbance mortality, and fishing mortality on nearshore metapopulation dynamics, and (2) to evaluate MPA effectiveness in recovering exploited nearshore metapopulations undergoing Allee effects.

Traditionally, growth of marine populations has been modeled with negative density dependent functions. However, growing empirical evidence indicates that depleted marine populations, especially those with limited adult movement, may undergo Allee effects, a positive density dependent relationship (Stoner and Ray-Culp 2000; Gascoigne and Lipcius 2004; Berec et al. 2007; Micheli et al. 2008). Allee effects can occur in nearshore populations before and after larval dispersal (pre- and post-dispersal, respectively). Pre-dispersal Allee effects occur when a species that spawns into the water column depend greatly on the presence of conspecific adults for fertilization success (Denny and Shibata 1989). Here, very low population densities result in reproduction failure. For instance, abalone species (*Haliotis* spp.) are characterized by aggregative behavior during their spawning season (Shepherd 1986). When abalone densities decline, their reproductive aggregations and fertilization success diminish (Shepherd and Brown 1993). Other broadcast spawners, such as red and purple sea urchins, have shown a decline in fertilization efficiency with low male density (Levitan 2002). Post-dispersal Allee effects occur when the presence of conspecifics influences survival of juvenile stages. For example, larvae of red sea urchins increase their survival when they settle under the spine canopy of adults (Tegner and Dayton 1977). Therefore, low adult densities might diminish survival of post-larvae and early juveniles.

Despite the empirical knowledge, only a few marine theoretical studies include Allee effects (e.g. Quinn et al. 1993; Myers et al. 1995; Pfister and Bradbury 1996; Gascoigne and Lipcius 2004). Quinn et al. (1993) used a Michaelis-Menten form to study metapopulations of sea urchins with pre- and post-dispersal Allee effects. Pfister and Bradbury (1996) modeled red sea urchin fisheries with a post-dispersal Allee effect. Myers et al. (1995) applied a modified version of the Beverton-Holt spawning and recruitment function to test for the occurrence of Allee effects in exploited fish stocks. Gascoigne and Lipcius (2004) incorporated this function into a transition matrix to evaluate persistence of marine benthic organisms in scenarios with pre-dispersal Allee effects and fishing mortality. I used Gascoigne and Lipcius's approach to construct a marine metapopulation model for nearshore species with potential pre- and post-dispersal Allee effects.

Marine ecosystems are under pervasive environmental and anthropogenic disturbance. Although overfishing is arguably the major cause of extinction in marine systems (Dulvy et al.

2003) environmental disturbance can also cause fluctuations in population size and local extinctions (Reed et al. 2006). However, the general assumption is that background extinction does not occur in marine systems because of the broad dispersal potential of many species. Some empirical studies report the contrary. In coastal sediments, many macrobenthic species show seasonal changes in abundance and habitat use (Armonies and Reise 2003). These species occupy only a portion of their suitable habitats, implying colonization failure or local extinctions. In kelp communities, seasonal storms and El Niño can cause local extinctions of kelp populations and reduce the canopy (Burgman and Gerard 1990; Reed et al. 2006; Gaines et al. 2007). Strong waves can remove and kill sea urchins (Tegner 2001), and El Niño high temperatures can increase abalone mortality (Moore et al. 2011). The marine metapopulation model developed here includes environmental disturbance, which makes natural mortality uneven across the seascape. As mentioned above, fishing pressure is another important source of mortality in marine systems. Traditionally, modeling efforts have assumed constant fishing effort. An exception is Man et al. (1995) who used a probability of extinction caused by fishing to test the role of MPAs in recovering patches. Fishing mortality, however, is neither constant nor stochastic; it mainly focalizes depending on the area and type of fishing (Parnell et al. 2010). Unfortunately, precise information on fishing spatial patterns is rarely available. For the purpose of this study the present model assumes fishing pressure as constant across the system. Nevertheless, the model can input more precise, heterogeneous information of fishing mortality.

Local larval retention and larval dispersal patterns are also important drivers that have been extensively modeled in marine metapopulation studies. Local larval retention, the amount of larvae that return to their parental patch, determines self-replacement of local populations. When larval retention is insufficient, populations rely on larval immigration to persist (Cowen et al. 2006; Hastings and Botsford 2006; White et al. 2010a). Theoretical studies have traditionally modeled nearshore organisms as large patchy populations, where each local population draws from a common pool of larvae of unspecified origin (e.g. Iwasa and Roughgarden 1986; Roughgarden and Iwasa 1986). Currently, larval dispersal is modeled using a Gaussian dispersal kernel as a function of the species' pelagic larval duration (PLD; e.g. Kaplan et al. 2009; White et al. 2010a). Here, larval dispersal is often symmetric, diffusion of larvae generally peaks at the parental local population, and alongshore advection may or may not occur. All these approaches provide valuable insights into the role of larval dispersal in nearshore population dynamics. Nonetheless, there is still debate on how to emphasize the complexity of larval dispersal in marine metapopulations. Theoretical studies suggest that population connectivity patterns play a fundamental role in metapopulation dynamics. Population connectivity is the exchange of individuals among subpopulations of a metapopulations (Cowen et al. 2007). Bode et al. (2009) found that asymmetric patterns of connectivity can increase the probability of metapopulation extinction. In nearshore metapopulations, larval connectivity depends on the PLD of the species. Watson et al. (2011) further showed that every species has a particular pattern of larval connectivity which can result in a different scheme of persistence. However, the effects of complex larval connectivity patterns and local larval retention on the dynamics of marine metapopulations with Allee effects are still poorly understood. For this study, I constructed a network model to generate larval connectivity patterns.

Network theory (graph theory in mathematics) has been used in landscape ecology to explore and analyze fragmented landscapes and habitat connectivity (Keitt et al. 1997; Urban and Keitt 2001; Minor and Urban 2007). A network or graph represents habitat patches as a set of nodes and dispersal pathways as edges (Keitt et al. 1997). Network analysis has been extensively applied in other disciplines to identify connectivity structure, explain local and global patterns, locate influential nodes, and examine network dynamics (e.g. Freeman 1978; Wasserman 1994; Broder et al. 2000). Many nearshore fish and invertebrates form a network of larval connectivity among local populations. For this reason, network theory has been recently used to study larval connectivity patterns (Treml et al. 2008; Artzy-Randrup and Stone 2010; Kininmonth et al. 2010), highlight important patches for conservation (Watson et al. 2011) and evaluate MPA configurations (Kininmonth et al. 2011). Despite these efforts, the use of network tools in marine research is still minimal. I modified the network approach by Watts and Strogatz

(1998) and integrated it with the transition matrix described above (Gascoigne and Lipcius 2004). With this algorithm larval connectivity patterns can be simulated from regular (symmetric) to random (asymmetric), and larval retention can vary from zero to full retention.

MPAs have been proposed as effective tools against overexploitation to prevent extinction of protected and unprotected populations, and sustain surrounding fisheries. However, the effectiveness of MPAs in recovering populations has been questioned. Halpern (2003) showed in an empirical meta-analysis that MPAs were not as effective as expected. Out of 70 MPAs 37% did not increase density and 24-41% did not increase diversity. Michelli et al. (2008) also found that red abalone densities did not increase inside MPAs. It seems that the effectiveness of MPAs in increasing abundances is modulated by the life history of organisms. Quinn et al. (1993) found that the strength of pre- and post-dispersal Allee effects can change MPA effectiveness. Later, Costello et al. (2010) and Watson et al. (2011) showed that including complex larval connectivity patterns in MPA network design could improve MPA effectiveness. To evaluate the effectiveness of MPAs in recovering nearshore metapopulations I examined two species with contrasting life histories, red abalone and red sea urchin. Red abalone *Haliotis rufescens* is considered a short-distance disperser, whereas red sea urchin *Strongylocentrotus franciscanus* is a long-distance disperser. Both red abalone and red sea urchin release their gametes into the water and may show a pre-dispersal Allee effect at low densities (Denny and Shibata 1989; Shepherd and Brown 1993; Levitan 2002; Gascoigne and Lipcius 2004). However, there is only evidence of a potential post-dispersal Allee effect for red sea urchin (Tegner and Dayton 1977).

In this study, I applied a network approach to determine the importance of multiple drivers in marine metapopulation dynamics and assess MPA effectiveness in recovering species undergoing Allee effects. My simulations use a linearized version of the central California benthic system and its current MPA configuration made by Kaplan et al. (2009; Fig. 1.1). This seascape region is characterized by upwellings, eddies, poleward and equatorward currents, and temporal variation in spatial patterns (Chelton et al. 1988). The linearized benthos can be transformed into a network of nodes with different habitat attributes (suitable, unsuitable, protected, and unprotected). Evaluating the interaction of these biological, environmental, and anthropogenic drivers in the presence of different MPA schemes may further clarify the effectiveness of MPAs in sustaining and recovering marine metapopulations with contrasting life histories.

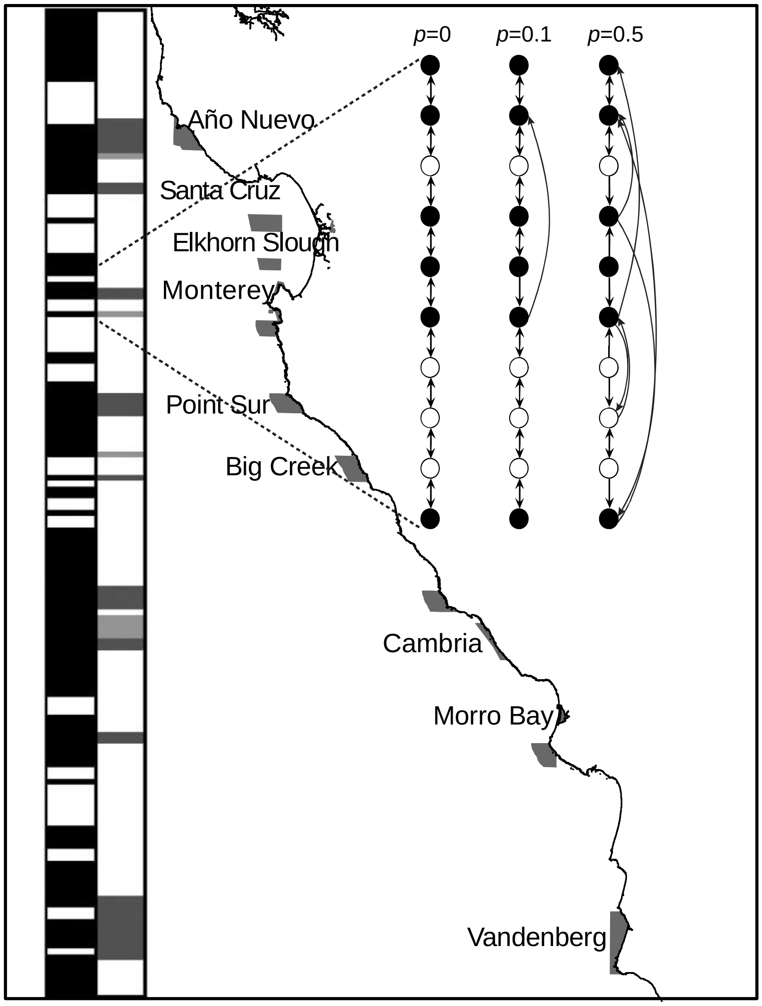
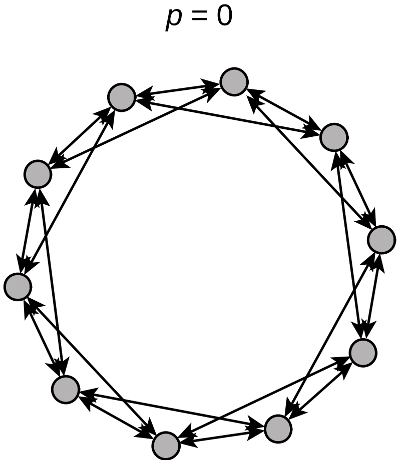


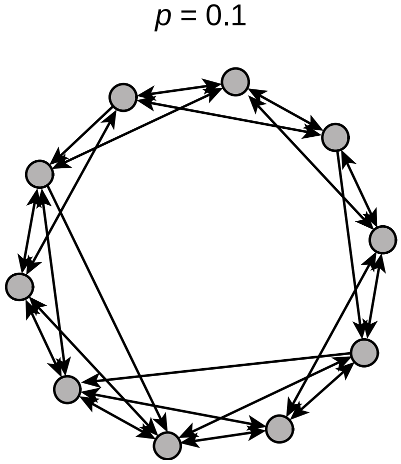
Figure 1.1: Linear representation of the central coast of California and mechanics of larval dispersal. Linearized benthic habitat corresponds to 0-30 m depth (first column from the left, where black areas are suitable habitat and white areas non-suitable habitat). MPAs are depicted in the second column from the left as grey areas. The linearized coast is divided into 2 km wide sections, each of which corresponds to a node in the network model. Edges (arrows) in the model represent potential dispersal pathways. Nodes (circles) are reconnected by randomizing the edges with a rewiring probability *p*.

METHODS

Model development

To simulate marine metapopulations I constructed an extension of the small world Watts-Strogatz model (Watts and Strogatz 1998). This new algorithm simulates local populations along the coastline as a linear set of nodes and larval exchange occurs through directed connections (Fig. 1.2). Larval dispersal pathways in the network can be modified by number and distance. Though the model itself is not limited to a circular layout, I chose a circular representation of the coastline to avoid edge effect.





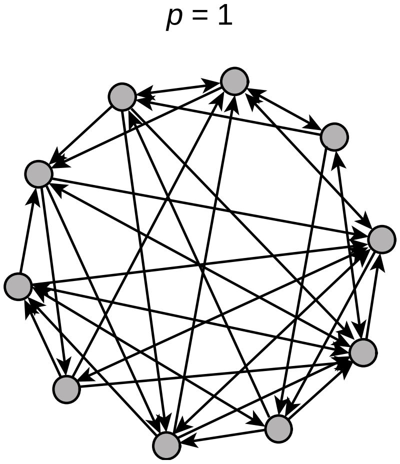


Figure 1.2: Mechanics of the directed small-world network algorithm in a one-dimensional lattice with 10 nodes. In the first network (left) rewiring probability p is 0, so each node is connected to its 4 nearest neighbors, 2 on each side. Increasing parameter p in the algorithm raises the probability of long-distance dispersal.

The coastal scenario used for the simulations corresponded to the upper subtidal region of the central coast of California (0–30 m deep). This part of the California coastline is approximately linear, making it easier to represent it as one-dimensional. Another important feature of this area is the presence of a set of MPAs. This region also comprises patches of rocky reefs of different sizes interspersed with soft-bottom areas (Fig. 1.1). Subtidal rocky reefs host kelp forest communities, characterized by a variety of benthic and demersal fish and invertebrates important for fisheries and conservation. Rocky-bottom areas were therefore chosen as suitable habitat in the simulations and all other seafloor types as unsuitable habitat. To obtain the number of nearshore sites to be simulated, I used the division of the upper subtidal in 2 km latitudinal bins published by Kaplan *et al.* (2009). In my network model, each bin corresponded to a single node. Thus, the resulting network included nodes with suitable and unsuitable habitat. Out of a total of 169 nodes, 115 had suitable habitat, 37 of which fell within MPAs (protected nodes) and 78 outside the MPAs (unprotected nodes).

I generated larval connectivity patterns with the network model and stored them in $n \times n$ matrices denoted by **C**, where n is the number of nodes or local populations within the network. The generated network begins with a regular ring lattice of n nodes ($n_1,\dots, n_i$) each connected to k adjacent nodes, $k/2$ on each side, through k links (n_i, n_j) with $j = \{i - k,\dots, i - 1, i + 1,\dots, i + k\}$ and $i \neq j$. For every node n_i the end of every link (n_i, n_j) is rewired with probability p (rewiring probability). The link is replaced with a randomly chosen link (n_i, n_l) where l is chosen from all possible values avoiding loops ($i \neq l$) and link duplication (n_i, $n_{l'}$) with $l' = l$ (Fig. 1.2). Thus, rewiring probability p controlled the asymmetry of the generated larval connectivity patterns and number of links k adjusted the number of nodes connected to a node of origin. As p approaches 1, the asymmetry in the connectivity pattern and the probability of long-distance dispersal increase. In the larval connectivity matrix **C**, column sums correspond to immigration and row sums to emigration. Local larval retention (LLR) is contained in the main diagonal of **C**. When LLR is 1 all individuals generated every year return to their parental site, whereas when LLR is 0 all individuals are exported to other sites. In the model, a percentage of juveniles generated every year stays in their parental node for LLR and the remaining are distributed according to the number of links k leaving the node ($(1 - \text{LLR})/k$). A constant LLR along the coastline is assumed for simplicity.

Juvenile and adult densities were stored in the $n \times 1$ vectors N_j and N_a, respectively. Pre- and post-dispersal Allee effects were included in the model with a modified Beverton-Holt function (Gascoigne and Lipcius 2004):

$$R_x = x^{\delta-1} / (1 + \beta \cdot x^{\delta}) \qquad (1)$$

where the parameter δ governs the strength of the Allee effect: when $\delta = 1$ the expression models standard negative density dependence; $\delta > 1$ leads to the Allee effect, where greater values intensify the effect (Fig. 1.3). β (= 45) is used as a scaling factor to make density curves look similar at high values.

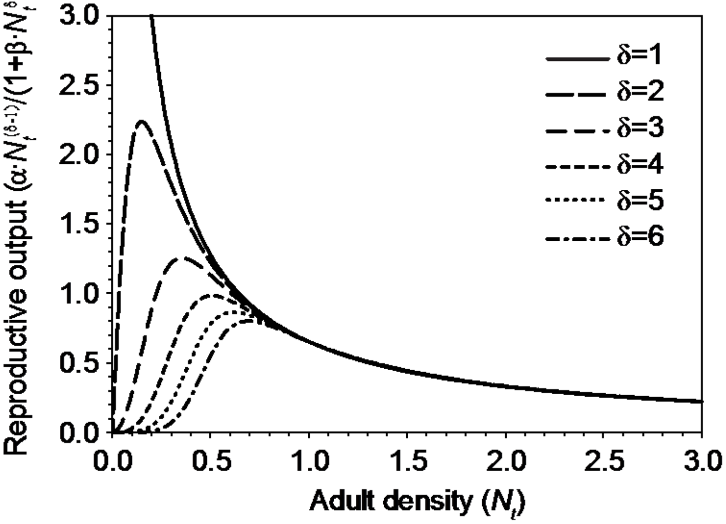


Figure 1.3: Effect of increasing the Allee effect strength δ in the modified Beverton-Holt function (modified from Gascoigne and Lipcius 2004).

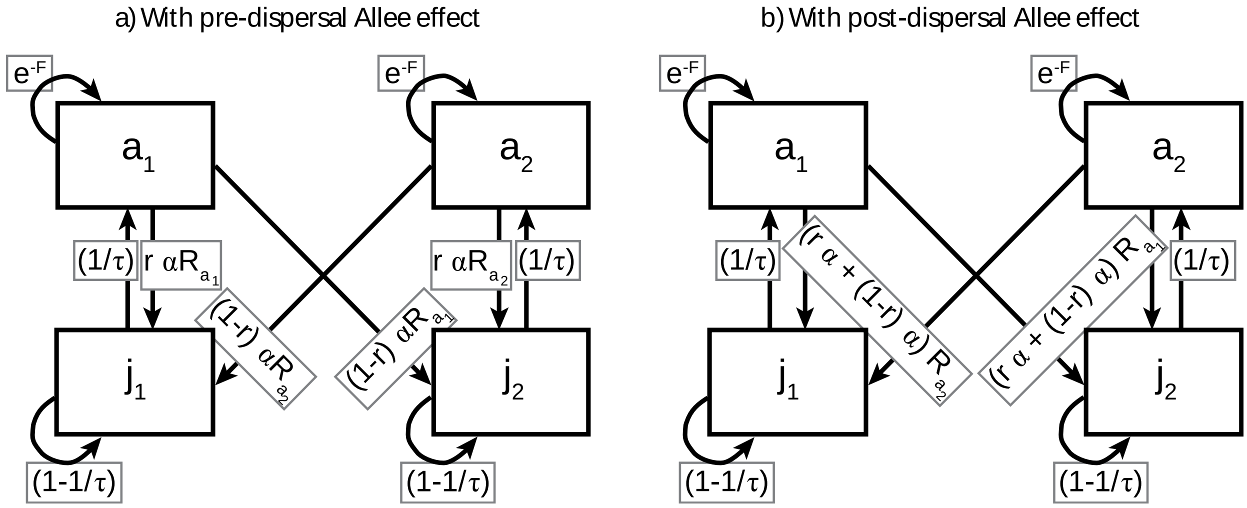


Figure 1.4: Schematic of two-patch metapopulation models with pre- and post-dispersal Allee effects. The schematic is based on equations 1 – 4 described in the Methods section excluding disturbance survival (*r* is local larval retention).

