Landscape Ecol (2017) 32:1643–1656
DOI 10.1007/s10980-017-0532-9

RESEARCH ARTICLE

Step-wise drops in modularity and the fragmentation of exploited marine metapopulations

Tania S. Peña · James R. Watson · Laura I. González-Guzmán · Timothy H. Keitt

Received: 23 October 2016 / Accepted: 14 May 2017 / Published online: 24 May 2017

Abstract
Context Many nearshore species are distributed in habitat patches connected only through larval dispersal. Genetic research has shown some spatial structure of such metapopulations and modeling studies have shed light onto possible patterns of connectivity and barriers. However, little is known about human impact on their spatial structure and patterns of connectivity.
Objectives We examine the effects of fishing on the spatial and temporal dynamics of metapopulations of sedentary marine species (red sea urchin and red abalone) interconnected by larval dispersal.
Methods We constructed a metapopulation model to simulate abalone and sea urchin metapopulations experiencing increasing levels of fishing mortality. We performed the modularity analysis on the yearly larval connectivity matrices produced by these simulations, and analyzed the changes of modularity and the formation of modules over time as indicators of spatial structure.
Results The analysis revealed a strong modular spatial structure for abalone and a weak spatial signature for sea urchin. In abalone, under exploitation, modularity takes step-wise drops on the path to extinction, and modules breakdown into smaller fragments followed by module and later metapopulation collapse. In contrast, sea urchin showed high modularity variation, indicating high- and low-mixing years, but an abrupt collapse of the metapopulation under strong exploitation.
Conclusions The results identify a disruption in larval connectivity and a pattern of collapse in highly modular nearshore metapopulations. These results highlight the ability of modularity to detect spatial structure in marine metapopulations, which varies among species, and to show early changes in the spatial structure of exploited metapopulations.

Keywords Larval connectivity · Southern California Bight · Allee effect · Marine metapopulation · Seascape ecology · Spatial structure · Red abalone · Red sea urchin

Introduction

Many nearshore species are distributed along coastlines over a patchy mosaic of suitable habitat such as rocky or coral reefs and kelp forests. They disperse between these habitat patches mainly as newly born

---

Electronic supplementary material The online version of this article (doi:10.1007/s10980-017-0532-9) contains supplementary material, which is available to authorized users.

T. S. Peña (✉) · L. I. González-Guzmán · T. H. Keitt
Department of Integrative Biology, University of Texas at Austin, 2415 Speedway, Stop C0390, Austin, Texas 78712-0253, USA
e-mail: taniasarith@utexas.edu

J. R. Watson
Stockholm Resilience Centre, Stockholm University, Kräftriket 2B, 106 91 Stockholm, Sweden

larvae, moving with ocean currents sometimes hundreds of kilometers (Kinlan and Gaines 2003). For such metapopulations, there is evidence of spatial genetic structure, but with conflicting results such as no geographic correlation or discordance between different genetic markers (Moberg and Burton 2000; Debenham et al. 2000; Gruenthal et al. 2007; Miller et al. 2008; De Wit and Palumbi 2013). Information gained from larval dispersal modeling has shed light onto possible patterns of connectivity between habitat patches (Cowen et al. 2006; Planes et al. 2009; Watson et al. 2010; Paris et al. 2013) and the barriers that separate them (Caley et al. 1996; Bell et al. 2001; Goodsell and Connell 2002; Deza and Anderson 2010; Bonin et al. 2011). For the most part, however, these studies have not gauged the (possibly strong) effect of fishing pressure on patterns of connectivity and spatial structure, as nearshore metapopulations become more and more depleted.

Strong fishing pressure can decrease local densities (Jackson et al. 2001; Pauly 2009; FAO 2012), which might have consequences on larval dispersal, genetic exchange and spatial structure of marine populations. It has been observed that coastal areas show high human impact across the globe (Halpern et al. 2008). This makes nearshore metapopulations crucial systems when studying the effects of fishing. A well-known effect is population decline, which in turn may have consequences on the recovery potential of nearshore metapopulations. For example, Allee effects, i.e. a drop in fitness at low densities, may intensify causing reproductive and recruitment failure (Gascoigne and Lipcius 2004; Berec et al. 2007). Allee effects are therefore important when studying nearshore benthic species. Another effect is the decrease of larval exchange (Kaplan et al. 2009), which is key for species that only disperse through their pelagic larvae. In their review, Ciannelli et al. (2013) highlight that overfishing can alter the dynamics of marine metapopulations by eroding their spatial structure and affecting colonization. In the present study, we want to further analyze these effects on nearshore metapopulations by focusing on their larval connectivity patterns.

Network modularity, a tool from network theory, has been used in both terrestrial and marine systems to assess spatial structure and analyze connectivity of metapopulations. In network theory, habitat patches within a metapopulation are represented by nodes and dispersal connections by edges (Keitt et al. 1997). Modularity has been used in the study of fragmented landscapes as a measure of the structure of the network that detects modules, i.e. densely connected groups of nodes (Keitt et al. 1997; Girvan and Newman 2002; Newman 2006a; Minor and Urban 2007). High modularity means that nodes within a module are more densely connected, but sparsely connected to nodes in other modules. Although its application in marine systems is recent, modularity has successfully identified groups of locations (nodes) as subpopulations (Jacobi et al. 2012), sub-patches (Cavanaugh et al. 2014) or emergent geographic clusters (Crandall et al. 2014) by using connectivity matrices. In that way, these studies have shown a spatial structuring on nearshore metapopulations, with patches that exchange more larvae within their module than with other modules. However, no study have yet focused on their spatial and temporal dynamics, nor in the effects of fishing pressure.

In this study, we simulated nearshore metapopulations of red abalone (*Haliotis rufescens*) and red sea urchin (*Strongylocentrotus franciscanus*) experiencing increasing levels of fishing mortality, and performed a modularity analysis to determine the effects of fishing on their spatial and temporal dynamics. Red abalone (a short-distance disperser) and red sea urchin (a long-distance disperser), henceforth abalone and sea urchin, are nearshore sedentary species that disperse only through pelagic larvae. These characteristics added to their high unit value that make them prone to overfishing, make them interesting for the application of graph theory. Here, we used previously published modeled estimates of larval connectivity within the Southern California Bight (SCB) for abalone (Watson et al. 2010) and sea urchin (Watson et al. 2011). We constructed a nearshore metapopulation model to simulate their spatial and temporal dynamics under fishing pressure. Changes in modularity and formation of modules over time were used as indicators of spatial structure. Given that abalone has a short pelagic larval duration (PLD) (Carlisle 1962) and sea urchin a long PLD (Kato and Schroeter 1985), we expect abalone to show a more defined spatial structure. Nevertheless, other life history strategies, such as age at maturity and fecundity, might also influence spatial structuring.

Methods

Focal species

H. rufescens and *S. franciscanus* are dioecious, broadcast-spawning species with pelagic larvae and sedentary juvenile and adult phases. They both live on subtidal rocky reefs associated with kelps, yet they differ in some aspects of their life histories. Abalone in the SCB spawns throughout the year (Leighton 1974) and their larvae remain in the water column for 4–7 days (Carlisle 1962). Females reach maturity at sizes above 100 mm in northern California (6 years old) (Rogers-Bennett et al. 2004; Leaf et al. 2008). Sea urchins spawn mainly from December to February and their larvae stay 6–7 weeks in the water (Kato and Schroeter 1985). Females can be induced to spawn at 1–2 years old, but the production of gametes is minimal (Kato and Schroeter 1985), hence age at maturity is generally assumed at 3 years old (White et al. 2010). As broadcast spawners, both species may be prone to pre-dispersal Allee effects, a decrease in fertilization at low adult densities (Kikuchi and Uki 1974; Denny and Shibata 1989; Levitan 2002).

Although individuals of both species live on hard substrate, they tend to occupy different depths. Abalone juveniles and adults in Southern California live preferably in the upper subtidal at 10–25 m deep (Leighton 1974), whereas sea urchins dwell mainly on mid to deep subtidal regions to a depth of 50 m (Kato and Schroeter 1985). However, they both can be found in deeper regions. Both species feed on drift macroalgae (Leighton 1966; Rogers-Bennett 2013), but when a shortage occurs only sea urchins become active foragers that denude standing kelps to leave only stipes (Harrold and Reed 1985). Their main predators are sea otters and humans (Leet et al. 2001).