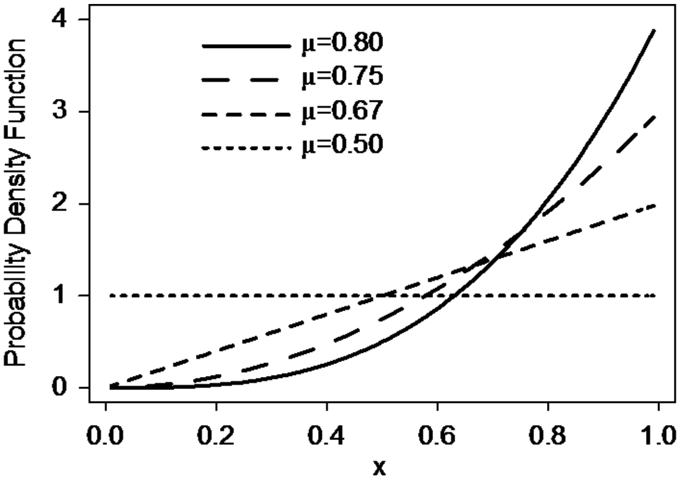


Figure 1.5: Curves obtained with the probability density function of the beta distribution for different shape parameters. The shape of the curve is set by 2 positive shape parameters, α and β, that give the mean of the distribution $\mu = \alpha/(\alpha + \beta)$.

Thus, in a marine metapopulation with a potential pre-dispersal Allee effect the growth equation for juveniles is:

$$N_{j,t+1} = \Big((1 - 1/\tau) \cdot N_{j,t} + C_{ji} \times \big(\alpha \cdot N_{a,t} \cdot \mathrm{R}_{N_a}\big)\Big) \cdot B_t \qquad (2)$$

with a potential post-dispersal Allee effect the growth equation for juveniles is:

$$N_{j,t+1} = \Big((1 - 1/\tau) \cdot N_{j,t} + \big(C_{ji} \times \alpha \cdot N_{a,t}\big) \cdot \mathrm{R}_{N_a}\Big) \cdot B_t \qquad (3)$$

and the growth equation for adults in both cases is:

$$N_{a,t+1} = \Big((1/\tau) \cdot N_{j,t} + e^{-F} \cdot N_{a,t}\Big) \cdot B_t \qquad (4)$$

where F is fishing mortality, α is the adjusted yearly *per capita* reproductive rate that accounts for the larvae and post-larvae lost in the first year (henceforth *per capita* reproductive output), τ is the age at maturity, and C_{ji} represents potential larval connectivity values from site *j* to *i* stored in a $n \times n$ matrix (Fig. 1.4). B_t is a $n \times 1$ vector containing random deviates drawn from a Beta distribution with mean μ. In the context of this study, these deviates corresponded to survival rate after environmental disturbance (henceforth disturbance) that affected local dynamics after dispersal. μ is the average fractional disturbance survival (Fig. 1.5). The beta distribution incorporates variation within the interval [0, 1] and is denoted by 2 positive shape parameters, α and β, that give the mean of the distribution $\mu = \alpha/(\alpha + \beta)$. I used the rbeta function from the stats package of the free software R (R Development Core Team 2009).

Evaluation of model parameters

To assess the role of multiple biological, environmental, and anthropogenic drivers in exploited nearshore metapopulations, I simulated two scenarios pre- and post-dispersal Allee effects. The drivers tested were four biological factors: Allee effect strength (δ), age at maturity (τ), adjusted yearly *per capita* reproductive rate (α), and local larval retention (LLR); three environmental factors: rewiring probability or asymmetry (p) number of links (k), and average fractional disturbance survival (μ); and one anthropogenic factor: fishing mortality (F).

There are many methods to evaluate the health of a metapopulation based on patch measurements (Ovaskainen and Hanski 2003), lifetime of a metapopulation (Frank and Wissel 2002), the sum of connectivity strengths (Urban and Keitt 2001), among others. I chose to measure habitat occupancy, i.e. the proportion of occupied suitable habitat at the end of a simulation time. Since natural and fishing mortalities combined with Allee effects can cause local extinctions, quantifying habitat occupancy is a good measure to determine nearshore metapopulation dynamics. In all simulations, every suitable node started as fully occupied. All simulations were arbitrarily run for 200 years. Every exercise was repeated 500 times to obtain the average habitat occupancy.

Fishing pressure and effectiveness of MPAs

To assess the impact of fishing pressure and the effectiveness of MPAs in recovering nearshore metapopulations, I used the model constructed here to simulate two nearshore species: red abalone *H. rufescens* and red sea urchin *S. franciscanus*. Both species are economically important, but red abalone is considered a short-distance disperser and red sea urchin a long-distance disperser.

Red abalones are dioecious species found on subtidal rocky reefs with kelp from Oregon to Baja California. They are distributed from the intertidal to the shallow subtidal in central and northern California (Leet et al. 2001). In Southern California, red abalones are found exclusively in the subtidal at 10-25 m deep (Leighton et al. 1974). Red abalone was abundant across the central coast of California, but intense fishing and the later return of sea otters, its main predator, depleted these populations (Karpov et al. 2000; Leet et al. 2001). This abalone can reach about 31 cm of shell length. Females reach maturity at sizes above 100 mm in northern California (Rogers-Bennett et al. 2004), which corresponds to older than 6 years old (Leaf et al. 2008). In this model, female abalones start spawning at 6 years old. The *per capita* reproductive rate (α) of 30 juvenile females per adult female corresponds to the largest size class estimated by Rogers-Bennett and Leaf (2006). As broadcast spawners, red abalone populations may undergo a pre-dispersal Allee effect at low densities (Denny and Shibata 1989; Shepherd and Brown 1993; Gascoigne and Lipcius 2004; Micheli et al. 2008). Red abalone larvae stay 4 – 7 days in the water column (Carlisle 1962). For this reason, this species is considered a short-distance disperser. Larvae of blacklip abalone *H. rubra* with a similar PLD can disperse up to 15 m (Prince et al. 1987; Shanks et al. 2003). Nevertheless, larval dispersal simulations have shown that red abalone larvae can potentially disperse farther (Watson et al. 2010).

Red sea urchins are also dioecious species found on subtidal rocky reefs from Alaska to Baja California (Ebert et al. 1999). They mainly occupy mid intertidal to deep subtidal regions to a depth of 50 m, but red sea urchins have been found in deeper regions (Kato and Schroeter 1985). This species is harvested in northern and southern California, but in central California their abundances are kept low because of predation by sea otters (Leet et al. 2001). In California, red sea urchin can reach about 130 mm. Red sea urchins can be induced to spawn at 1 – 2 years old or ~40 mm (Kato and Schroeter 1985), but at these ages the production of gametes is minimal. In my model, female sea urchins start spawning at 3 years old (similar to White et al. 2010b). Since there is no information on *per capita* reproductive rate (α) of any sea urchin species, I assumed the same value used for red abalone, 30 juvenile females per adult female. As broadcast spawners, sea urchins can also undergo a pre-dispersal Allee effect (Denny and Shibata 1989; Levitan 2002). Adults' spine canopy may also increase survival of post-larvae and early juveniles (Tegner and Dayton 1977). Therefore, it is possible that a post-dispersal Allee effect occurs at low adult densities. Red sea urchin larvae stay in the water column for 6 – 8 weeks (Kato and Schroeter 1985). They can potentially disperse long distances (~200 km according to Shanks et al. 2003) and are more likely driven by complex water current patterns.

To assess the impact of fishing pressure, habitat occupancy was measured in unexploited (F=0) and exploited (F=0.1) red abalone and red sea urchin metapopulations. This exercise was carried out for two scenarios: potential pre- and post-dispersal Allee effects. Given that red abalone is considered a short-distance disperser, I assumed a small number of links in the network (k=4, a minimum dispersal distance of 4 km). However, for red sea urchin, which is a long-distance disperser, I used a great number of links (k=12, a minimum dispersal distance of 12 km). For each scenario, I measured habitat occupancy after 200 years across the ranges of LLR (zero to complete larval retention) and rewiring probability (symmetric to completely random larval connectivity patterns).

To evaluate MPA effectiveness, habitat occupancy was quantified at increasing values of fishing mortality and suitable habitat as MPA (fraction of suitable habitat within MPAs). Fishing mortalities (F) ranged 0–0.5 (corresponding to survival 100% – 60.6%) and the fraction of suitable habitat in MPAs from 0 to 1. In this exercise, I assessed metapopulations of red abalone with a moderate pre-dispersal Allee effect (δ=3), and metapopulations of red sea urchins with moderate pre- and post-dispersal Allee effects (δ=3). To make the analysis more realistic and evaluate recovery from exploitation, I ran the simulations without MPAs for 30 years and with MPAs for 170 years to complete 200 years. MPAs were randomly chosen from the list of nodes with suitable habitat. The current MPA design in the central coast of California corresponds to ~32% of the coastline. For the short-distance disperser, red abalone, I assumed strong larval retention 90%, few dispersal links (k=4), and a more symmetric connectivity pattern with few long-distance dispersal shortcuts (p=0.05). For the long-distance disperser, red sea urchin, I assumed a greater number of dispersal links (*k*=12) and a more asymmetric connectivity pattern with many long-distance shortcuts (*p*=0.30). Cowen et al. (2006) obtained that self-recruitment of other long-distance dispersers vary from 9 to 55.2% of the total recruitment. Therefore, as local larval retention for red sea urchin I assumed an intermediate value 30% in the model (Table 1.1).

For these exercises, average fractional disturbance survival (μ) was assumed 0.80. Every simulation started with all suitable nodes as fully occupied and ran for 200 years. Every scenario was run 500 times to obtain the average habitat occupancy.

Table 1.1: Summary of red abalone and red sea urchin parameters chosen for the model to evaluate MPA effectiveness. References and detailed description of the values chosen is in the text.

Parameter	**Red abalone**	**Red sea urchin**
Local larval retention (LLR)	0.9	0.3
Number of connections (*k*)	4	12
Rewiring probability (*p*)	0.05	0.3
Age at maturity (τ)	6	3
Per capita reproductive rate (α)	30	30
Pre-dispersal Allee effect (δ)	3	3
Post-dispersal Allee effect (δ)	3	3
Average fractional disturbance survival (μ)	0.80	0.80

All codes were written in the free software R (R Development Core Team 2009). Because replicate runs produce stochastic results, I computed the average of replicates locally within the parameter space using a thin-plate spline (Fields Development Team 2006). The degree of smoothing is determined by cross-validation, which generates an optimal tradeoff between smoothing and retention of sharp transitions (see surface plots presented in Results).

RESULTS

Evaluation of model parameters

Simulated nearshore metapopulations could present either pre- or post-dispersal Allee effects. The coastal system simulated corresponded to a one-dimensional habitat configuration of the upper subtidal (0–30 m deep) of central California. A series of larval connectivity patterns were generated by changing two parameters of the network model: number of dispersal links (k), and rewiring probability (p, probability of long distance dispersal). I evaluated the role of Allee effect strength (δ), age at maturity (τ), *per capita* reproductive rate (α), local larval retention (LLR), rewiring probability (p), number of dispersal links (k), average fractional disturbance survival (μ), and fishing mortality (F) on metapopulation dynamics. Habitat occupancy after 200 years, i.e. the proportion of occupied suitable habitat, was quantified as the response variable.

The generic model results show that Allee effects modulate the response of nearshore metapopulations to larval retention. The response depends greatly on both strength and type of the Allee effect. In general, habitat occupancy decreases more rapidly in the post-dispersal Allee effect scenario than in the pre-dispersal Allee effect scenario (Figs. 1.6-1.8). As the Allee effect strength increases, habitat occupancy decreases (Fig. 1.6a-b). Given that more larvae may be lost when local larval retention decreases, habitat occupancy is expected to decrease as larval retention diminished. In fact, my results show that habitat occupancy tends to increase as larval retention increases. Strikingly, when larval retention is high, habitat occupancy decreases rapidly (Fig. 1.6).

Habitat occupancy decreases in metapopulations of species with moderate Allee effects (δ=3) that reproduce at older ages (Fig. 1.6c-d). Habitat occupancy also decreases with lower *per capita* reproductive output (Fig. 1.6e-f). In all cases, metapopulations with strong larval retention show lower habitat occupancy.

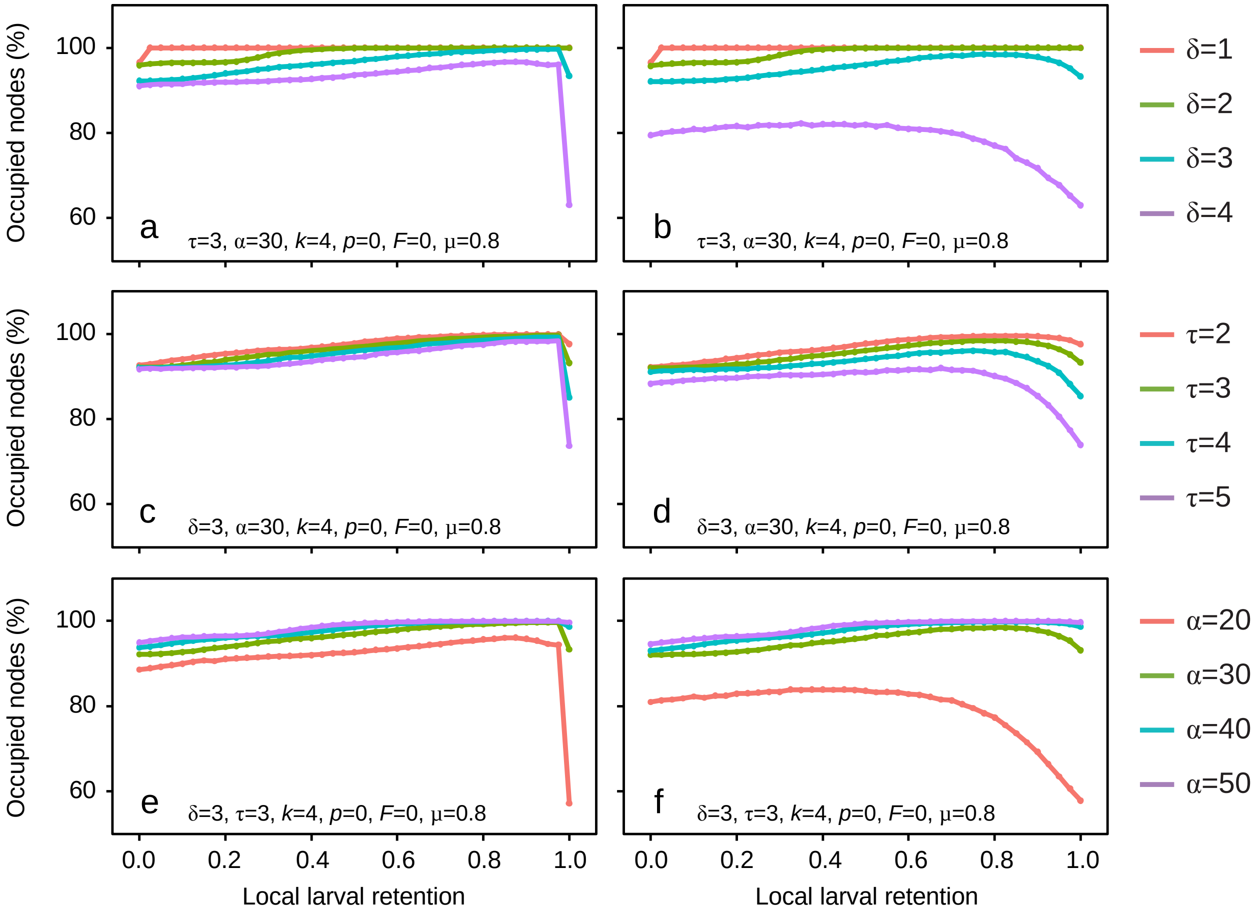


Figure 1.6: Habitat occupancy as a function of local larval retention and three other biological factors: Allee effect strength (δ), age at maturity (τ) and per capita reproductive output (α). (c-f) are results of metapopulations with moderate Allee effects (δ=3). Habitat occupancy decreases with stronger Allee effects (a and b), older age at maturity (c and d) and lower per capita reproductive output (e and f). Parameters used are in respective plots.

The parameters that control larval connectivity patterns in systems with potential Allee effects, rewiring probability (*p*) and dispersal links (*k*), show little effect on habitat occupancy (Fig. 1.7a-d). Here, the importance of asymmetric connectivity patterns (*p*) and the number of dispersal links (*k*) in the dynamics of nearshore metapopulations diminishes as local larval retention increases.

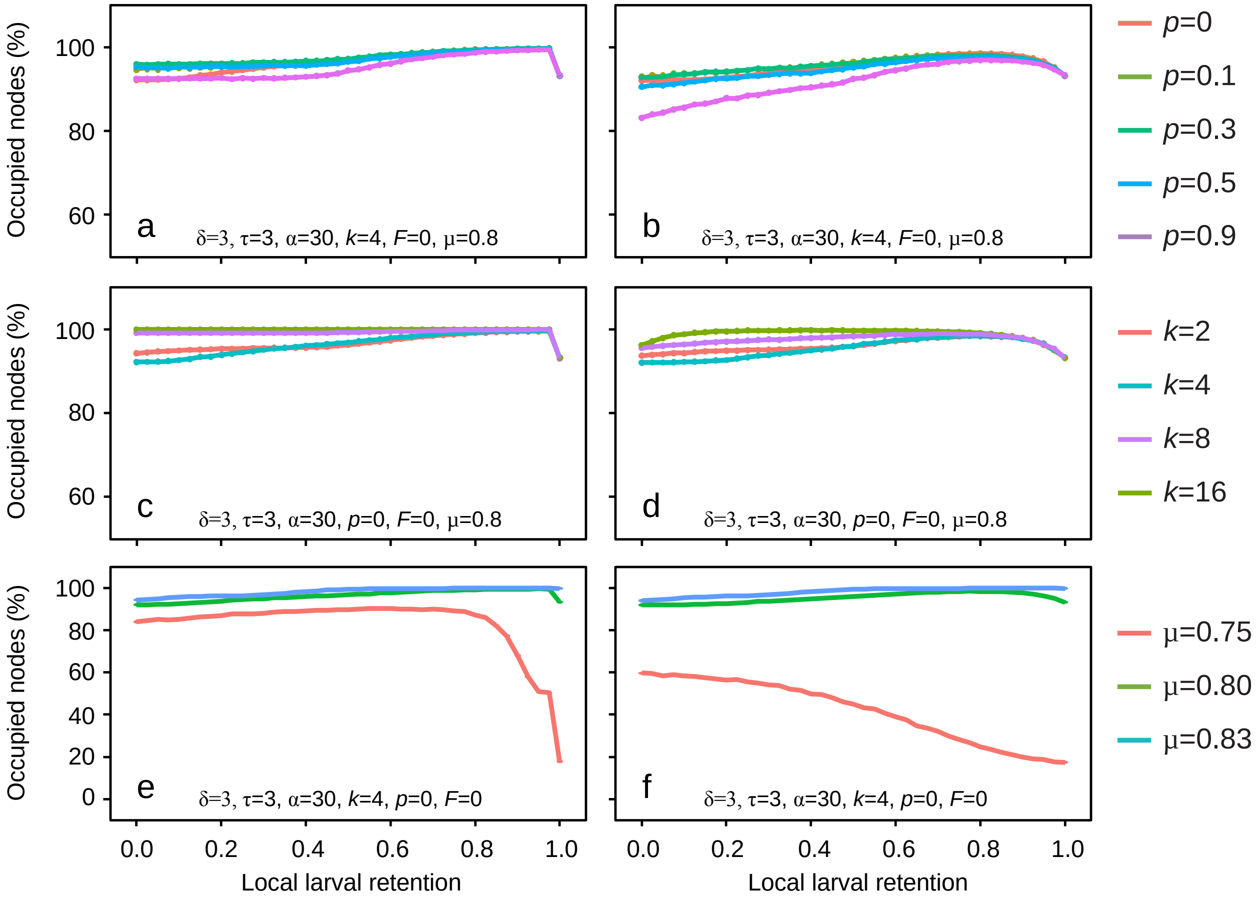


Figure 1.7: Habitat occupancy as a function of local larval retention, and three environmental parameters: rewiring probability (*p*), connection number (*k*) and average fractional disturbance survival (μ). (a-d) are results of metapopulations with moderate Allee effects (δ=3). Habitat occupancy decreases slightly with greater rewiring probability (a and b) and connection number (c and d), and rapidly with greater disturbance mortality (e and f). Parameters used are in respective plots.