Larval connectivity data

We used previously published estimates of potential larval connectivity developed from Lagrangian particle simulations in the Southern California Bight (Mitarai et al. 2009; Watson et al. 2010, 2011). Potential larval connectivity is the probability that a larva released from a particular location, at a given time will disperse to another location over a given advection time (species' PLD) (Mitarai et al. 2009). In these simulations, Lagrangian particles (larvae) were released from 135 circular nearshore patches, each with a 10 km diameter, distributed uniformly throughout the SCB coastline, the Northern and Southern Channel Islands (Mitarai et al. 2009). The Lagrangian particles were then transported passively by modeled ocean currents, produced from a Regional Oceanic Modeling System (ROMS) solution to the Southern California Bight for the period 1996–2002 (Shchepetkin and McWilliams 2005; Dong et al. 2007; Dong and McWilliams 2007; Dong et al. 2009; Mitarai et al. 2009). Potential connectivity to and from each nearshore patch was then calculated from the Lagrangian particle trajectories, resulting in a potential connectivity matrix. We refer the reader to Mitarai et al. (2009) and Watson et al. (2010) for more information on these Lagrangian particle simulations and the derivation of potential connectivity.

From these Lagrangian particle simulations we obtained 135 × 135 potential larval connectivity matrices for abalone and sea urchin, defined by their spawning month, year and PLD (Tables S1, S2, Supporting Information), for the period 1996–2002 (Watson et al. 2010). Since abalone spawns year-round in the SCB, we calculated the yearly potential connectivity by taking 12 monthly averages. In contrast, for sea urchin, the yearly potential connectivity was calculated as the average of December (from the previous year), January and February, which covers its spawning period.

In addition to these estimates of potential connectivity, we constructed spatial maps of the distributions of abalone and sea urchin in the SCB using substrate type, kelp bed cover and depth GIS layers from the California Department of Fish and Wildlife (https://www.dfg.ca.gov/marine/gis/downloads.asp) and the California Seafloor Mapping Program (Johnson et al. 2013). We overlaid hard substrate, kelp cover and the 30- and 60-m-deep isolines for abalone and sea urchin, respectively (Fig. S1, Supporting Information). To linearize the coastline of Southern California, we used the approach used by Kaplan et al. (2009) and divided it into 2-km-wide latitudinal and longitudinal bins (the substrate-type GIS layer shows 2-km grids). In general, horizontal sections of the coastline (mainland and islands) were divided into longitudinal bins; the rest was divided into latitudinal bins. To capture small isolated patches, bins with more than 0.1 km^2 of hard substrate or kelp cover were considered with suitable habitat. Each bin corresponded to a node in the network. This approximation captures the spatial distribution of the habitat, simplifies the computational analysis, and suits better the potential connectivity data described above. We obtained a total of 379 bins: 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 bins, 291 contained suitable habitat for abalone and 293 for sea urchin. The final step was to assign the probability that a larva in site *i* ended in site *j*, by interpolating the nearest potential connectivity values. This resulted in a 379×379 potential connectivity matrix **C** which we then used in the metapopulation simulations described below.

Simulation of nearshore metapopulations

We have developed a general model of nearshore metapopulation dynamics for sedentary species, whose parameterization leads to species-specific results (Tables S1, S2, Supporting Information). In the model, larval dispersal follows the potential connectivity matrix, where some larvae are lost in the system and some find suitable habitat to settle. Settlement is followed by the juvenile phase that groups all individuals before reaching age at maturity, thus natural mortality is very high. All individuals that have reached age at maturity are in the adult phase, which can be subject to natural and fishing mortality. Reproduction is subjected to a pre-dispersal Allee effect at low densities.