Disturbance (Fig. 1.7e-f) and fishing mortalities (Fig. 1.8) have a strong impact on nearshore metapopulations with potential Allee effects. Habitat occupancy, especially in the post-dispersal Allee effect scenario, decreases rapidly as mortality increases. Nearshore metapopulations with high larval local retention show greater sensitivity to decreased survival (Figs. 1.7f and 1.8b). The peak of habitat occupancy is displaced towards lower larval retention as survival decreases. If fishing mortality is intense enough (*F*=0.20) habitat occupancy decreases as larval retention increases in the post-dispersal Allee effect scenario (Fig. 1.8b).

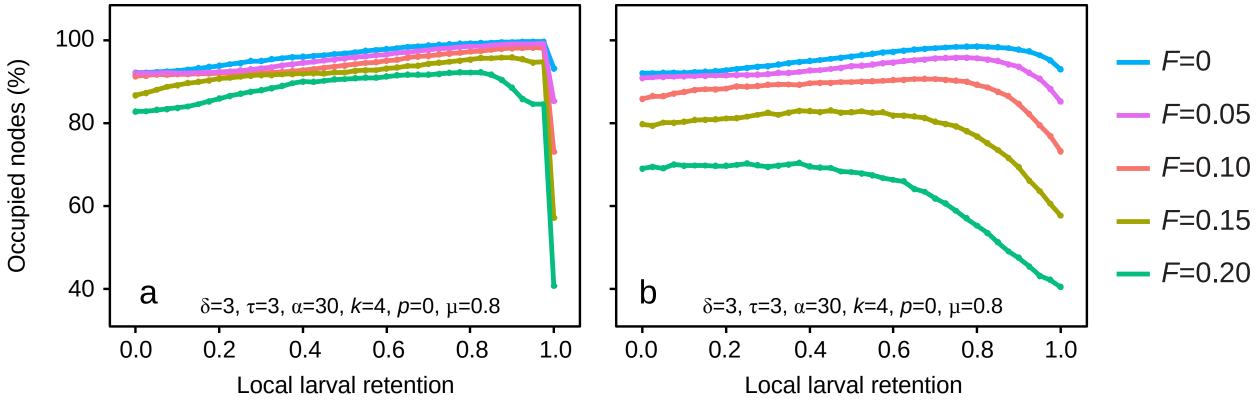


Figure 1.8: Habitat occupancy as a function of local larval retention and fishing mortality (*F*). Simulated metapopulations have potential moderate Allee effects (δ=3). Habitat occupancy decreases rapidly with more intense fishing mortality.

Fishing pressure and effectiveness of MPAs

To assess the impact of fishing pressure and the effectiveness of MPAs in recovering nearshore metapopulations with potential Allee effects, I contrasted two species: red abalone and red sea urchin. Abalone species tend to disperse shorter distances and reproduce at older ages compared to sea urchin species.

Changing asymmetry and local larval retention have little or no effect on unexploited red abalone metapopulations with pre-dispersal Allee effects (Fig. 1.9). Only strong larval retention (LLR > 95%) results in lower habitat occupancy. The highest habitat occupancy (~98%) occurs at around 90% of LLR. Larval retention determines how much larval connectivity patterns affect metapopulation dynamics. Fishing pressure can cause red abalone extinction if larval retention is low and larval connectivity patterns are more asymmetric (Fig. 1.9). Abalone metapopulations with high larval retention may suffer a decrease in habitat occupancy, but they do not go extinct. In a scenario where red abalone underwent a post-dispersal Allee effect, the metapopulation would be quickly depleted (Fig. 1.9).

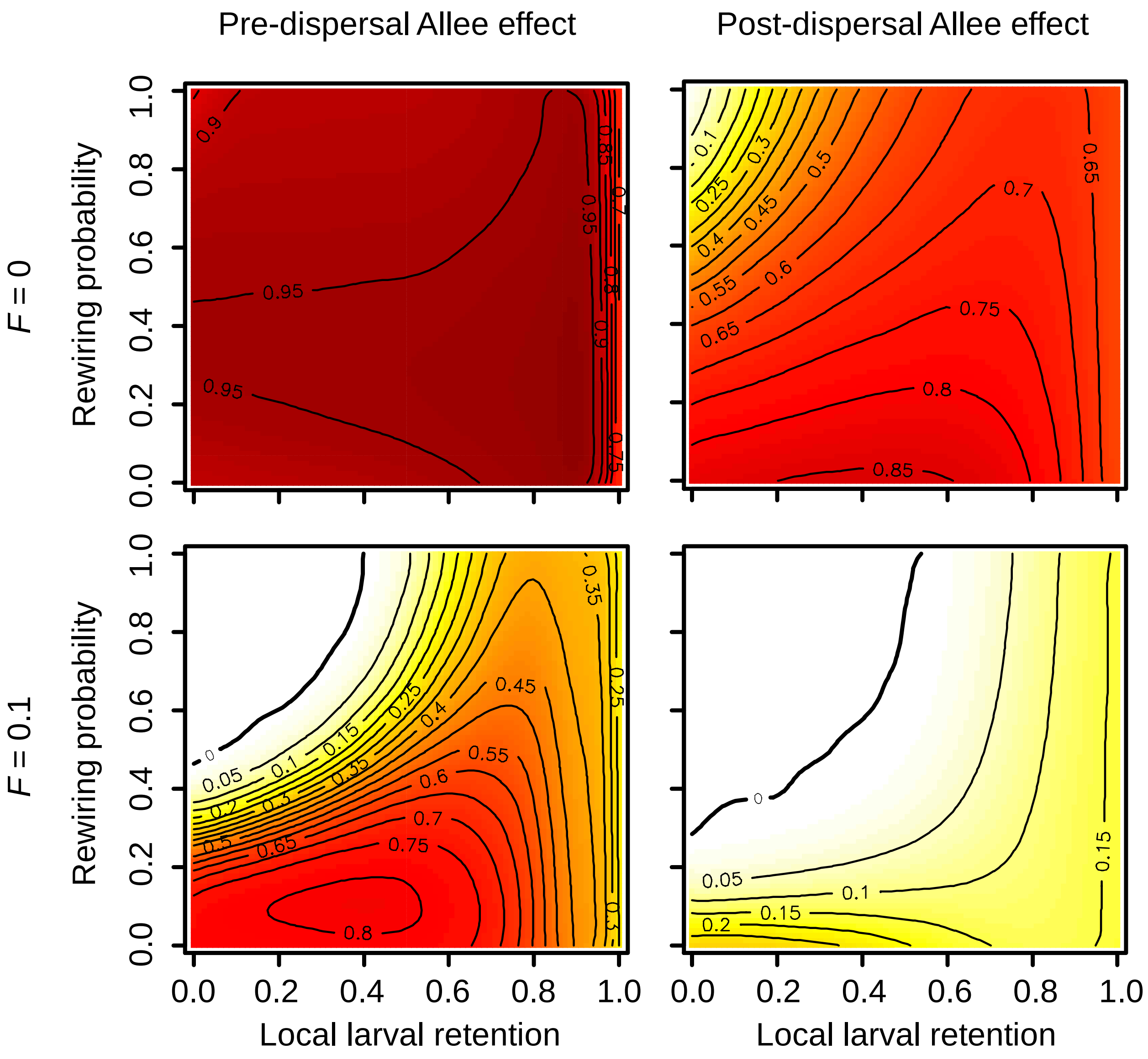


Figure 1.9: Habitat occupancy in red abalone metapopulations as a function of local larval retention, rewiring probability, fishing mortality and Allee effect. Fishing mortality (lower row) has a dramatic effect on habitat occupancy.

Dispersal asymmetry (rewiring probability) and larval retention have negligible effect on unfished red sea urchin metapopulations regardless of the Allee effect scenario (Fig. 1.10). Most suitable habitat remains occupied. As in the case of red abalone, fishing mortality has a greater impact in a scenario with a post-dispersal Allee effect. Nearshore metapopulations go extinct rapidly if larval connectivity is more asymmetric and larval retention is low.

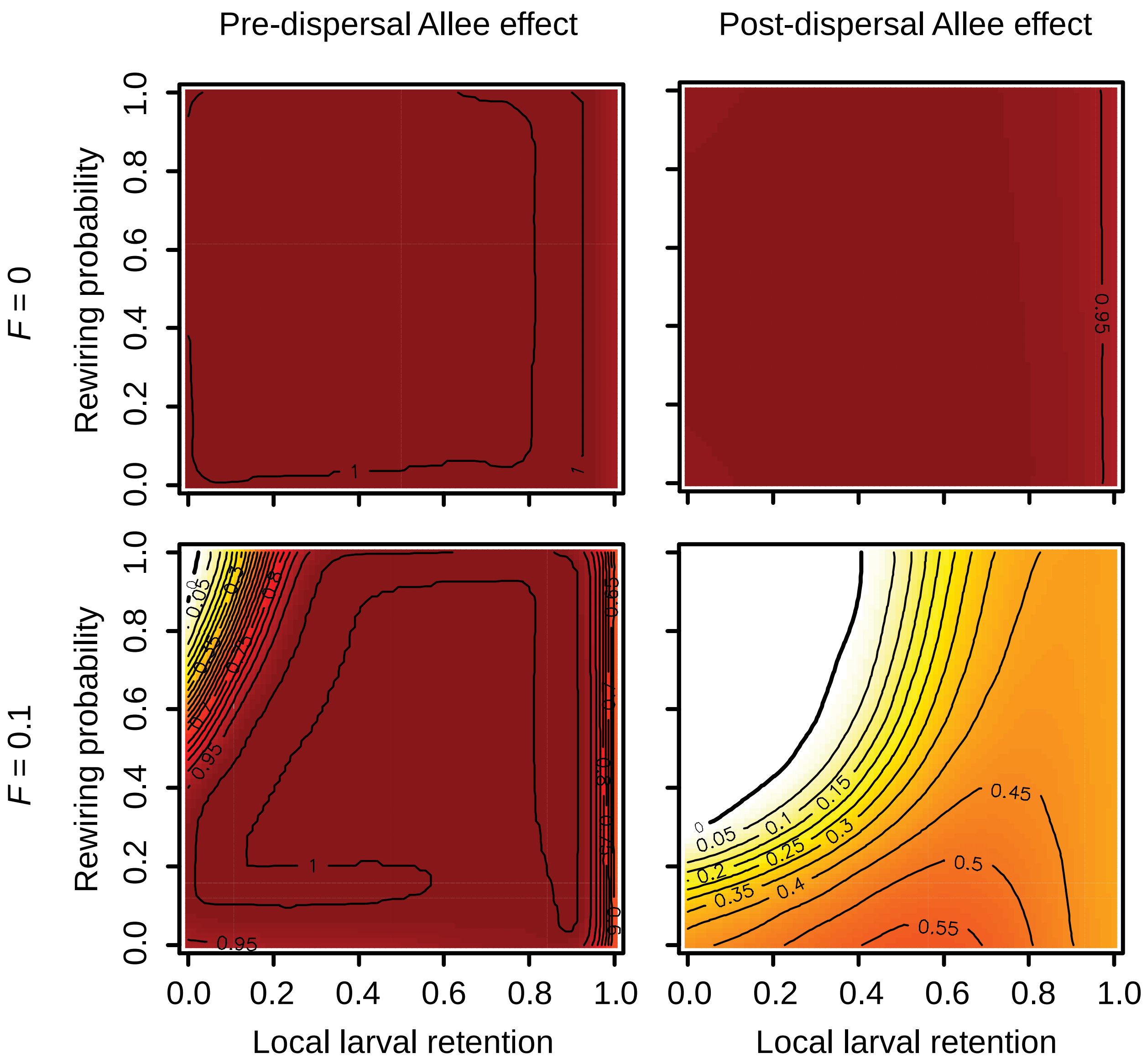


Figure 1.10: Habitat occupancy in red sea urchin metapopulations as a function of local larval retention, rewiring probability, fishing mortality (*F*) and Allee effect. Fishing mortality (lower row) has a dramatic effect on habitat occupancy, especially in the post-dispersal Allee effect scenario.

The results of the model are consistent with life history features of both red abalone and red sea urchin. The short pelagic larval duration (PLD) of red abalone (4–7 days) favors high larval retention and more symmetric larval connectivity patterns. Small amounts of larval exchange in abalone metapopulations with pre-dispersal Allee effects seem enough to keep less than half of habitat occupied after 200 years of light fishing (*F*=0.1; Fig. 1.9). However, the metapopulation does not completely go extinct. The long PLD of red sea urchin (6 – 8 weeks) favors low larval retention and more asymmetric larval connectivity patterns (rewiring probability). However, exploitation may have a greater impact on these metapopulations if they undergo Allee effects. As seen above, habitat occupancy decreases with greater stochasticity in the larval connectivity patterns (rewiring probability) and low larval retention (Fig. 1.10). In all cases, increasing fishing mortality will have a stronger impact in scenarios with high larval dispersal rates.

When assessing MPA effectiveness in recovering nearshore metapopulations from past exploitation, the results show some local populations may not recover from overexploitation (Fig. 1.11). Protecting a fraction of habitat from harvesting can prevent complete extinction of the metapopulation and in some cases increase habitat occupancy. Nevertheless, pre- and post-dispersal Allee effects have strong negative repercussions on abalone and sea urchin metapopulations, respectively (Fig. 1.11).

Protecting more suitable habitat areas improved abalone occupancy of unprotected areas, but MPA effectiveness depends greatly on fishing pressure before and after the establishment of protected areas (Fig. 1.11). Some protected populations seem to go extinct when fishing mortality exceeds 0.3 and the fraction of suitable habitat within MPAs is below 32% (similar to the current fraction of protected habitat in the central coast of California). Furthermore, red abalone metapopulations cannot fully recover from intense fishing pressure even after closing the entire coast to fishing. However, habitat occupancy decreases slowly as fishing mortality increases and the fraction of protected habitat decreases. Thus, complete metapopulation extinction can only occur when there are no protected areas.

Unlike abalone metapopulations, red sea urchin metapopulations with potential pre-dispersal Allee effects can completely recover and sustain fished areas after establishing MPAs (Fig. 1.11). This result is likely due to the younger age at maturity of red sea urchins compared to red abalone's age at maturity. Having 32% of habitat in MPAs (the current fraction of MPAs) seems to sustain populations in most of the suitable habitat. However, sea urchin metapopulations can still go extinct when less than 10% of habitat is protected. If red sea urchins undergo post-dispersal Allee effects, the fraction of protected habitat and fishing pressure make a big difference. Like in the case of red abalone, the metapopulation cannot fully recover from intense fishing, even after protecting the entire coast (Fig. 1.11). Unfortunately, in this scenario habitat occupancy decreases rapidly as fishing mortality increases and the metapopulation goes extinct.

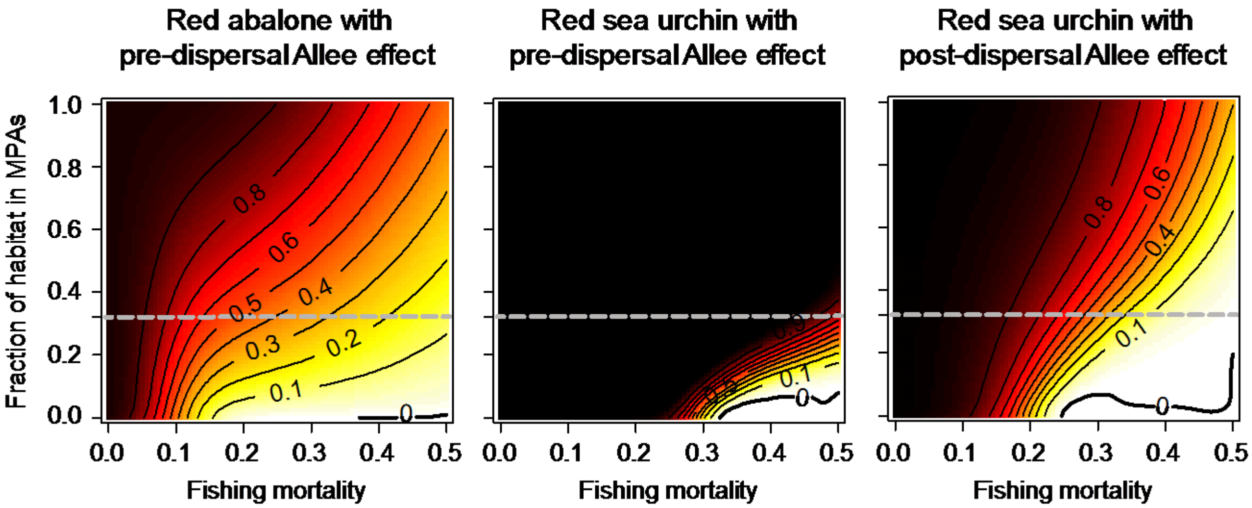


Figure 1.11: Evaluation of the effectiveness of the fraction of habitat in MPAs against fishing mortality in red abalone and red sea urchin metapopulations with moderate Allee effects. Isolines in the surface plot represent suitable habitat occupancy. Parameters used are in Table 1.

DISCUSSION

The network assessment presented here shows the interaction of different environmental (larval connectivity patterns, and disturbance), biological (age at maturity, *per capita* reproductive rate, pre- and post-dispersal Allee effect strength) and anthropogenic drivers (fishing pressure, and MPAs) and their importance on persistence of marine metapopulations. My results indicate that type and strength of an Allee effect changes the relationship between occupied habitat and larval retention. Habitat occupancy in metapopulations with potential Allee effects decreases with high larval retention; in the presence of fishing pressure, however, habitat occupancy also diminishes with low larval retention. Asymmetric connectivity patterns also seem to have a negative relationship with local occupancy, something more evident in the post-dispersal Allee effect scenario. Thus, long-distance dispersers such as sea urchins go extinct more rapidly under heavy fishing intensity. Species with potential post-dispersal Allee effects seem to be more susceptible to environmental and anthropogenic disturbance. Although the models oversimplify real scenarios, they show that MPAs may be a great tool to sustain overexploited marine metapopulations, but not always to recover original densities or empty patches. Further, species with potential post-dispersal Allee effects may be less likely to recover from overexploitation.

The combination of Allee effects and disturbance mortality generates metapopulation responses to local larval retention that differ from previous studies. Kaplan et al. (2009) showed that the patchy configuration of marine habitats favors persistence of short-distance dispersers, i.e. greater local larval retention favors the chances of settling on suitable patches. According to our results this relationship holds only when there is zero Allee effect or no disturbance. If marine metapopulations display spatial and temporal fluctuations, a condition that could be observed in nature due to environmental and demographic stochasticity, then species with limited dispersal capabilities are more sensitive to potential Allee effects. The mechanism supporting these results was described in Keitt et al. (2001): when an Allee effect occurs, empty patches need to receive enough immigration from their neighbors to pass above the Allee effect threshold if they are to reach an upper steady-state. Therefore, local populations that by chance decrease beyond the Allee effect threshold can only recover if there is enough larval supply from other sites.

Another major result is that persistence of fished metapopulations with Allee effects is ameliorated by greater larval dispersal rates. Kaplan et al. (2009) using a model with symmetric larval dispersal and zero Allee effects found that long distance dispersers (characterized by lower larval retention) had lower persistence due to increased larval loss to unsuitable areas. Quinn et al. (1993), on the contrary, showed that persistence of metapopulations without MPAs undergoing intense fishing and an Allee effect went extinct within the same number of time units regardless of the amount of dispersing larvae. I suggest that as fishing pressure intensifies the peak of occupied suitable habitat moves from greater to lower values of local larval retention because more larvae are necessary to surpass the Allee effect threshold and compensate for fishing mortality.

Interestingly, intense harvesting and Allee effects have an additional consequence: the system becomes more susceptible to complex connectivity patterns. Simulation studies have shown a negative correlation between dispersal asymmetry and metapopulation persistence (Vuilleumier and Possingham 2006; Bode et al. 2008). However, my results evidence that increased mortality and Allee effects can intensify this negative correlation and increase extinction probability of metapopulations with asymmetric, strong dispersal. Exploitation lowers population size below the Allee effect threshold, increases local extinction rate, and makes populations more dependent on emigration to persist. Asymmetric connectivity, in turn, may increase the loss of larvae to unsuitable habitat. I hypothesize that under these conditions extinction rate exceeds colonization probability and marine metapopulations are more likely to go extinct. This effect may be especially important for persistence of long-distance dispersers such as sea urchins, whose larvae have a long PLD and are more likely to be affected by the asymmetric movement of coastal and oceanic currents. Conversely, persistence of red abalone metapopulations, characterized by a short PLD, may be affected by fishing pressure and the Allee effect, but the effect of dispersal asymmetry may be weaker.

My results also indicate that post-dispersal Allee effects have a stronger negative impact on the persistence of unfished and fished metapopulations. These contrasting results may be explained by the fact that pre-dispersal Allee effects depend directly on the amount of adults, whereas post-dispersal Allee effects depend on both the number of immigrant larvae and the presence of adult conspecifics. As such, fishing pressure (which decreases adults), and poor larval retention and stochastic connectivity patterns (which decrease the arrival of larvae to suitable habitat) have a greater negative impact on metapopulations with a potential post-dispersal Allee effect.