Population dynamics are iterated forward in discrete annual intervals and defined by juvenile (*J*) and adult (*A*) growth equations:

$$J_{t+1} = \left(e^{-M_J} \cdot (1 - 1/\tau) \cdot J_t + \mathbf{C} \times (\alpha \cdot A_t \cdot \mathrm{R}_t)\right) \cdot B_t, \quad (1)$$

$$A_{t+1} = \left((1/\tau) \cdot J_t + e^{-(M_A+F)} \cdot A_t\right) \cdot B_t \quad (2)$$

where J_t and A_t are vectors over space with juvenile and adult densities at time *t*, M_J and M_A are natural juvenile and adult mortalities, and *F* is fishing mortality. α is the number of mature eggs produced by a female in a year, and τ is the age at maturity. **C** is the transposed of the potential larval connectivity matrix described above, which in the model is multiplied times the production of new individuals ($\alpha\ A_t\ R_t$), resulting in the realized larval connectivity matrix **L**, Therefore **L** contains the amount of larvae coming to place *j* from place *i*. Every time step (year) the algorithm randomly chooses one matrix **C** from the 7-year period quantified in the previous section and calculates its corresponding matrix **L**. B_t is a vector containing 379 random deviates drawn from a Beta distribution with mean μ, which determine individual mortality due to environmental stochasticity. R_t is a modified version of the Beverton–Holt function that describes the Allee effect (Myers et al. 1995; Gascoigne and Lipcius 2004):

$$R_t = \mathrm{x}_t^{\delta-1}/(1 + \beta \cdot \mathrm{x}_t^{\delta}) \quad (3)$$

where δ controls 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 result in stronger Allee effects. β (=45) is a scaling factor that makes density curves look similar at high values (Gascoigne and Lipcius 2004). As broadcast spawners both abalone and sea urchin were simulated with moderate Allee effects $\delta = 3$. The minimum value within a node is 0.0001, below which the node goes extinct.

Modularity and spatial structure

The modularity index indicates whether any division of the network exists and takes values most often within the 0–1 interval (Newman 2006a; Fortunato 2010). Larger values generally indicate that the number of connections within the groups of populations is greater than the connections between the groups. In this study we used the walktrap algorithm, which is based on the criterion a random walker tends to be trapped in dense parts of a network (Pons and Latapy 2006). The walktrap community function of the igraph package in R (Csardi and Nepusz 2006) implements this algorithm to calculate the number of modules or communities (M), the modularity index (Q) and the membership vector. This algorithm is advantageous because it can be used for weighted networks (Pons and Latapy 2006) and is less computationally costly than other algorithms, but performs well at identifying community structure (Steinhaeuser and Chawla 2010; Yang et al. 2016). In our exercise, we used 4 steps as the length of the random walks. The algorithm used weights, but not directionality of edges.

To detect spatial structure of abalone and sea urchin, we calculated the average of the seven potential connectivity matrices of each species and performed the modularity analysis. This average will give us a spatial–temporal baseline of the modularity of the metapopulations, while only considering larval dispersal. We also performed the modularity analysis on each yearly potential connectivity matrix to observe its temporal changes without the simulated fishing pressure.

Modularity and fishing pressure

To explore the temporal changes of modularity under fishing pressure, we used our metapopulation model to simulate various fishing scenarios ($F = 0$, 0.3, 0.4, 0.5) for abalone and sea urchin. In each case, we performed 1000 simulations over a time span of 200 years; in this way we had a large time span to observe any change even at low fishing pressure. Here, all nodes (bins) started with the same high density and fishing mortality along the coast. Even though fishing mortality was constant in our model, it was proportional to local density; hence more was taken in denser locations. Our algorithm quantified occupancy of the node, to detect the occurrence of local extinctions, and the realized larval connectivity matrix for each time step. With the matrix we obtained the average larval connection strength of the network and performed the modularity analysis to calculate the modularity index and the number of modules. We chose one simulation of both abalone and sea urchin with similar time-span under strong fishing pressure ($F = 0.5$) to visualize and compare the dynamics of the nearshore metapopulations and the realized larval connectivity patterns.