The efficiency of MPA networks in recovering and sustaining marine metapopulations depends on the interaction among life history, larval dispersal, environmental disturbance, and fishing pressure before and after the establishment of protected areas. Kaplan et al. (2009) found that long-distance dispersers benefited less from the establishment of several small protected areas because larvae could fall in unsuitable or fished areas. When comparing a short- vs. a long-distance disperser, I found that within the same pre-dispersal Allee effect scenario long-distance dispersers may be more benefited because it ensures enough larval supply to prevent population sizes falling below the Allee threshold. Furthermore, species with earlier ages at maturity may do better under heavy harvesting because of their faster turnover rates. A crucial caveat is that some organisms, such as red sea urchins, may undergo an Allee effect during settlement (Tegner and Dayton 1977) which could make them more sensitive to fishing mortality than red abalone and less likely to recover. Another important caveat is that depleted populations especially of red abalone may persist within protected areas, but due to their limited dispersal rates these populations may never recover in areas where they go extinct. This scenario has been observed in the central coast of California where depleted populations of red and black abalones persist at very low densities within no-take reserves (Micheli et al. 2008). Micheli et al. propose that high natural mortality, the Allee effect, and possibly illegal take may be the reason for the failure of these populations to recover. I hypothesize that additionally low larval exchange may be preventing full recovery of these populations.

Whether these simulation results easily translate to natural systems needs to be further studied, but they enhance the importance of including biological, environmental, and anthropogenic features that are often overlooked when designing MPAs. This study shows that populations may be increasingly more dependent on the amount and patterns of larval connectivity. Even small amounts of incoming larvae, particularly from protected areas, can be crucial to prevent complete extinction of marine metapopulations. The excess of larval export can also make metapopulations more susceptible to strong asymmetric dispersal and post-dispersal Allee effects. An important point to consider when designing networks of MPAs is that small isolated patches may not receive enough larvae from other sites to prevent an Allee effect, and protecting such small patches or very small areas may not be a good strategy. Another important point is the estimation of the Allee effect parameter. Many marine populations are under heavy exploitation. Therefore, there is an increasing need to understand processes that affect population dynamics and population performance at low densities. Estimating the Allee effect parameter may help prevent depletion of marine populations and determine the effectiveness of plans to recover endangered species. The incorporation of processes such as the Allee effect or environmental disturbance may be decisive when planning resource management and measuring the effectiveness of MPAs.

Chapter 2: Complex connectivity patterns, fishing exploitation, and Allee effects change predictability of marine metapopulation persistence

INTRODUCTION

Population connectivity, the movement of individuals among patches, plays an important role in local and metapopulation dynamics, patch isolation, and resilience of populations to human exploitation (Hanski 1998; Botsford et al. 2001; Segelbacher et al. 2003). Theoretical studies increasingly suggest that quantifying patterns of larval connectivity is crucial for improving management of nearshore metapopulations (Botsford et al. 1994; Siegel et al. 2008; Costello et al. 2010; Watson et al. 2012). Watson et al. (2011) proposed using larval connectivity patterns to find crucial local populations for conservation. The importance of local populations however may change under heavy exploitation given that more productive patches are usually the target of fisheries. Intense fishing pressure can deplete populations causing Allee effects and local extinctions (Stoner and Ray-Culp 2000; Gascoigne and Lipcius 2004; Dulvy et al. 2003). The Allee effect is a decrease in reproduction or survival at low population densities (Stephens et al. 1999). The results from Chapter 1 show that nearshore metapopulations under exploitation and Allee effects depend greatly on larval dispersal to persist. In Chapter 2, I assessed the importance of larval connectivity patterns in preventing extinctions of local populations due to exploitation and Allee effects. To quantify the relationship between local population dynamics and larval connectivity I used network theory tools.

A network (called a graph in mathematics) is a collection of nodes joined by edges (Newman 2010). Network theory is the study of networks as representations of complex interacting systems. Networks have been used to represent patches of habitat as nodes and dispersal pathways as edges in a landscape (e.g. Keitt et al. 1997). In landscape ecology, network theory tools have been traditionally used to analyze fragmented landscapes. Network studies address issues regarding dispersal pathway lengths, dispersal patterns, and influential patches (Keitt et al. 1997; Urban and Keitt 2001; Minor and Urban 2007; Watson et al. 2011). Given that many nearshore fish and invertebrates disperse solely through a pelagic larval stage, nearshore metapopulations can be represented as networks of local populations connected by larval dispersal. The complexity of larval connectivity and the interest in designing networks of marine protected areas (MPAs) (Lubchenco et al. 2003; Gaines et al. 2010) has increase the application of network theory in marine ecology. Marine ecologists have applied network theory to describe larval connectivity patterns (Treml et al. 2008; Kininmonth et al. 2010), determine metapopulation persistence (Artzy-Randrup and Stone 2010), analyze MPA configurations (Kininmonth et al. 2011) and find critical regions to prevent stock collapse (Watson et al. 2011). Nevertheless, there is still plenty of scope for further use of network theory tools in marine ecology.

Network theory has a set of measures and metrics to quantify the structure of a network, i.e. the arrangement of nodes and edges (Newman 2010). One of these metrics is centrality. Within the scope of network theory, the concept of centrality is a family of network metrics used to identify the level of influence of individual nodes based on their structural position relative to other nodes in the network (Wasserman and Faust 1994; Estrada and Bodin 2008). In ecology, centrality metrics calculate the importance of individual patches in relation to their impact on the metapopulation (Urban and Keitt 2001; Estrada and Bodin 2008). Centrality also measures isolation and contribution of individual habitat patches to the landscape connectivity (Estrada and Bodin 2008; Economo and Keitt 2010). Centrality metrics have been proposed as tools to find regions for conservation. In nearshore metapopulations, Watson et al. (2011) identified local populations with high centrality whose protection can reduce the risk for stock collapse. Kininmonth et al. (2010) showed that individual coral reefs can play a consistent role in maintaining high larval flow through time. These consistently important reefs could be considered for conservation. In the present study, I evaluate the importance of centrality vs. isolation in determining local occupancy in exploited nearshore metapopulations. Local occupancy measures how frequently a particular site is occupied within a timeframe. The centrality of a patch depends on the emphasis on dispersal paths within and beyond the local neighborhood and how these paths are interpreted.

In metapopulations with complex connectivity patterns there are different patch configurations based solely on connectivity. Patches that receive more immigrants may be considered more important in the metapopulation. Patches may also benefit from dispersal paths beyond immediate neighborhood when they receive immigrants from strongly connected patches. Some patches may act as stepping stones, being the only link between different parts of a landscape and whose removal could break the landscape into smaller sections (Minor and Urban 2007). The distance of a patch to all other patches may also be an important factor for its occupancy. Any of these patch types may be more useful to predict those patches more resilient to intense fishing. Centrality metrics can categorize patches based on short range or long range connections and the interpretation of connection paths (Economo and Keitt 2010). I use centrality metrics to quantify the structural position of local populations in numerous sets of nearshore metapopulations. My objective here is to obtain graph metrics that better explain local occupancy in nearshore metapopulations. The findings of this study can be used for conservation planning.

METHODS

I used different centrality metrics that characterize the importance of local populations to see if they correlate with local occupancy in exploited nearshore metapopulations. Since several depleted coastal species have failed to recover possibly due to Allee effects, the scenarios tested include the Allee effect at reproduction. These metrics are calculated *a priori* (using the potential larval connectivity matrix) for different larval connectivity patterns and local larval retention.

Generating larval connectivity patterns and simulating metapopulation dynamics

The model used here to simulate nearshore metapopulation dynamics is the one constructed in Chapter 1. This algorithm incorporates fishing pressure and Allee effects to local dynamics and uses a directed network to generate dispersal patterns (Fig. 2.1). The directed network, my own version of a small world Watts-Strogatz network (Watts and Strogatz 1998), generates $n \times n$ matrices containing dispersal rates. These matrices are henceforth named *potential connectivity matrices*. Specifically, a potential connectivity matrix contains the proportion of individuals generated in node i that will disperse to node j for a metapopulation with n nodes. The main diagonal of the matrix contains the proportion of individuals generated in node i that return to the same node or local larval retention. For the purpose of this study, each node represents a local population. The first assumption of this metapopulation model is two life-stages, juveniles and adults. Adults start spawning at the age of maturity of the species (τ). Generated larvae spend some time in the water column depending on the species' pelagic larval duration (PLD). Surviving larvae settle to mature into juveniles and then into adults. In a period of a year, each adult produces α new juveniles (adjusted yearly *per capita* reproductive rate). The second assumption is that dispersal occurs after the first year, so that in the model the juvenile stage disperses according to the connectivity matrix. This assumption was made because in general the number of larvae generated and their survival rate is unknown. In this way, the larval stage can be simplified. The third assumption is that larval dispersal rates depend exclusively on local larval retention and the number of dispersal links from a focal node towards k other nodes.

The network model used here can generate a variety of network structures, from regular structures, where nodes are connected to their closest neighbors, to complex structures, where dispersal shortcuts are created between distant nodes. Network structure is controlled by a rewiring probability p that increases the number of dispersal shortcuts and the asymmetry of the network. The number of links leaving a node k remains constant. Because individuals that reach unsuitable habitat are lost and unsuitable habitat remains empty, rows and columns of the potential connectivity matrix that correspond to unsuitable habitat are set to zero. Nodes that contain unsuitable habitat are also set to zero density in every time step. The working system corresponds to the subtidal rocky reefs off the central coast of California. I also used the assumptions from Chapter 1 based on biological information of two different sedentary invertebrates, red abalone and red sea urchin (Table 1.1).

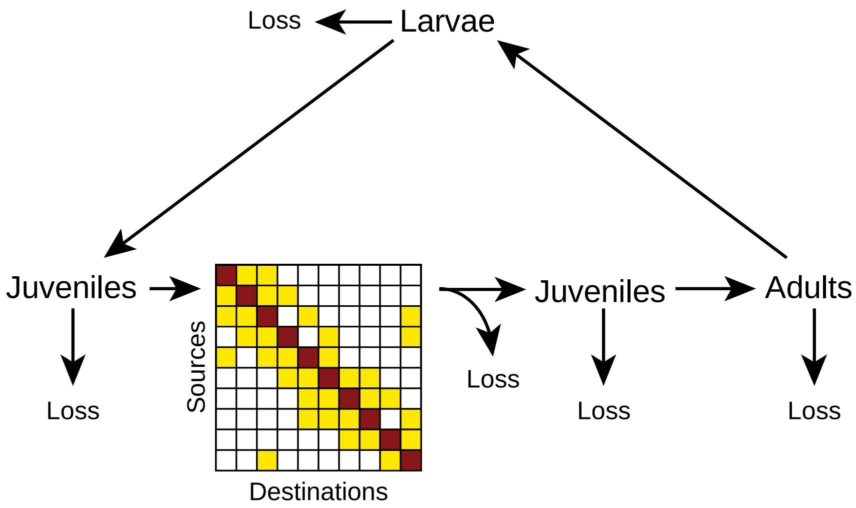


Figure 2.1: Conceptual flow chart of the metapopulation model. Within a year most larvae die and some settle to become juveniles. Juveniles can reach suitable or unsuitable habitat depending on the potential connectivity matrix. Population densities in unsuitable habitat are set to zero. Juveniles are prone to disturbance mortality, and adults to disturbance mortality and fishing.

Calculating the centrality metrics

Within the scope of network analysis, node centrality is the inverse of node isolation (Economo and Keitt 2010). In a seascape, it is expected that populations receiving more larvae stay occupied for a longer time compared to more isolated populations. However, direct inflow of larvae may not be the only factor determining local occupancy. Local occupancy may depend on the importance of the local populations that provide the larvae or the position of a local population in the seascape. Centrality captures these particular features within a network structure. To quantify the importance of a node in a marine metapopulation, I chose three of the most common centrality measures used, degree, betweenness, and closeness, and two less commonly used, Kleinberg’s hub and authority scores.

Degree centrality is the number of links connected to a node or the sum of their weights (Fig. 2.2). In directed graphs, each node has in-degree and out-degree, which are the sum of incoming and outgoing links respectively. In marine metapopulations of sedentary benthic organisms, each link corresponds to the flux of larvae from one site to another. I chose weighted in-degree (henceforth *degree*) because it measures the immediate amount of immigrants that a particular site receives. As mentioned above, local occupancy should be higher as larval inflow increases (high degree), especially if local populations require larval supply to surpass the Allee effect threshold to persist. In turn, local populations with low degree may be more vulnerable to extinction. To measure weighted in-degree, I used the function degree() of the igraph package for the R software (Csardi and Nepusz 2006).

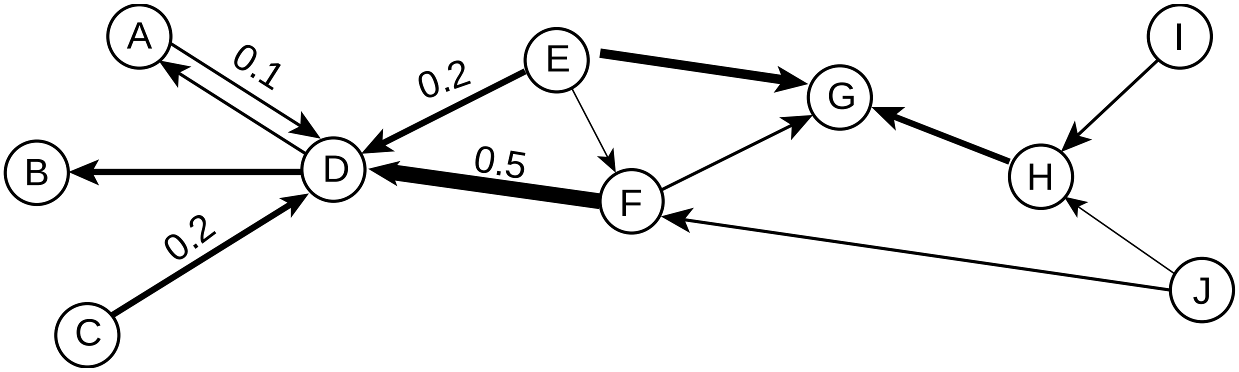


Figure 2.2: Illustration of a weighted directed graph, where A-I are the nodes and arrows are the edges. The weighted in-degree is the sum of the incoming connection weights (1.0 for node D). Nodes D and G, pointed by other nodes with high centrality, are authorities. Nodes E and F are important nodes providing strong connections to authorities D and G. Node D, which connects two sides of the network, has high betweenness centrality.

Besides direct larval inflow, local occupancy may also increase if the local populations that supply larvae also receive a great amount of larvae. Here, the centrality measure should consider direct and indirect larval dispersal paths. Eigenvector centrality is a metric that ranks nodes based on the importance of their neighbors (Newman 2003). However, it works best for undirected networks. There are several variants of the eigenvector centrality that can be used for directed networks. Kleinberg put forward the idea of two different centralities, *authorities* and hub (Kleinberg 1999). Authorities give a node a high score if it is pointed by other nodes with high centrality as well (nodes D and G in Fig. 2.2). Hubs accords a node a high score if it points to others with high authority centrality (nodes E and F in Fig. 2.2) (Kleinberg 1999). Authority and hub scores are defined as the principal eigenvector of $\mathbf{A}^T\mathbf{A}$ and $\mathbf{A}\mathbf{A}^T$ respectively, where $\mathbf{A}$ is the adjacency matrix of the network. In a nearshore metapopulation, authorities are patches that receive larvae from patches that also receive many larvae, and hubs are patches that sustain important patches. To calculate hubs and authorities of the network, I used the functions hub.score() and authority.score() from the igraph package (Csardi and Nepusz 2006).

The previous centrality measures rank nodes based on the amount of dispersal. A very different concept of centrality is *betweenness centrality*, which measures the number of geodesic paths that cross a node to connect other nodes (Freeman 1978). In a landscape, some patches connect different parts of the landscape which otherwise would be isolated; an example is node D in Fig. 2.2 (Minor and Urban 2007). These patches are known as stepping stones. I used betweenness given that local occupancy may also increase in nodes where more dispersal paths lie. The function used from igraph was betweenness() set for weighted directed graphs (Csardi and Nepusz 2006).

Another different centrality measure is *closeness centrality*, which scores nodes based on how close they are to all other nodes in the network (Freeman 1978). This measure identifies patches that have a more central position in the landscape and from where dispersal can occur more quickly. Given that the system evaluated here has disconnected components, I used a modification of the original closeness equation, the sum of inversed distances to all other nodes (Opsahl et al. 2010). The tnet package from R contains the function closeness_w() that applies this modified equation and calculates closeness measures for weighted directed networks (Opsahl 2009).

Correlation analysis

To find out whether network metrics can be used to evaluate marine metapopulation dynamics undergoing exploitation and Allee effects, I calculate Spearman's rank correlation coefficients of the set of network metrics and local occupancy. Spearman's rank correlation coefficient is a nonparametric measure that assesses whether two variables relate in a monotonic function, i.e., when one variable increases so does the other and vice-versa. I estimate these centralities on the potential matrices where connections coming from or going to unsuitable habitat are removed. Local occupancy is measured by using the number of times that densities within a particular node n_i, initially fully occupied, fall below 1×10^{-4} within 1,000 years.

Occupancy vs. local larval retention and rewiring probability

Correlation coefficients are calculated between average time of local occupancy and the centrality metrics described above (degree, authorities, hubs, closeness, and betweenness) for 10,000 initial conditions randomly chosen within the ranges of local larval retention and rewiring probability. Greater rewiring probability increases the amount of dispersal shortcuts in the metapopulation. I compare marine metapopulations with different numbers of larval connections (k=4, 12, 40). All simulated metapopulations have the same number of nodes with suitable (115) and unsuitable habitat (54), the same fishing mortality (F=0.35), Allee effect strength (δ=3), *per capita* reproductive rate (α=30), age at maturity (τ=3), and average fractional disturbance survival (μ=0.83), but differ in the number of connections k. I fitted a thin plate splice surface to the occupancy results for each scenario. The degree of smoothing is determined by cross-validation, which generates an optimal tradeoff between smoothing and retention of sharp transitions (Fields Development Team 2006).

Occupancy vs. fishing mortality

The analyses was carried out for two types of metapopulations: red abalone and red sea urchin. Red abalone is characterized by a short PLD and an old age at maturity (Carlisle 1962; Rogers-Bennett et al. 2004). Red sea urchin on the other hand has a longer PLD and starting reproducing at younger ages (Kato and Schroeter 1985). The values used for the model parameters are similar to those in Chapter 1 (Table 1.1). Therefore, in the model red abalone had high local larval retention (LLR=0.90), few dispersal shortcuts (*p*=0.05), few dispersal paths (*k*=4), and old age at maturity (τ=6). Red sea urchin had low local larval retention (LLR=0.30), several dispersal shortcuts (*p*=0.30), various dispersal links (*k*=12), and early age at maturity (τ=3). The other parameter values are the same for both species: the adjusted yearly *per capita* reproductive rate (α=30), the Allee effect strength (δ=3), and the average fractional disturbance (μ=0.83). The correlation analyses are performed at many different initial values of fishing mortality. Every exercise was repeated 10,000 times to obtain the average local occupancy.

RESULTS

Correlation analysis

Harvesting affects average time of local occupancy in nearshore metapopulations greatly depending on the rewiring probability, which creates dispersal shortcuts, and local larval retention (Fig. 2.3). In nearshore metapopulations with few dispersal paths (*k*=4), average time of local occupancy decreases rapidly as dispersal shortcuts become more frequent. Here, more habitat stays occupied for a longer time. However, strong larval retention (above 0.8) results in shorter average local occupancy. This relationship changes as the number of dispersal links increase. The first change is that local occupancy increases within the upper range of larval retention (above 0.8). The second change is that local occupancy becomes more even across the values of rewiring probability. Here, greater average local occupancy is found within the intermediate range of larval retention.

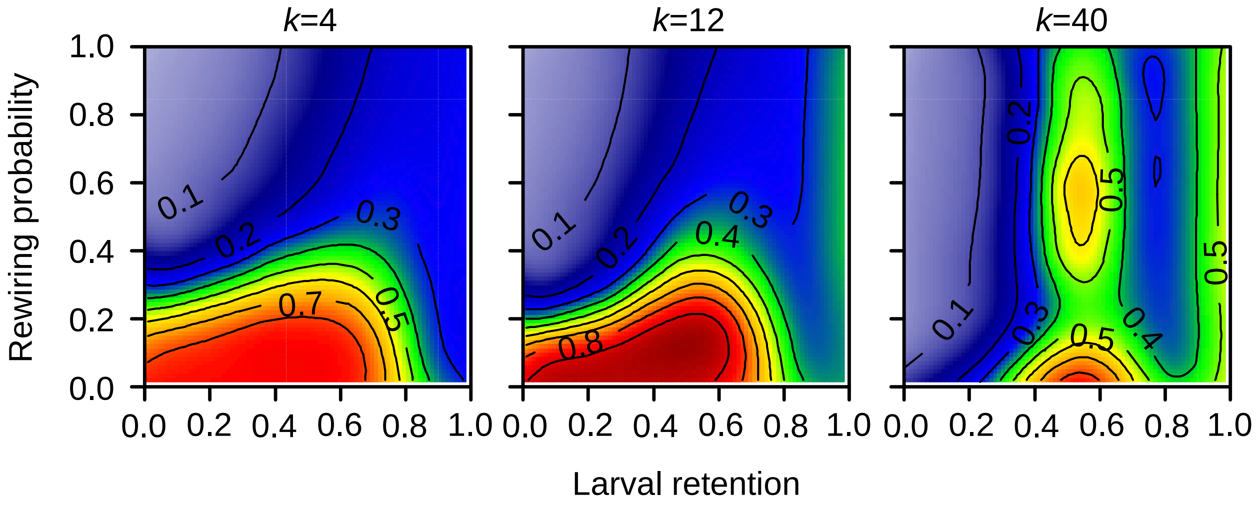


Figure 2.3: Average time of local occupancy as a function of local larval retention and rewiring probability in harvested marine metapopulations with Allee effects. Fishing mortality (F=0.35) has a dramatic effect on habitat occupancy as larval connectivity asymmetry increases. Isolines in the surface plots correspond to average time of local occupancy.

Occupancy vs. local larval retention and rewiring probability

The first experiment evidences the importance of connectivity patterns and local larval retention on local occupancy in metapopulation with intense fishing mortality (F=0.35) and moderate Allee effects (δ=3). The predictive power of all centrality measures is maintained more or less constant across the larval retention values tested except when local larval retention is extremely high (Figs. 2.4-2.8). The number of dispersal paths (k) in the metapopulation also has a great influence on predictive power. However, the results depend greatly on the rewiring probability (p) which creates more dispersal shortcuts as it approaches one.

Among all centrality metrics, degree, authorities, and betweenness correlate better with local occupancy when nearshore metapopulations have fewer dispersal paths (Figs. 2.4-2.5, 2.8). However, as the number of dispersal paths go up and rewiring probability stays below 0.5, authorities, hubs, and closeness predict better local occupancy (Fig. 2.5-2.7). If rewiring probability is above 0.5, correlation coefficients drop drastically.

The results show that centrality metrics that measure local (degree) and beyond local incoming dispersal paths (authorities) seem to predict well the dynamics of exploited nearshore metapopulations (Figs. 2.4-2.6). Degree works best for systems with few dispersal paths (*k*=4; Fig. 2.4). Kleinberg's authorities reach high correlation coefficients (above 0.6) regardless the number of dispersal links (Fig. 2.5). Nonetheless, low correlation values occur in systems where dispersal paths (*k*=40) and shortcuts (*p*>0.5) are frequent. Kleinberg's hubs, which gives good scores to nodes that receive and provide larvae to important nodes, also show strong correlation. However, these values decrease as the number dispersal shortcuts increase (rewiring probability approaches one), regardless the number of dispersal links (Fig. 2.6).

Betweenness and closeness show correlation coefficients below 0.4 in most of the parameter ranges tested. Betweenness seems to be a good metric only when there are few dispersal paths in the metapopulation (*k*=4; Fig. 2.8). Closeness on the contrary appears to work better when there are numerous dispersal paths in the metapopulation (*k*=40; Fig. 2.7).

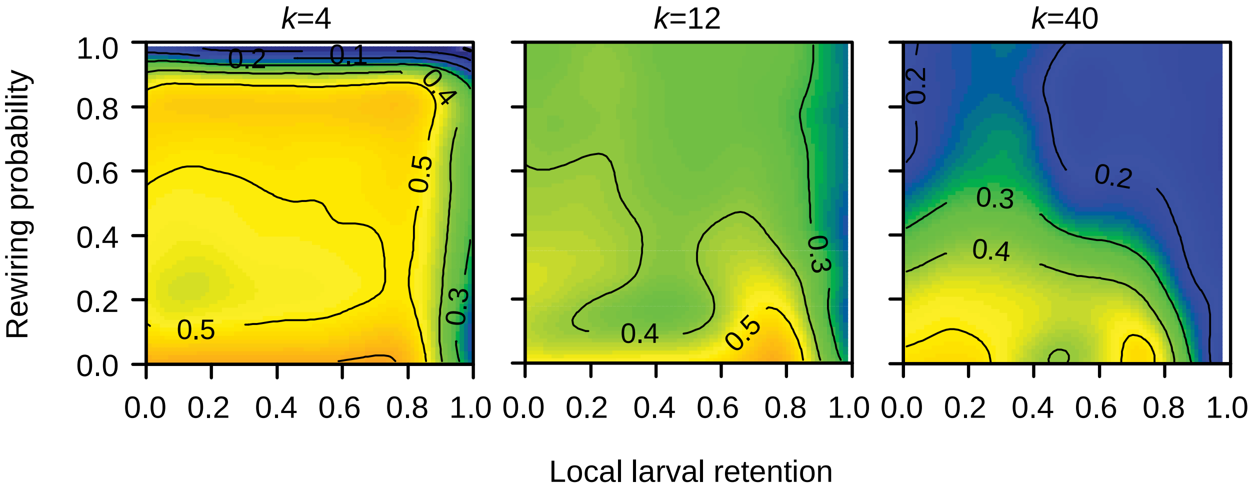


Figure 2.4: Performance of degree centrality. Spearman rank correlation coefficients with local occupancy at different initial conditions of local larval retention, rewiring probability (dispersal shortcuts), and connection number (*k*). Isolines in the surface plots correspond to average correlation coefficients.

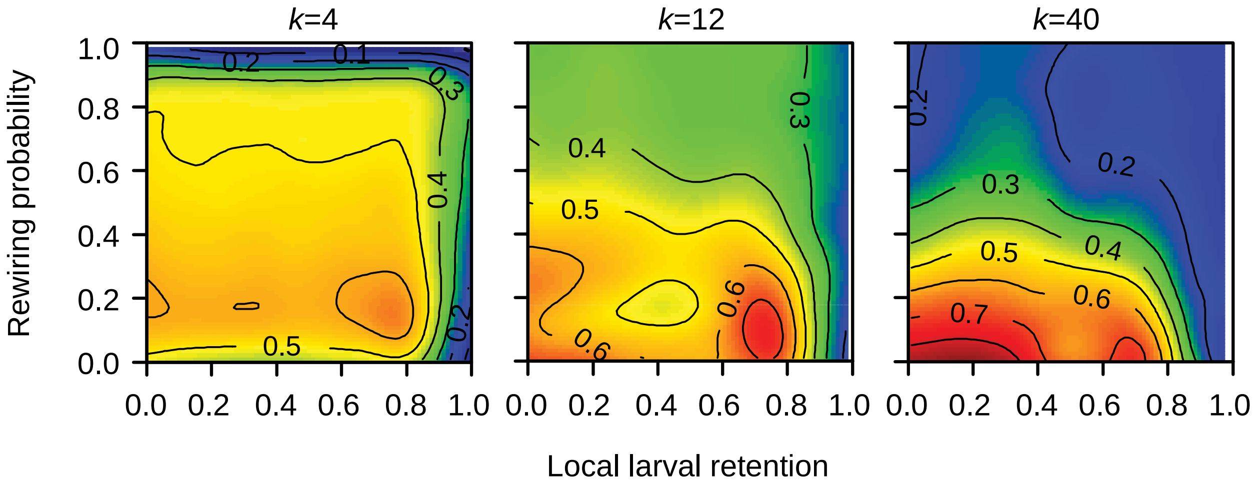


Figure 2.5: Performance of Kleinberg's authority scores. Spearman rank correlation coefficients with local occupancy at different initial conditions of local larval retention, rewiring probability (dispersal shortcuts), and connection number (*k*). Isolines in the surface plots correspond to average correlation coefficients.

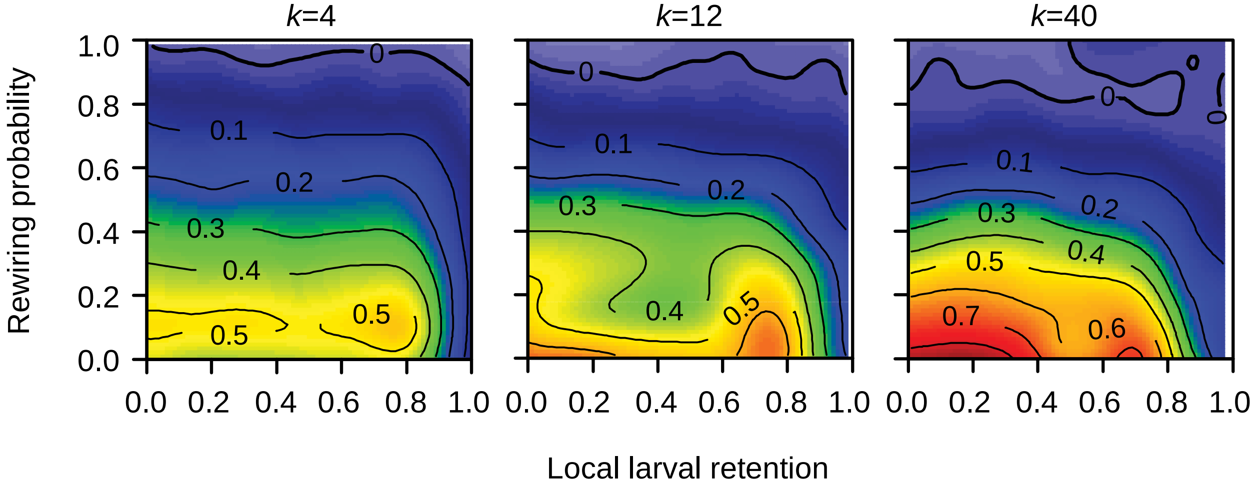


Figure 2.6: Performance of Kleinberg's hub scores. Spearman rank correlation coefficients with local occupancy at different initial conditions of local larval retention, rewiring probability (dispersal shortcuts), and connection number (*k*). Isolines in the surface plots correspond to average correlation coefficients.

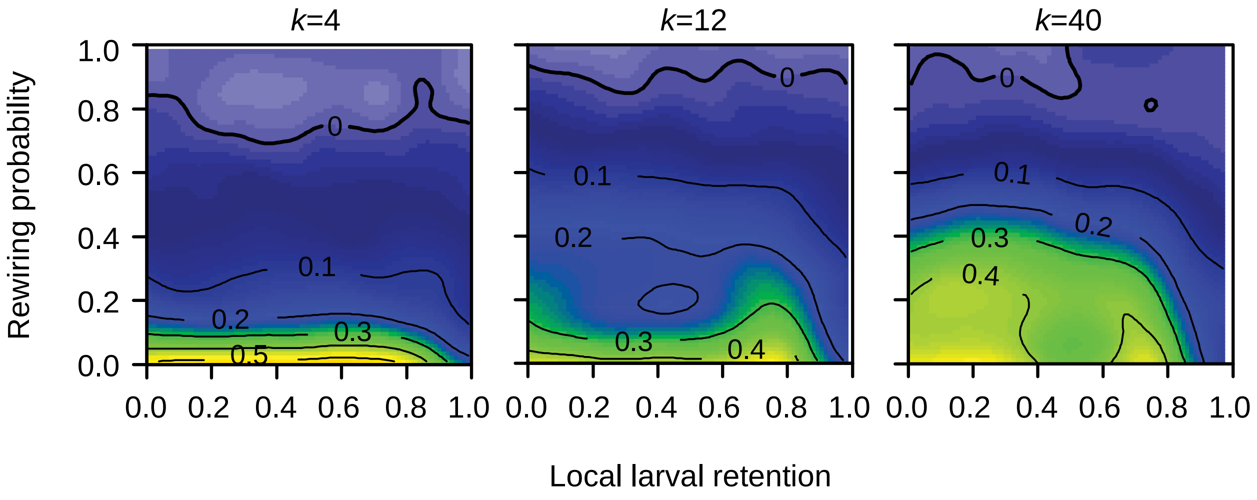


Figure 2.7: Performance of closeness centrality. Spearman rank correlation coefficients with local occupancy at different initial conditions of local larval retention, rewiring probability (dispersal shortcuts), and connection number (*k*). Isolines in the surface plots correspond to average correlation coefficients.

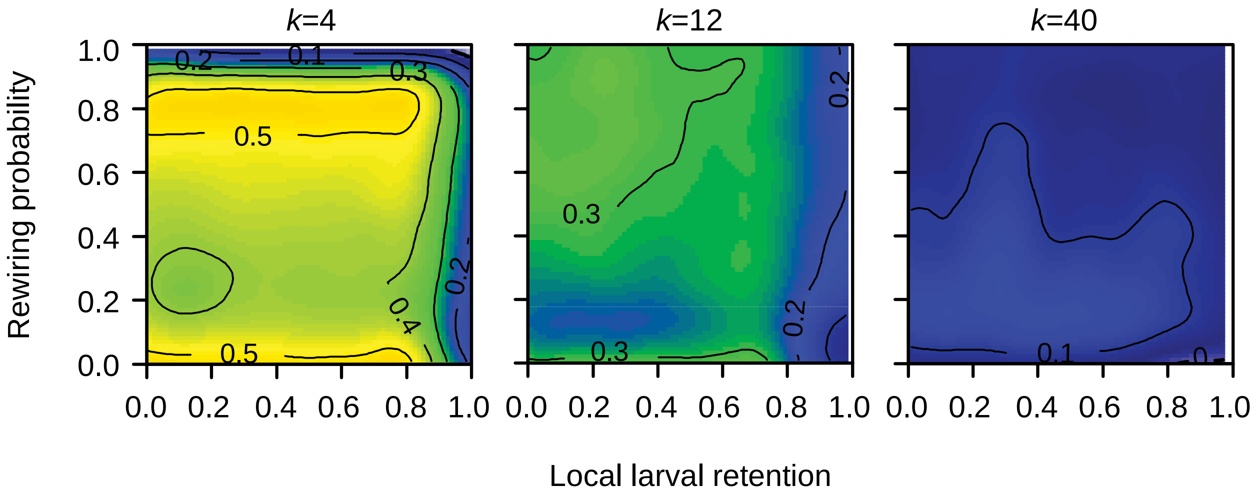


Figure 2.8: Performance of betweenness centrality. Spearman rank correlation coefficients with local occupancy at different initial conditions of local larval retention, rewiring probability (dispersal shortcuts), and connection number (*k*). Isolines in the surface plots correspond to average correlation coefficients.

Occupancy vs. fishing mortality

From the second experiment, it is immediately clear that centrality of a local population is important for local occupancy in exploited marine metapopulations (Fig. 2.9). Fishing intensity, depending on the life history of the species, can differentially change how influential a local population is in a nearshore metapopulation. The red abalone example (simulated with limited and more symmetric larval dispersal) shows their highest correlations within a small range of low fishing mortalities (0 – 0.1). Degree centrality shows the highest average correlation coefficients and narrowest confidence intervals. The red sea urchin case (simulated with greater and more asymmetric larval dispersal) shows high correlations only with fishing mortalities above 0.35. The highest average correlation coefficients are reached with Kleinberg's authority. Betweenness shows better correlation with red abalone than with red sea urchin, and closeness has the lowest correlations for both species.

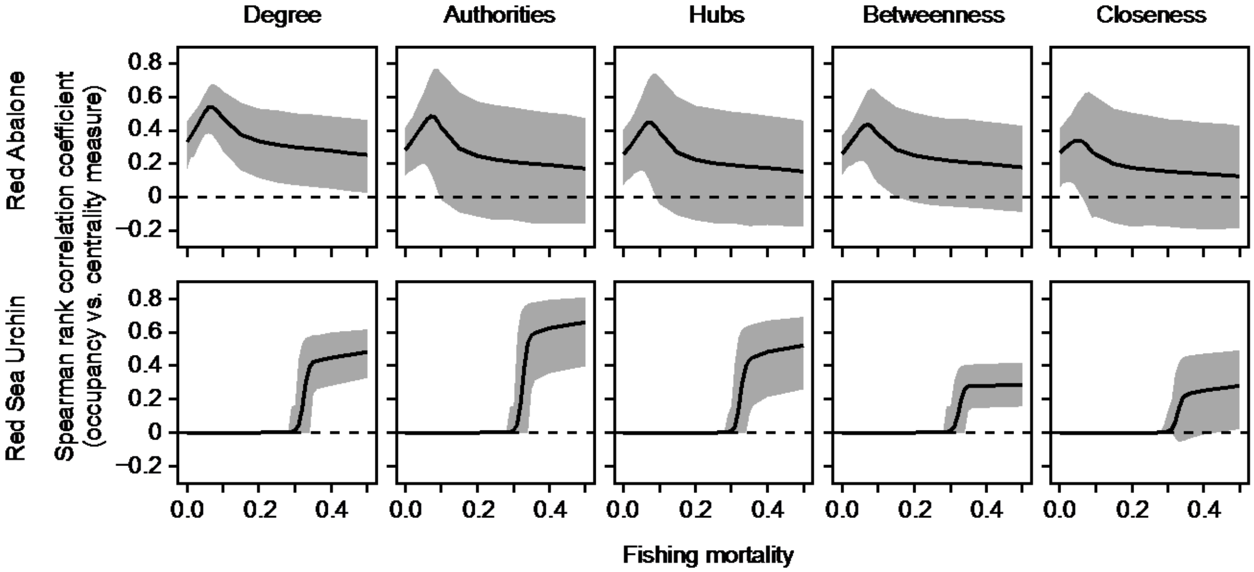


Figure 2.9: Performance of five centrality metrics across fishing mortality values. Spearman rank correlation coefficients between occupancy and centrality measures are plotted for two scenarios: abalone (short-distance disperser) and sea urchin (long-distance disperser). The black solid line is the average correlation coefficient of 10,000 simulations, and grey areas correspond to the 95% non-parametric confidence intervals.

In the red abalone example, at low fishing intensity nodes with low centrality go extinct faster and remain unoccupied, whereas at high fishing intensity nodes go extinct regardless of their centrality measure (Fig. 2.10). Degree centrality seems to be a better predictor of metapopulation dynamics than the other centralities. In the sea urchin case, nodes with low centrality also go extinct faster and highly central nodes remain occupied longer (Fig. 2.11). However, as fishing mortality increases the difference between minimum and maximum times of occupancy diminish rapidly. In all cases closeness centrality show the lowest correlations.

It is clear that local occupancy and centrality have generally a positive correlation, so that isolated local populations go extinct more rapidly and nodes with higher centrality remain occupied longer. However, intense exploitation of species with limited dispersal capabilities prone to suffer Allee effects can cause local extinction regardless of their centrality. In these scenarios predictability of centrality metrics will depend greatly not only on the complexity of larval connectivity patterns, but also on the species distinct life history.

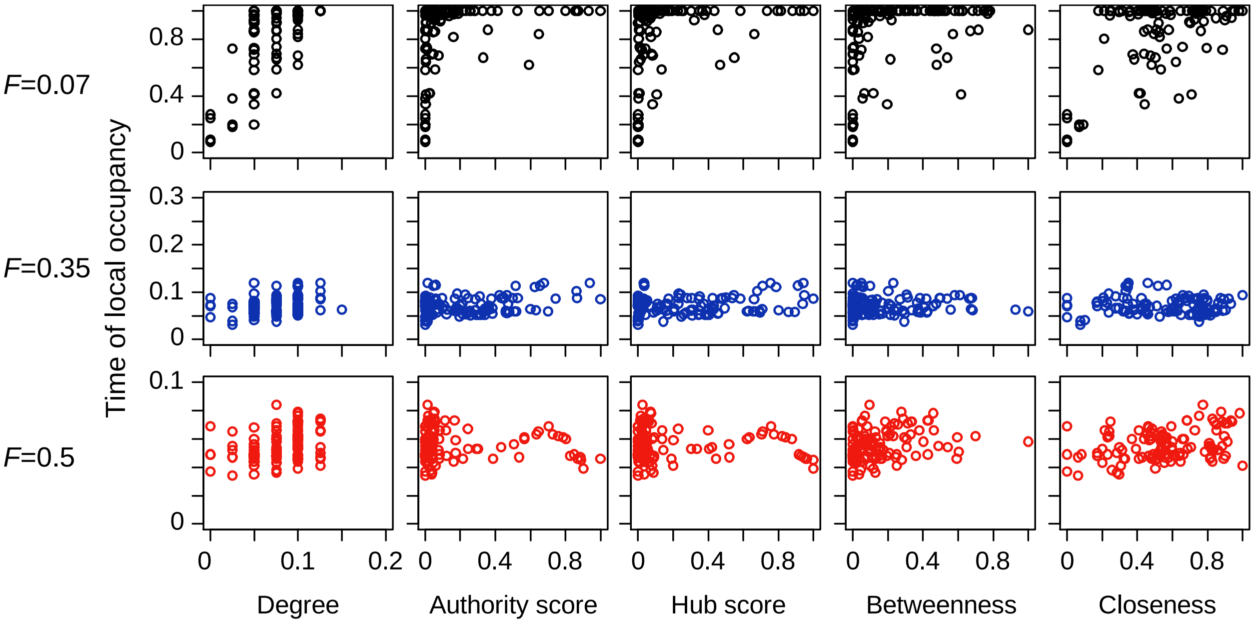


Figure 2.10: Local occupancy in red abalone metapopulations plotted as a function of five centrality metrics (one example for each case). Increasing fishing mortality appears to decrease the slope. *F* is fishing mortality.