Results

Modularity and spatial structure

Modularity analysis revealed a strong spatial signature for abalone in both its average ($Q = 0.5320$) and yearly larval connectivity patterns ($Q = 0.5268 \pm 0.0277$ SD). We found 6 modules in the averaged patterns and 4–8 modules in the yearly patterns (Fig. 1). All connectivity patterns showed two persisting breaks along the coastline that divided the SCB mainland into 3 modules: southern, central and northern. These breaks coincided with large areas of soft substrate, i.e. unsuitable habitat (Fig. S1, Supporting Information). Only in 1996 the southern module split near Carlsbad, an area with suitable habitat, indicating an important change in connectivity patterns that year (Fig. 1).

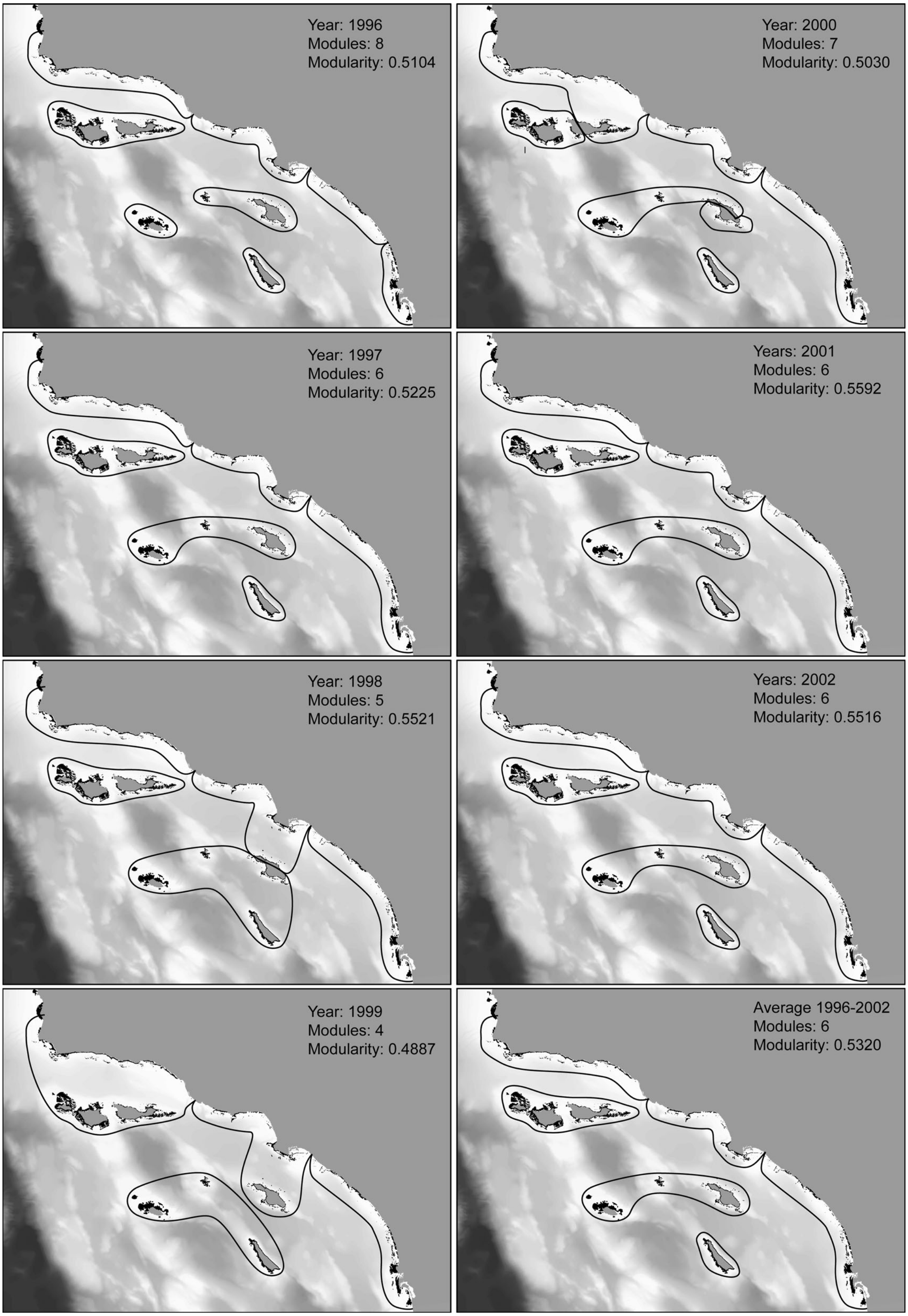
The Northern Channel Islands form one single module in the averaged patterns and 5 of the 7 years analyzed (Fig. 1). In 1999 they joined the northern module, and in 2000 only Anacapa I. and part of Santa Cruz I. joined the northern module. These results show significant larval exchange between these areas than with any other area of the SCB.