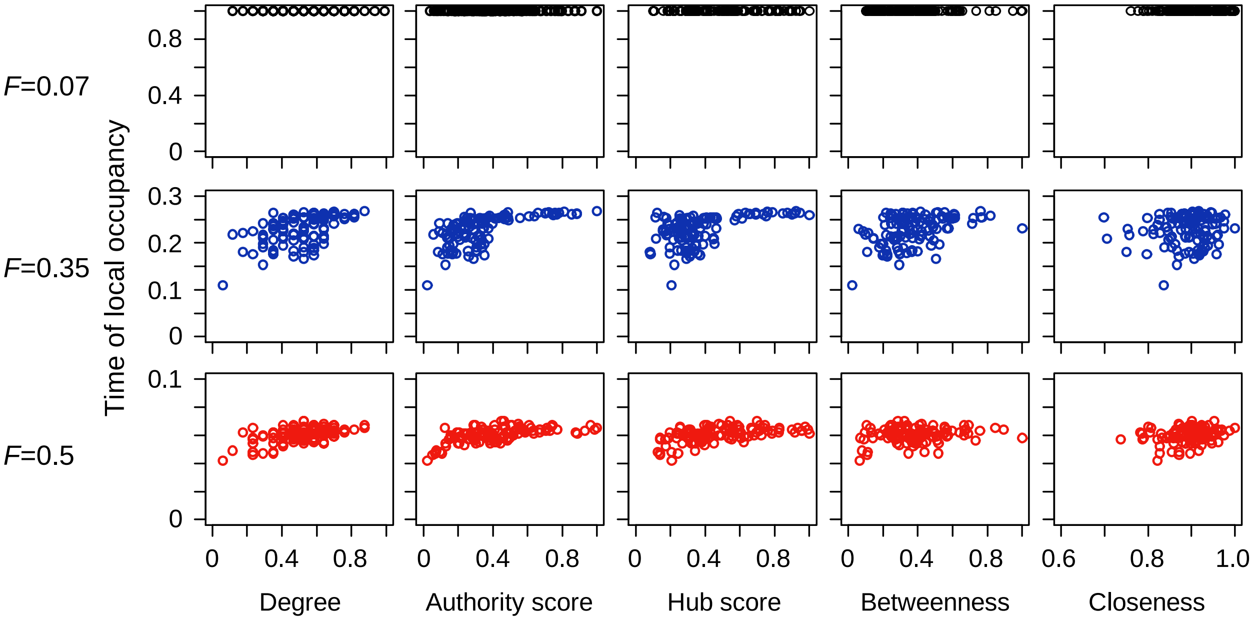


Figure 2.11: Local occupancy in red sea urchin metapopulations plotted as a function of five centrality metrics (one example for each case). Increasing fishing mortality appears to decrease the slope and dispersion of points. *F* is fishing mortality.

DISCUSSION

These results emphasize the importance of connectivity structure, isolation, life history, and exploitation in nearshore metapopulation dynamics and the predictive power of graph theory metrics. Although all centrality measures capture the general idea that more isolated local populations go extinct faster, those that quantify within (degree) and beyond local (authorities) inflow of individuals seem to predict better local occupancy. Further, there seems to be a threshold of larval retention above centrality does not correlate with local occupancy. Life history of the species and fishing intensity in turn can change the correlation between local occupancy and the centrality metric.

The centrality measures used in this study show that in general central populations are less likely to go extinct over time. However, their performances depend greatly on the species' dispersal strategies. The low correlation between local occupancy and all centrality measures at very low larval retention reveals that local populations depend greatly on larval supply most likely to overcome fishing and the Allee effect. This finding coincides with Keitt et al. (2001)

where patches require immigrants to surpass the Allee effect threshold and recover. My results however show that not only the flow of immigrants from neighbor locations (degree centrality) favor longer local occupancy, but also the amount of immigrants arriving at these neighbor sites (authority centrality). All centrality metrics seem to be correlated with each other most likely because all use incoming dispersal information although focus in a different feature of the network structure. For this reason, local occupancy also shows some positive correlations with the other centrality measures, hubs, betweenness, and closeness. However, these metrics not only use information of incoming individuals; hubs use emigrant information, betweenness focuses on the number of dispersal paths crossing, and closeness quantifies a node based on its position in the landscape. In most cases, correlations decrease as the number of dispersal shortcuts, possibly because as more dispersal shortcuts occur, local occupancy decreases, and the importance of nodes in the system evens out.

All centrality metrics were calculated using weighted connections between local populations, i.e. the amount of dispersing larvae for each dispersal path. Metapopulation dynamics are therefore not well captured when there is strong larval retention. These results are relevant because larvae have been traditionally considered susceptible to offshore transport, especially in productive regions with strong upwelling (Scheltema 1986; Caley et al. 1996). The longer larvae stay in the water column, the more likely they are to be carried away from their natal locations (Shanks et al. 2003). Nevertheless, larvae possess active mechanisms that exploit water circulation patterns. These adaptations may help even species with long PLD remain closer to their parental populations, and increase local retention and self-recruitment (Cowen 2002; Cowen et al. 2006; Morgan et al. 2009). Cowen et al. (2006) included active larval movement in their simulations and found that self-recruitment increased substantially. The centrality metrics are however more likely to give good results when studying the dynamics of most nearshore metapopulations because complete larval retention is less likely to occur in marine metapopulations.

These results also emphasize the importance of the entire connectivity structure on local occupancy and metapopulation persistence. Kleinberg’s authoritativeness is a function of long range connections; it ranks local populations by the direct inflow of larvae from other local populations that are in turn enhanced or diminished by inflow of larvae from other sites. In metapopulations where larval exchange is strong, authority scores capture better the impact of connectivity structure on metapopulation dynamics. Highly stochastic and well-connected connectivity structures create more complex connections that may still level off authority scores and diminish their resolution power. Watson et al. (2011) used eigenvector centrality to identify local populations important for the persistence of marine metapopulations at the Southern California Bight. Removing network nodes based on eigenvector centrality rank proved to impact more on the metapopulations than random removal. I chose the HITS algorithm (hubs and authorities) over eigenvector centrality because of its better suitability for directed networks. Further, even though similar algorithms for directed networks such as PageRank could be used to identify important patches for conservation, Kleinberg’s scores was useful because it provided me an additional metric, the hub scores, which emphasize those local populations that sustain important local populations. Even though hub scores show more variation in the correlation analysis, they still capture some important dynamics in well-connected metapopulations that can be useful when identifying local populations that sustain important sites for fisheries.

The other centrality measures—betweenness and closeness—that also quantify regional node position in the network do not show such strong predictive power and are more sensitive to complex connectivity patterns. Watson et al. (2011) also found that betweenness did not catch metapopulation structure and dynamics as well as eigenvector centrality. Nevertheless, betweenness and closeness centralities can be useful to categorize patches according to their position in the marine metapopulation (Treml et al. 2008; Kininmonth et al. 2010) for later consideration in conservation planning.

Ultimately, network metrics can be powerful tools to predict spatial dynamics of nearshore species, especially measures that quantify the amounts of larvae that arrive to a local population and how well supplied these source populations are. Nonetheless, there are three caveats. First, if fishing pressure is heavy, metapopulation structure and dynamics may be more difficult to predict based solely on connectivity patterns. Second, different life histories of the species can define which centrality measure is better to predict its own spatial dynamics. Patches that maintain other patches connected (betweenness), that are closer to other patches (closeness), or that provide larvae to important local populations (hubs) seem to be less important for the health of a marine metapopulation. And third, for most marine ecosystems, there is no information on larval connectivity patterns. In this case, the findings of the present study show that locations where more larvae arrive are more likely to persist. Along the coastline there are sites where more larvae are retained (White et al. 2010a). This is generally evidenced *in situ* by the amount of early juveniles present in those patches. Identifying these zones of larval retention is therefore relevant when planning the establishment of MPAs if we want to ensure that protected sites will be less likely to go extinct.

Chapter 3: Network modularity reveals spatial subdivision and increase in fragmentation in harvested marine metapopulations

INTRODUCTION

Natural populations have become increasingly fragmented due to anthropogenic activities. Human impact on terrestrial ecosystems has restricted the spatial distribution of many species, disjoined previously continuous populations, and increased isolation among habitat patches. In marine ecosystems, ocean currents suggest that larvae of marine organisms can potentially disperse across long geographic distances, resulting in little isolation among distant populations (Scheltema 1970; Waples 1987). However, if nearshore larval retention is greater than expected as recent studies have found (Cowen et al. 2006; Morgan et al. 2009), nearshore metapopulations may present spatial structures that have not yet been investigated. Exploitation, a key anthropogenic factor in marine ecosystems, may additionally affect the spatial structure of nearshore metapopulations. Although overfishing is arguably the main cause for stock reduction and extinction in the marine realm (Reynolds et al. 2002), it is unknown how fishing pressure affects the spatial structure of nearshore metapopulations. In this study, I quantified the spatial and temporal subdivision of nearshore metapopulations of two economically important species, red abalone and red sea urchin, and evaluated the impact of exploitation on spatial structure based on a key process, larval dispersal.

In the past, the concept of panmitic populations was accepted for nearshore species based on the apparent absence of barriers, pelagic larvae, and some genetic evidence (Scheltema 1970; Ryman et al. 1984; Waples 1987). Finding spatial patterns and subdivisions in nearshore metapopulations however is crucial for fisheries management and the design of marine protected areas (MPAs). Although larvae of nearshore species can potentially be carried away long distances by ocean currents, nearshore metapopulations have been found to show some spatial subdivision (Edmands et al. 1996; Moberg and Burton 2000; del Río-Portilla and González-Aviles 2001; Luttikhuizen et al. 2003). These findings coincide with increasing evidence that local larval retention may be more common than previously assumed (Cowen et al. 2000;

Swearer et al. 2002; Jones et al. 2005; Morgan et al. 2009). Consequently, some marine metapopulations may show modular spatial structures, where some local populations are more interconnected than others. Here, I use the concept of modularity, a tool from social sciences, to identify partitioning of nearshore metapopulations. Modularity (Q) is a measure of the structure of networks that quantifies the goodness of partitions of a network into clusters or modules (Fortunato 2010). The modularity index can take either positive or negative values, most often within the 0-1 interval (Newman 2006). More positive values indicate a better partitioning of the network; values near zero correspond to poor partitioning.

Modularity analysis has been rarely applied in population ecology even though it has been proven to be a useful tool to detect and characterize community structure (Fortunato 2010). Fortuna et al. (2009) used genetic data of four Mediterranean woody plant species in a highly fragmented forest mosaic in Southern Spain and found that three of them showed high partitioning. Bodin and Norberg (2007) quantified compartmentalization of habitat patches in fragmented dry forests in southern Madagascar using modularity analysis. Fletcher et al. (2013) used individual movement data of cactus bug and the Everglades snail kite, and population genetic data of bullfrog and the Florida black bear to perform the modularity analysis. They identified significant spatial modularity in 3 of the species, revealing critical meso-scales, above the patch and below the landscape scale. In marine environments, Cavanaugh et al. (2014) applied modularity to southern California giant kelp (*Macrocystis pyrifera*) forests in order to delineate local populations. They maintain that their spatial analysis identifies patches better than other methods. There are no studies however on nearshore invertebrates or fish due to the difficulty in obtaining larval connectivity data and the conflicting patterns found with genetic markers.

In recent years, coupled biophysical models have been used to obtain potential connectivity of nearshore species (e.g. Cowen et al. 2006; Mitarai et al. 2009; Watson et al. 2010). These potential connectivity patterns have been useful to identify important local populations whose protection may prevent stock collapse (Watson et al. 2011). These studies have revealed that marine metapopulations have spatially complex patterns of larval connectivity. However, the degree at which marine metapopulations are modular and the influence of exploitation in modular systems has never been studied. My goal is to address these issues and explore the impact of fishing pressure on nearshore metapopulations.

For this study, I obtained patterns of potential larval connectivity of two nearshore sedentary invertebrates with distinct life histories: the red abalone *Haliotis rufescens* and the red sea urchin *Strongylocentrotus franciscanus*. Both species have pelagic larvae, yet red abalone has a shorter pelagic larval duration (PLD) than red sea urchin (Carlisle 1962; Kato and Schroeter 1985). Dispersing larvae in the Southern California Bight were simulated using a Lagrangian probability density function method (Mitarai et al. 2009; Watson et al. 2010). I used these data to perform a modularity analysis to capture spatial subdivisions for these two populations. For the modularity analysis, I used a 7-year average potential connectivity matrix and annual averages of potential connectivity in order to obtain temporal variation in the formation of modules. I simulated metapopulation dynamics of red abalone and red sea urchin to assess spatial partitioning and the effect of fishing on metapopulation structure through time. To create temporal dynamics, I used the 7 years of potential larval connectivity and performed the modularity analysis on the realized larval connectivity patterns.

METHODS

Focal species

I analyzed larval connectivity data for two species, the red abalone (*H. rufescens*) and the red sea urchin (*S. franciscanus*), from simulation approaches that captured the effects of complex ocean circulation in the Southern California Bight (Mitarai et al. 2009). Both red abalone and red sea urchin are dioecious, broadcast spawners, and have sedentary juvenile and adult phases that live on subtidal rocky reefs associated with kelps. They differ in some aspects of their life histories. Red abalone larvae remain in the water column from 4 – 7 days (Carlisle 1962) and spawn throughout the year in the Southern California Bight (Leighton 1974), whereas red sea urchin larvae persist 6 – 8 weeks in the water and spawn mainly from December to February (Kato and Schroeter 1985). In Southern California, red abalone stay in the upper subtidal at 10-25 m deep (Leighton et al. 1974), whereas red sea urchin occupies mid to deep subtidal regions to a depth of 50 m (Kato and Schroeter 1985). Both species feed on drift macroalgae (Leighton 1966, Rogers-Bennett 2013), but when a shortage of drift algae occurs red sea urchins become active foragers that denude standing kelps leaving only stipes (Harrold and Reed 1985). Therefore, production of larvae and connectivity are tightly bound to the occurrence and productivity of kelp beds.

Potential larval connectivity

I used high-resolution ocean circulation simulations of the Southern California Bight from a 3-dimensional numerical hydrodynamic model (the regional oceanic modeling system ROMS; Shchepetkin and McWilliams 2005). Potential larval connectivity was calculated using the method of Mitarai et al. (2009), where parcels of water are released from a nearshore spawning site for a given time (PLD) over a given period (spawning period of the species). In the model, red abalone larvae disperse up to 7 days and red sea urchin larvae disperse up to 56 days. Lagrangian probability density functions were used to quantify the probability of a larva to travel from one site to another. Nearshore sites used for this assessment corresponded to areas with a 5-km radius along the mainland (sites 1-62; from south to north), Northern Channel Islands (sites 63-96), and Southern Channel Islands (sites 97-135). This process generated 135 × 135 potential connectivity matrices for the spawning months of each species in the years 1996 through 2002 (Watson et al. 2010). Annual potential connectivity for abalone was then calculated by averaging 12 matrices for each year. Because of its seasonal spawning, annual potential connectivity for sea urchin was obtained by averaging the matrices of 3 months, December of the previous year and January and February of the actual year (1996 only had

January and February). Overall average connectivity matrices were calculated by averaging all monthly connectivity matrices for both abalone and sea urchin.

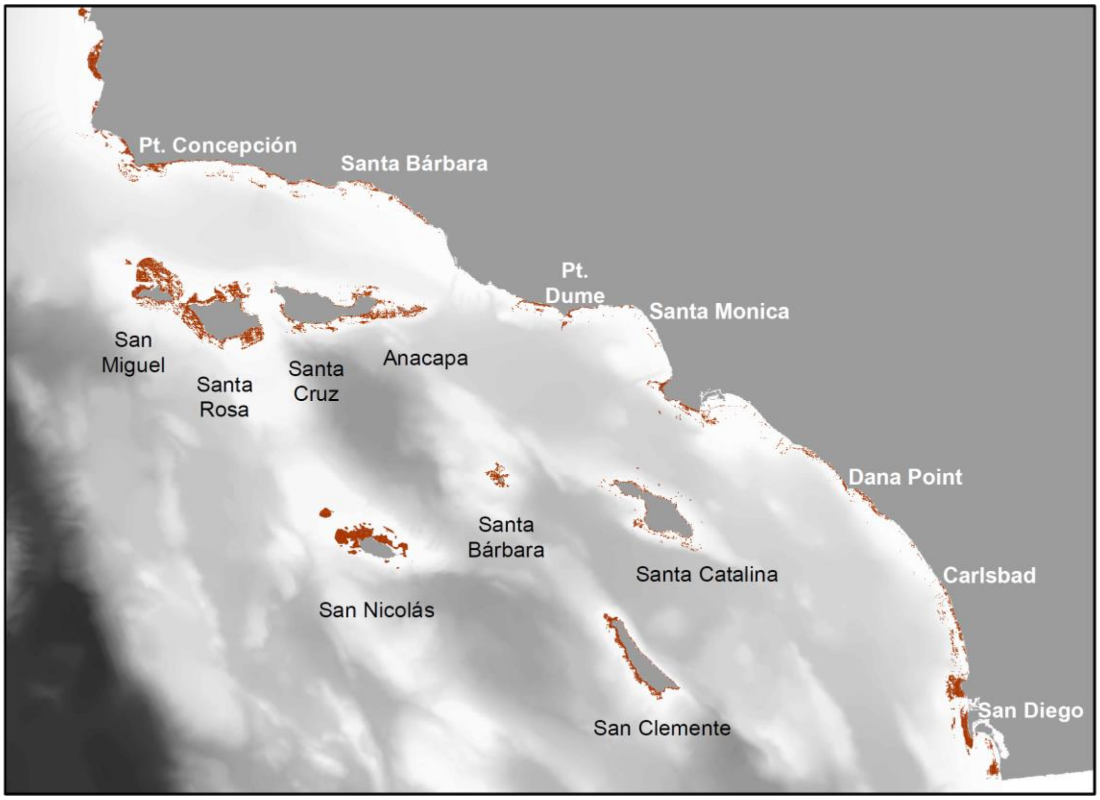


Figure 3.1: Southern California Bight with hard-bottom habitat (brown). This figure also depicts bathymetry of the study area, where darker is deeper, the Southern California mainland, the Northern Channel Islands (San Miguel, Santa Rosa, Santa Cruz, and Anacapa), and the Southern Channel Islands (San Nicolás, Santa Bárbara, Santa Catalina, and San Clemente). Hard-bottom is suitable habitat for abalone and sea urchin species.

I constructed spatial maps to delimit abalone and sea urchin distribution in the Southern California Bight using substrate type and depth GIS layers obtained from the California Department of Fish and Wildlife (https://www.dfg.ca.gov/marine/gis/downloads.asp). Both species live on subtidal rocky reefs (Fig. 3.1). Predicted substrate layers were gridded by 2 × 2 km oriented along latitude and longitude for Southern California. I assigned each grid suitable habitat as long as it had at least a third of hard surface. This part of California (unlike central California) has an irregular coastline and islands; nevertheless, I converted it into a 1-D representation. In general, grid points in portions of the mainland and islands that were horizontal were grouped in 2 km wide longitudinal bins, the rest were grouped in 2 km wide latitudinal bins. Although this approximation has its disadvantages because of the irregularity of the shelf, it captures the spatial distribution of the habitat, simplifies the computational analysis, and suits better the potential connectivity data described above. I assayed a total of 379 grids in six regions: 1-195 (mainland), 196-299 (Northern Channel Islands), 300-331 (Santa Catalina I.), 332-360 (San Clemente I.), 361-374 (San Nicolás I.), and 375-379 (Santa Bárbara I.). Of the 379 grids, 299 contained suitable hard-bottom habitat. Since the parcels of the larval simulation are 5-km radius and these tend to overlap, each grid was assigned its closest corresponding potential connectivity. The final potential connectivity matrix was 379 × 379.

Metapopulation dynamics

To simulate metapopulation dynamics I used a slightly modified version of the model constructed in Chapter 1 (Fig. 3.2). This modification adds juvenile and adult mortalities ($M_j = 5$ and $M_a = 0$, respectively) to the juvenile growth equation

$$N_{j,t+1} = \left(e^{-M_j} \cdot (1 - 1/\tau) \cdot N_{j,t} + C_{ji} \times \left(\alpha \cdot N_{a,t} \cdot \mathrm{R}_{N_a}\right)\right) \cdot B_t \qquad (1)$$

and the adult growth equation

$$N_{a,t+1} = \left((1/\tau) \cdot N_{j,t} + e^{-(M_a+F)} \cdot N_{a,t}\right) \cdot B_t \qquad (2)$$

where F is fishing mortality, α is the number of mature eggs produced by a female in a year, τ is the age at maturity, and C_{ji} is the potential larval connectivity from site j to i stored in a $n \times n$ matrix. B_t is a $n \times 1$ vector containing random deviates drawn from a Beta distribution with mean μ (the average fractional disturbance survival), which in the model I used 0.83. $N_{j,t}$ and $N_{a,t}$ are $n \times 1$ vectors of juvenile and adult densities per time step. β (= 45) is used as a scaling factor to make density curves look similar at high values. All sites with unsuitable habitat are set to zero density. $\mathrm{R}_x = x^{\delta-1} / (1 + \beta \cdot x^{\delta})$, where the parameter δ governs the strength of the Allee effect; I used $\delta = 3$ to simulate a moderate Allee effect on reproduction.

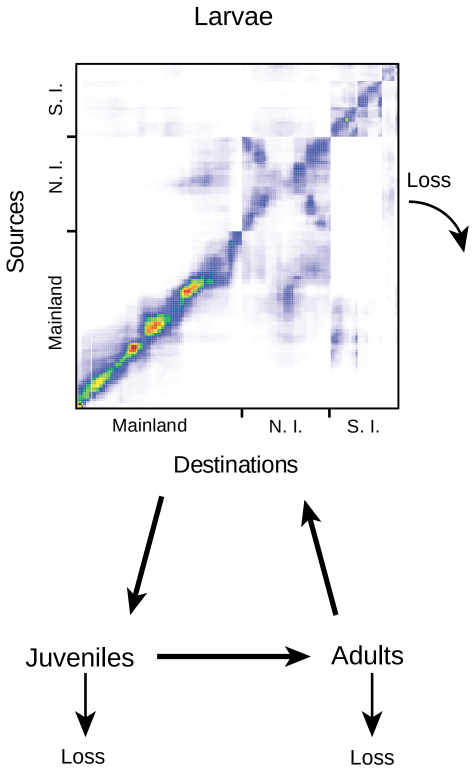


Figure 3.2: Conceptual flow chart of the metapopulation model. I use realistic potential larval connectivity matrices for every year. The matrix accounts for the loss of larvae in the system before settlement. During settlement however some larvae can be lost to unsuitable habitat, so the metapopulation model assigns 100% mortality for larvae that reach these sites. Larvae that settle in suitable habitat become juveniles and the ones that survive this stage become adults.

Modularity analysis

I used modularity, a powerful approach to detect modules or communities within networks, to quantify the structure of the larval connectivity networks of red abalone (a short-distance disperser) and red sea urchin (a long-distance disperser). I then characterized the impact of fishing intensity on the structure (modularity) of these two metapopulations over time.

Modularity is a measure of the structure of networks which evaluates the goodness of partitions of a graph into communities (also called modules, clusters, or subgraphs; Fortunato et al. 2010). I used the walktrap algorithm to find densely connected communities. The walktrap algorithm measures similarities between nodes based on the criterion that random walks tend to stay inside densely connected parts or communities (Pons and Latapy 2006). The walktrap.community function of the igraph package (Csardi and Nepusz 2006) calculated the modularity index, the partitioning, and the number of modules in the network for weighted, directed networks. This function is less computationally costly than other algorithms, but performs well at identifying the true community structure (Steinhaeuser and Chawla 2010).

The first exercise consisted in detecting communities in the two metapopulations (abalone and sea urchin). I constructed two spatial networks with the two 7-year average potential connectivity matrices, where nodes with unsuitable habitat were set to zero.

The second exercise was to detect differences between communities over the seven years (1996-2002) for which there is potential larval connectivity data. I constructed 7 spatial networks for each species, where nodes with unsuitable habitat were deleted.

The third analysis was a temporal modularity analysis to determine the impact of fishing pressure on the structure of the two metapopulations over time. For this analysis, I simulated abalone and sea urchin metapopulation dynamics over a time span of 200 years and obtained the realized larval connectivity of every year. The realized larval connectivity, the number of larvae spawned at a given site that successfully recruits at a destination site, is a product of the potential larval connectivity and the production of larvae, which in this study may undergo an Allee effect if population densities decrease ($C_{ji} \times \alpha \cdot N_{a,t} \cdot \mathrm{R}_{\mathrm{x}}$ in equation 1). Potential larval connectivity (**C**) is randomly chosen each time step from the 7-year period described above. With this simulation I obtained time series of the number of occupied sites, average weighted in-degree, modularity index, and number of modules.

The biological parameters used in these simulations were mainly obtained from the literature. Red abalone females in Northern California start spawning at 106 mm, which corresponds to approximately 6.8 years old (Rogers-Bennett et al. 2004; Leaf et al. 2008). In the model I used an age at maturity of 6 years. Their maximum fecundity 2850000 eggs y^{-1} is reached at a size of 215 mm (approximately 20 y old; Rogers-Bennett et al. 2004). I used in the model 1425000 eggs y^{-1}, half of the maximum fecundity. Red sea urchins mature younger and can be induced to spawn even at 40 mm or 1 – 2 years old (Kato and Schroeter 1985), but the production of gametes at this sizes is minimal. In the model, I set age at maturity to 3 years. Red sea urchin females spawn several millions of eggs at a time (Leet et al. 2001). I used 8000000 eggs y^{-1} in the model.

RESULTS

I performed a modularity analysis in two larval connectivity datasets that revealed spatial and temporal subdivisions of the metapopulations of red abalone and red sea urchin within the Southern California Bight. I also simulated red abalone and red sea urchin metapopulation dynamics and estimated the impact of fishing pressure on their modularity and partitioning of the metapopulations.

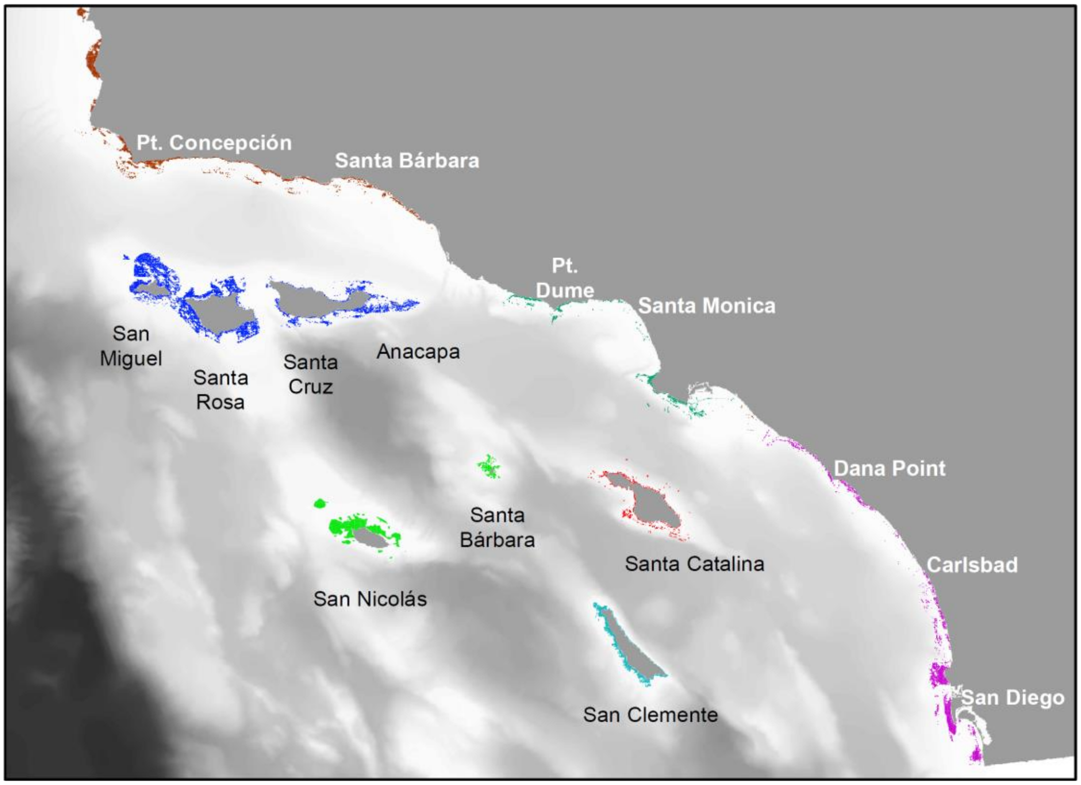


Figure 3.3: Map of the Southern California Bight showing 7 (color-coded) subdivisions for the red abalone metapopulation found with the modularity analysis. The Southern California mainland is divided into 3 patch communities, the Northern Channel Islands form another community, San Nicolás and Santa Bárbara form the fifth one, Santa Catalina the sixth one, and San Clemente the seventh one.

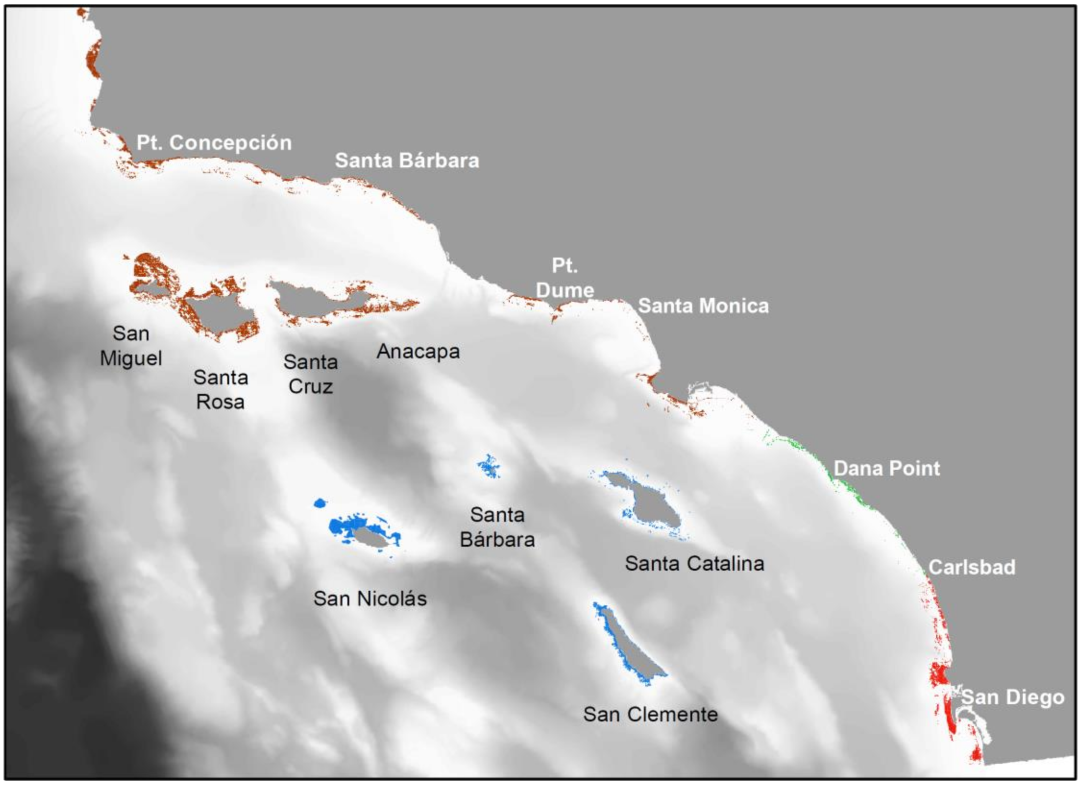


Figure 3.4: Map of the Southern California Bight showing 4 (color-coded) subdivisions for the red sea urchin metapopulation found with the modularity analysis. The south region of the Southern California coast is divided into 2 patch communities with the break point at Carlsbad, the central and north regions plus the Northern Channel Islands form another community, and all the Southern Channel Islands form one community.

The results show that the red abalone metapopulation exhibits greater modularity (Q) than the red sea urchin metapopulation ($Q_{abalone} = 0.525$ and $Q_{urchin} = 0.136$). The modularity index can reach a maximum of 1 which translates into high partitioning of the network into clusters. The high modularity index obtained for red abalone reveals the formation of clusters of local populations well connected with each other. The low modularity index for the red sea urchin metapopulation means that the formation of clusters is not as clear as in the case of red abalone. The analysis also reveals 7 distinct modules or clusters in the red abalone metapopulation (Fig. 3.3): three across the mainland (south, central, and north), one single cluster formed by the Northern Channel Islands (San Miguel, Santa Rosa, Santa Cruz, and

Anacapa), and three for the Southern Channel Islands (Santa Catalina, San Clemente, and San Nicolás – Santa Bárbara).

For the red sea urchin metapopulation, the analysis detected 4 modules (Fig. 3.4): two in the southern coast with a break around Carlsbad (CA), one formed by the central and northern sections of the coast and the Northern Channel Islands, and one formed by the Southern Channel Islands. All modules show a strong spatial signature, where patches in close geographic distance tend to aggregate in the same modules.

The results indicate that, within the period of 1996 through 2002, both the modularity index and module partitioning changed over time in these two marine metapopulations. Modularity in the red abalone metapopulation varies between 0.485 and 0.553, and in the red sea urchin metapopulation varies between 0.041 and 0.242. According to my analysis, the habitat patches with red abalone located in the southern and central regions of the mainland form two defined blocks; however, the northern region periodically mixes with the Northern Channel Islands (in 1996, 1999, and 2000). The Southern Channel Islands form three blocks as described above, but there seem to be periods of more mixing between them as well (1996 and 1999; Fig. 3.5). Within the period studied, the red sea urchin metapopulation showed considerable mixing among the sites and less defined patterns (Fig. 3.6). In 2000, the number of modules increased up to 6, with more undefined partitioning, which corresponded to an extremely low modularity (0.041). However, there seem to be a regular break between Northern and Southern Channel Islands. The most constant cluster of patches corresponded to the first four patches far south in the mainland.

Fishing mortality has a greater impact on the modularity of the red abalone metapopulation than the red sea urchin metapopulation. As fishing pressure increases and dispersing larvae and occupied habitat drop (Figs. 3.7-3.8), modularity in the abalone metapopulation decreases gradually until extinction, and the metapopulation is partitioned into smaller numerous modules which later go extinct (Figs. 3.9-3.10). On the contrary, the impact of fishing mortality on the red sea urchin metapopulation is more abrupt. When fishing mortality is strong, connection strength among sites gradually weakens, but all local populations collapse almost simultaneously (Figs. 3.7-3.8). Modularity in the red sea urchin metapopulation is lower than that in the red abalone metapopulation, but it shows a greater range of variation over time. There is no apparent decrease in modularity or increase in spatial subdivision before the metapopulation collapses due to fishing pressure (Figs. 3.9-3.10).

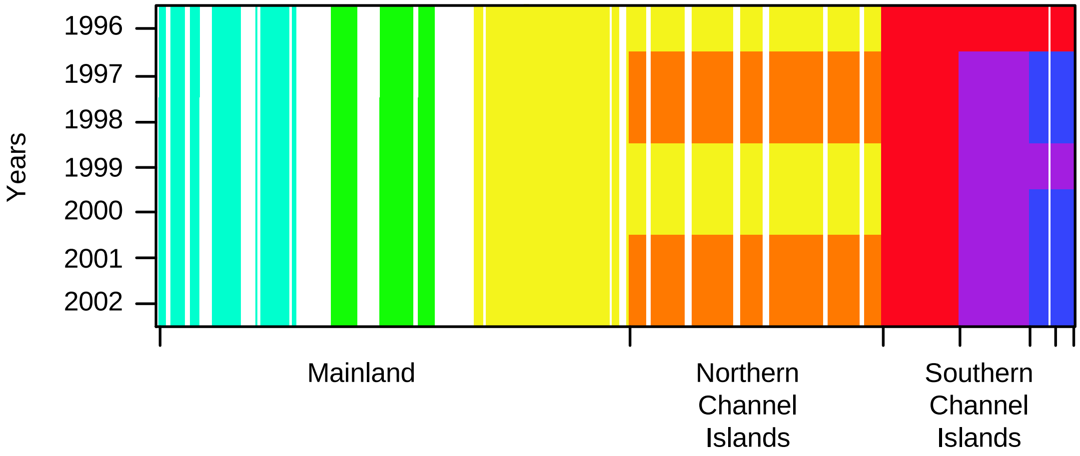


Figure 3.5: Temporal variation of the spatial structure of the red abalone metapopulation in the Southern California Bight. The mainland is subsequently split into 3 clusters. The northern cluster merges with the Northern Channel Islands in 1996, 1999 and 2000. The Southern Channel Islands usually form 3 clusters, except in 1996 and 1999.

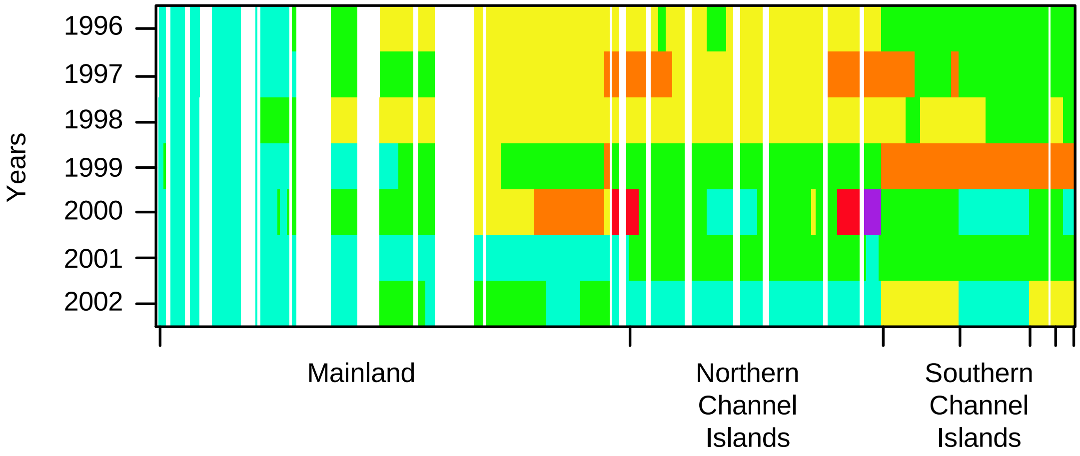


Figure 3.6: Temporal variation of the spatial structure of the red sea urchin metapopulation in the Southern California Bight. Patterns show considerable mixing between the different regions.