The Southern Channel Islands form two modules in the averaged patterns and 3 of the 7 years analyzed: Santa Catalina, Santa Barbara and San Nicolas Islands form one, and San Clemente I. another one (Fig. 1). However, in 1996 San Nicolas I. forms another module, in 1998 all islands form one module, but half of Santa Catalina I. joins the central module, and in 1999 Santa Catalina I. joins the central module and the other islands join as one module.

In the case of sea urchin, the average patterns have 4 modules ($Q = 0.1472$), but the yearly patterns show 3–8 modules ($Q = 0.1568 \pm 0.0666$ SD) (Fig. 2). The low modularity indexes indicated a weak spatial signature for sea urchin. Distant nodes can be grouped into modules, indicating low spatial correlation. Here, the averaged patterns show the northern and central coastal area and the Northern Channel Islands forming one single module, the Southern Channel Islands forming another one, and the southern coastal area splitting at around Carlsbad into two modules (Fig. 2). However, the yearly patterns show distant locations grouping into single modules. These results indicate more mixing among distant modules of the sea urchin metapopulation.

Modularity and fishing pressure

Without fishing mortality, the simulated abalone metapopulation showed a strong modular structure. The analysis showed the modularity index varying mainly between 0.43 and 0.55, and the number of modules between 5 and 10 (Fig. 3). When the metapopulation underwent moderate fishing pressure, the modularity index diminished and dropped below 0.45, but there was no metapopulation extinction as


Year: 1996
Modules: 8
Modularity: 0.5104
Year: 2000
Modules: 7
Modularity: 0.5030
Year: 1997
Modules: 6
Modularity: 0.5225
Years: 2001
Modules: 6
Modularity: 0.5592
Year: 1998
Modules: 5
Modularity: 0.5521
Years: 2002
Modules: 6
Modularity: 0.5516
Year: 1999
Modules: 4
Modularity: 0.4887
Average 1996-2002
Modules: 6
Modularity: 0.5320

◀**Fig. 1** Modules and modularity indexes based on potential larval connectivity estimates (Mitarai et al. 2009; Watson et al. 2010) of abalone in the Southern California Bight for the period 1996–2002

fishing continued. As fishing pressure increased, modularity showed a rapid drop between 30 and 50 years of fishing, followed by a plateau around 0.2, until the metapopulation collapses. When fishing pressure was strong, modularity decreased more rapidly after 20 years of fishing, to slow down after 30 years until metapopulation collapse. Therefore, before the extinction of abalone metapopulation, we can observe one important drop in modularity; as fishing pressure continues modularity drops until extinction.