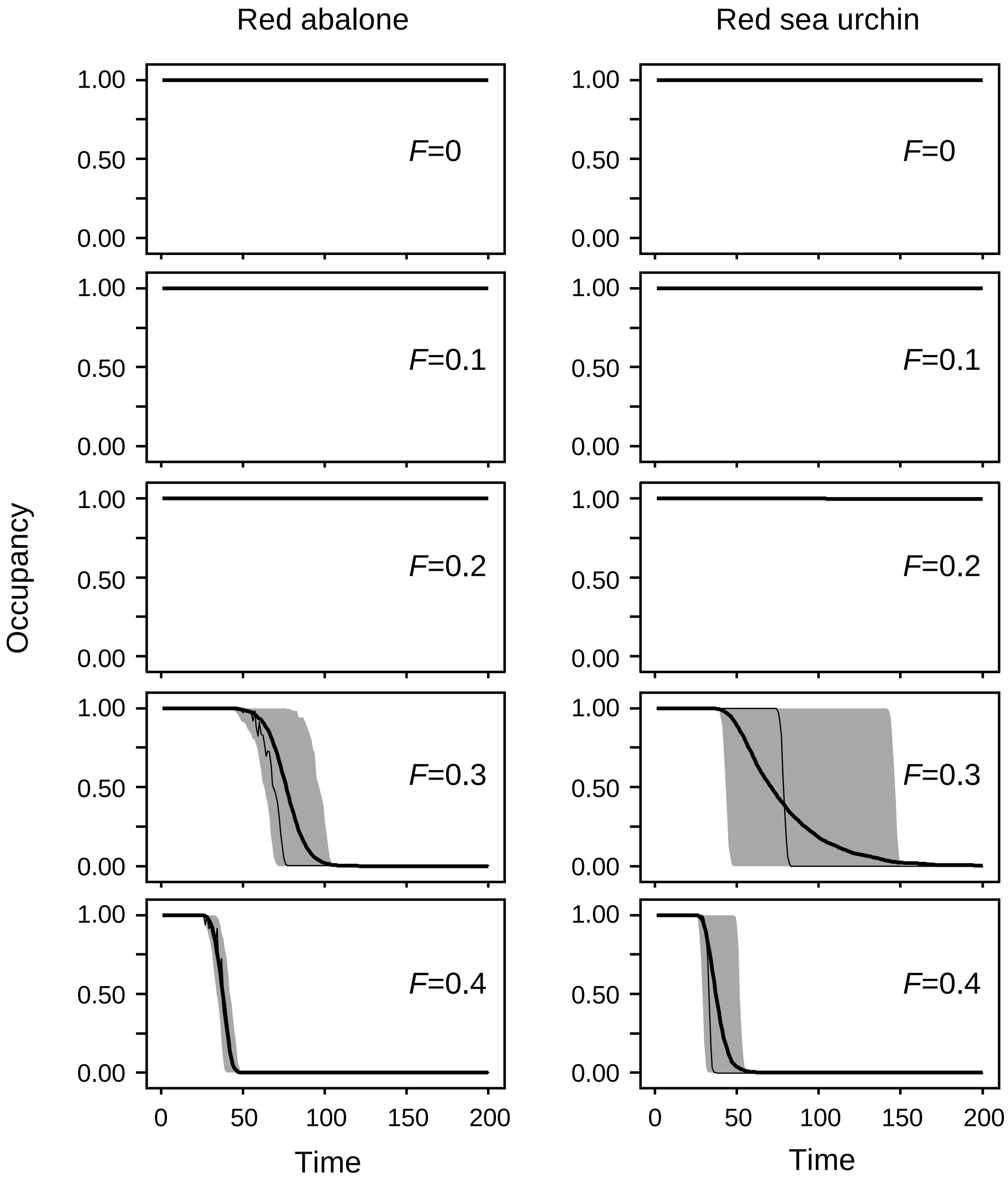


Figure 3.7: Effect of exploitation on habitat occupancy for red abalone and red sea urchin metapopulations in the Southern California Bight. At low densities, both metapopulations can undergo a pre-dispersal Allee effect. (Time unit is years.)

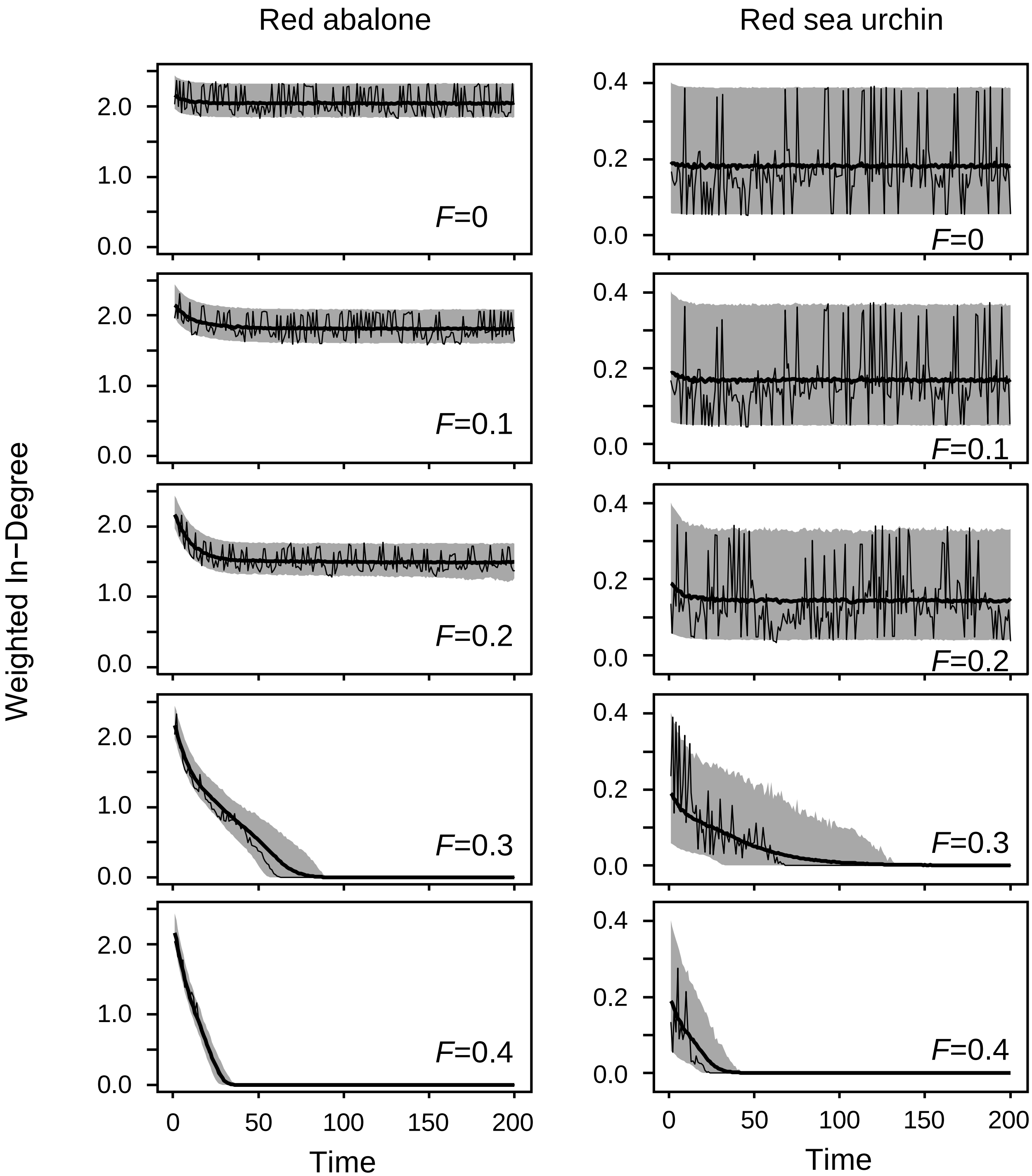


Figure 3.8: Effect of exploitation on weighted in-degree for red abalone and red sea urchin metapopulations in the Southern California Bight. The weighted in-degree is obtained by averaging the dispersal rates of all local populations. At low densities, both metapopulations can undergo a pre-dispersal Allee effect. (Time unit is years.)

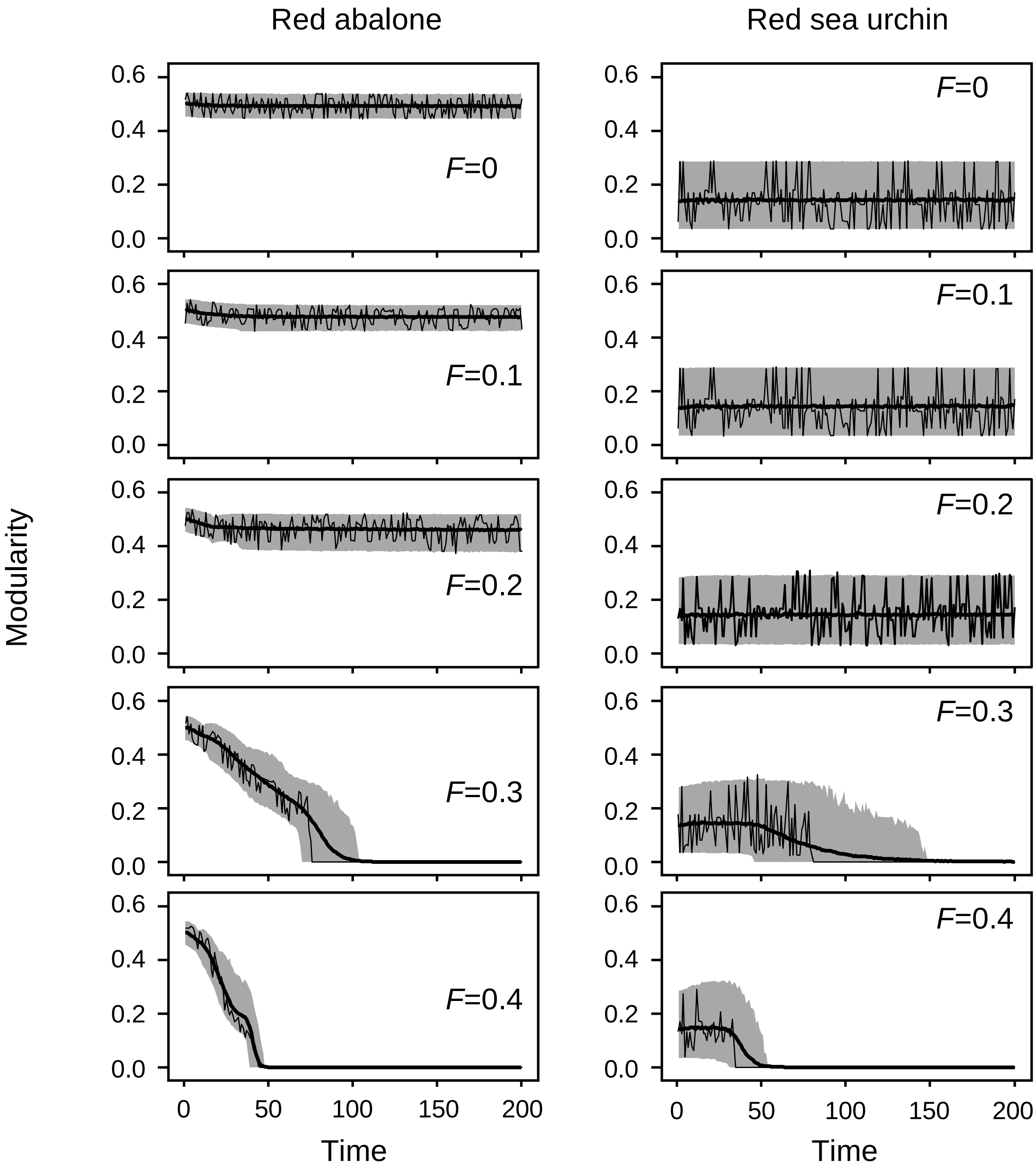


Figure 3.9: Effect of exploitation on modularity for red abalone and red sea urchin metapopulations in the Southern California Bight. The walktrap algorithm is used for community detection on the realized connectivity matrix of every time step. At low densities, both metapopulations can undergo a pre-dispersal Allee effect. (Time unit is years.)

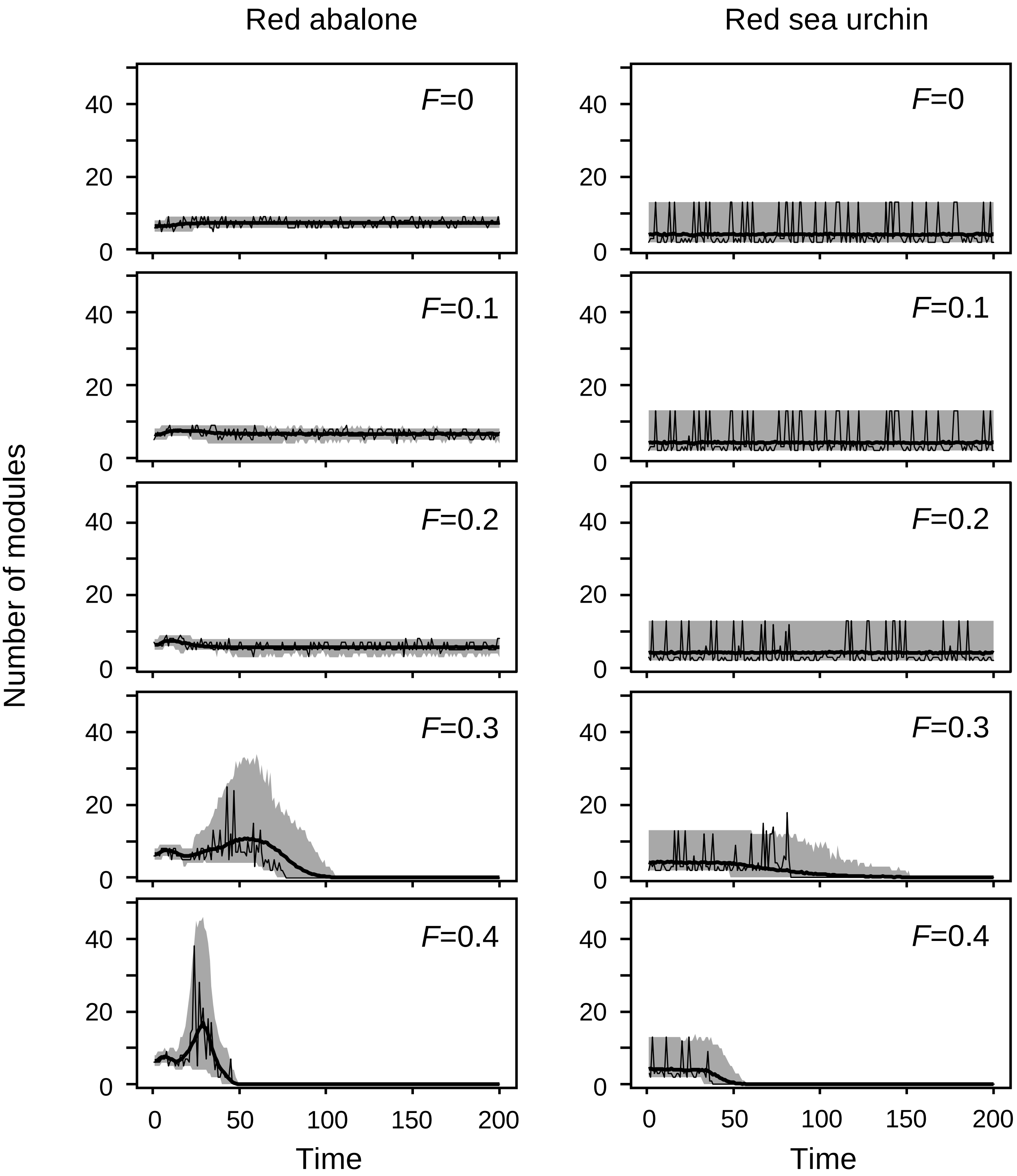


Figure 3.10: Effect of exploitation on the number of modules detected by the modularity analysis for red abalone and red sea urchin metapopulations in the Southern California Bight. Community detection is calculated every time step for each realized connectivity matrix. At low densities, both metapopulations can undergo a pre-dispersal Allee effect. (Time unit is years.)

DISCUSSION

The results highlight the ability of the modularity analysis to detect spatial subdivisions in the red abalone and red sea urchin metapopulations and the great impact of fishing pressure on the spatial structure of marine metapopulations. Although the red abalone metapopulation appears to have 7 well-defined modules compared to the 4 less clear modules found in the red sea urchin metapopulations, the walktrap algorithm for community (module) detection captures important break points for the red sea urchin metapopulation (e.g. Carlsbad ,CA). The modules however are not constant in the time frame 1998 – 2002; the red abalone metapopulation have 4 to 7 modules, whereas the red sea urchin metapopulation shows 3 – 6 modules. Increasing fishing pressure decreases modularity and increases fragmentation in the red abalone metapopulation, but not in the red sea urchin metapopulation.

In natural populations, it is common to find modular spatial structures due to the patchy configuration of many habitats (Keitt et al. 1997; Fortuna et al. 2009). Marine metapopulations may not be the exception. Even though genetic studies have not found defined spatial patterns for populations red and green abalone in California (Gruenthal et al. 2007; 2013; De Wit and Palumbi 2013), the red abalone metapopulation studied here shows clusters of patches based on larval dispersal patterns. It is important to remark however that other abalone species with similar life histories (short PLD) have shown differentiation between localities (Del Río-Portilla and González-Avilés 2000; Gruenthal and Burton 2008; Díaz-Viloria et al. 2009) and newer genetic tools may detect some spatial subdivision in the future. The modularity analysis also detects that in some years the metapopulation shows less partitioning, indicating more mixing between modules. In 1996 and 1999-2000, the north coast of Southern California and the Northern Channel Islands formed one block, which coincided with two La Niña events in those same years. Conversely, in 1997-1998 and 2002, the Northern Channel Islands and the mainland split, these years correspond to two El Niño events. Although the time series is too short to determine any relationship between these events and the variation of the spatial structure of the red abalone metapopulation, I think it is a remarkable coincidence that should be explored more thoroughly.

Due to its long PLD, the red sea urchin metapopulation is expected to be less modular than the red abalone metapopulation. However, the modularity analysis of the 7-year average potential connectivity found interesting breaks between patches. For instance, the split between modules at Carlsbad (CA) coincides with the findings of Moberg and Burton (2000) that show a break point of genetic differentiation between Oceanside and Dana Point. Edmands et al. (1996) found a significant break for purple sea urchin *Strongylocentrotus purpuratus* at a similar location, between Laguna Beach and La Jolla. The time series of potential connectivity analyzed does not show strong patterning overall, yet if local larval retention is greater than what is generally expected for a species with long PLD (Cowen et al. 2000; Morgan et al. 2009) the modularity analysis may show a better subdivision of the metapopulation.

In terrestrial ecosystems, fragmentation of populations has been mainly attributed to habitat fragmentation due to land conversion by humans. In marine ecosystems, exploitation has arguably the greatest impact on populations, but it does not necessarily cause habitat fragmentation. My results demonstrate that fisheries alter the spatial structure of modular systems such as red abalone metapopulations even without the loss of habitat. With intense fishing, modularity diminishes and the metapopulation becomes more fragmented. The rapid decrease in modularity of the red abalone metapopulation suggests that exploitation affects greatly larval dispersal within modules, plausibly more than dispersal between modules. This trend is not observed in the red sea urchin metapopulation. With intense fishing, the red sea urchin metapopulation simply collapses without any previous change in modularity or population fragmentation. This outcome is important because metapopulations of long-distances dispersers may give signs of being healthy and sustainable, albeit on the verge of collapsing. It should be pointed out however that self-recruitment in nearshore species may be greater if larval mechanisms for retention such as vertical migration behaviors were added to the dispersal simulation (Cowen et al. 2000; 2006). In this case, it is very likely that the red sea urchin metapopulation will present a more modular spatial pattern and that heavy fishing will have a similar effect as on red abalone.

Even though modularity analysis is useful to detect spatial subdivisions in natural populations, it suffers a resolution limit that may prevent it from detecting small clusters. In that case it is possible to adjust null models to reflect more relevant processes such as localized movement (Fortunato 2010). This approach also assumes non-overlapping modules, which may not be necessarily true for natural populations, especially marine populations. Another shortcoming may lie in the linearization of the coastline. This reduction from 2-D to 1-D has the advantage of being computationally simpler, yet it underestimates some patches while overestimating others. Nonetheless, Kaplan et al. (2009) maintains that 1-D representations still capture the essential spatial variability of the habitat which affects population persistence. Another important caveat is the use of a constant fishing mortality for all local populations. Fishing effort is usually aggregated and varies among sites (Parnell et al. 2010). However, historically, red abalone landings from the Southern California mainland and Northern Channel Islands have been relatively similar and constant for the first 20 years of the fishery with a similar decline afterwards (Karpov et al. 2000). This characteristic of red abalone fishery favors the assumption of homogeneous fishing pressure. Red sea urchin fishery in the Southern California Bight on the other hand has presented shifts of fishing effort between island groups (Kalvass and Hendrix 1997). It is likely that these fishing dynamics will increase fragmentation in this metapopulation, something that is not observed in my simulation. Kelp beds, in turn, show great temporal variation with extinctions and colonizations due to seasonal storms and El Niño (Burgman and Gerard 1990; Reed et al. 2006; Gaines et al. 2007). Although the disturbance survival parameter of the model accounts for these dynamics, fitness of both species and therefore larval connectivity may be greatly reduced. In this scenario, it is very likely that nearshore metapopulations will be more rapidly fragmented by fishing.

Overexploitation is noted as the main cause for stock collapse and extinctions in marine ecosystems. Nonetheless, the impact of fishing pressure on the spatial structure of marine populations has never been addressed. Here, modularity analysis revealed spatial subdivisions of marine metapopulations with complex connectivity patterns and evidenced interannual variations that may be related to the ENSO variability. Most importantly, exploitation showed a strong impact on the spatial structure of modular marine metapopulations (e.g. red abalone) by decreasing modularity and fragmenting the network even without habitat loss. These findings offer complementary information to the evaluation of population genetic structure for nearshore species, such as the scale at which genetic differentiation may be found. Delineating groups of patches and evaluating the resilience of individual modules may be useful when designing MPAs. Also, quantifying the modularity of exploited systems and its spatial subdivision may be an indicator of the health of the metapopulation before and after the establishment of MPAs. Therefore, this network theoretic approach may be important for conservation and management of marine metapopulations.

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