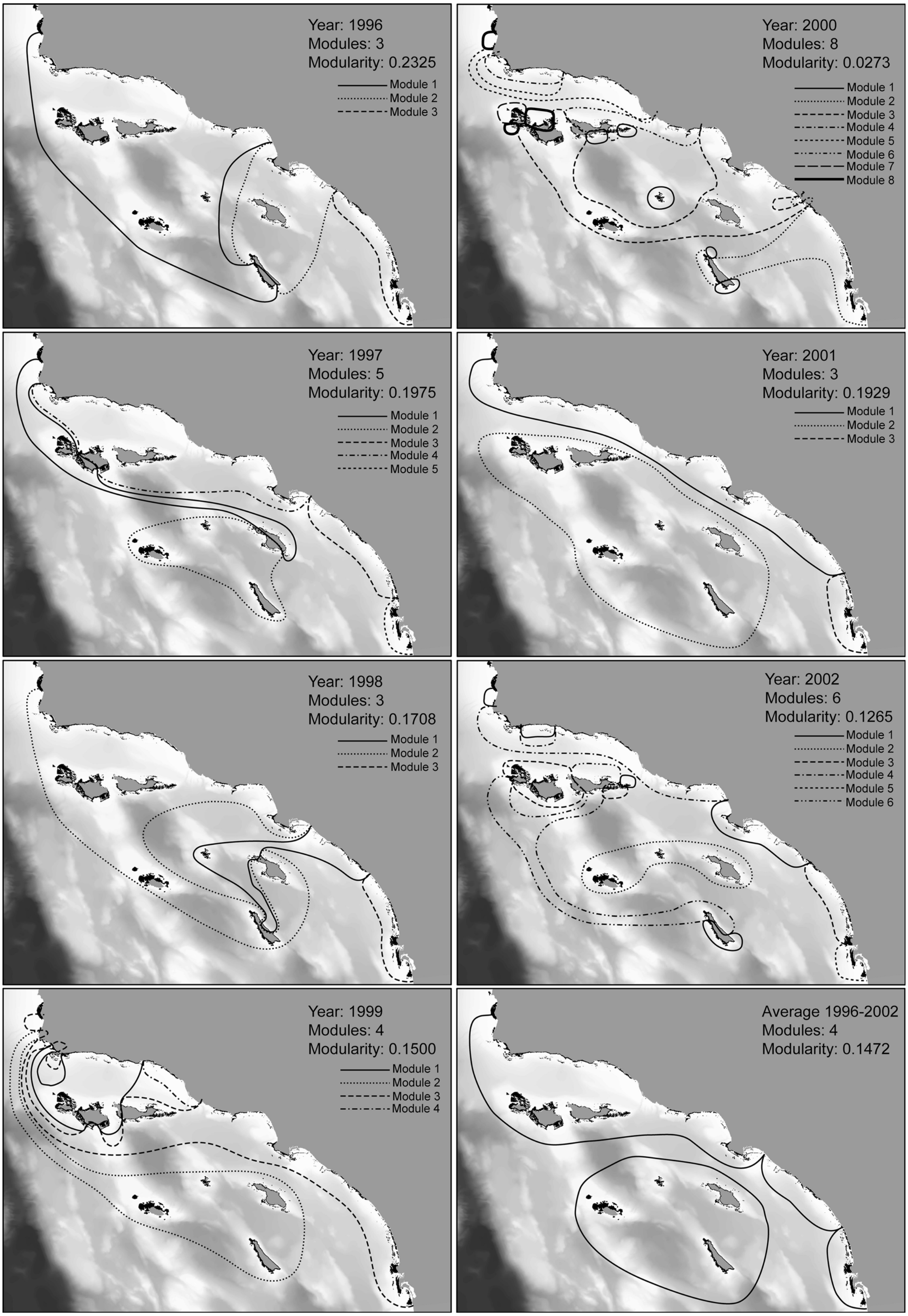
As modularity dropped there was a rapid increase in the number of modules detected by the algorithm, after which the number of modules decreased until extinction (Fig. 4). During these time spans, the average larval connection strength decreases and occupancy oscillates until it finally drops to extinction (Figs. S2, S3, Supporting Information). As fishing pressure increases, time to extinction becomes more uniform (Fig. S3, Supporting Information). These results indicate a decrease in the ratio of within-module connections and between-module connections of the simulated abalone metapopulations. Moreover, large modules, such as the southern module, breakdown into smaller modules of weakly interconnected nodes that go extinct rapidly (Fig. 5). Despite the collapse of the southern module, the northern modules (mainland and Northern Channel Islands) and those nodes connected to them seem to last longer under strong fishing pressure.

For the sea urchin metapopulation, the picture is different. Without fishing mortality, the analysis revealed relatively low modularity compared to abalone. Over the course of time, modularity oscillated widely between 0.03 and 0.33, where modules fluctuated between 2 and 16 (Figs. 3, 4). When fishing mortality increased, modularity behaved similarly over time, stopping abruptly when metapopulations collapsed (Fig. 3). There was no clear indication of modules splitting over time; only in about 3% of the simulations we observed large picks 2–4 years before collapse (Fig. 4). The largest pick for $F = 0.4$ and 0.5 appear 12 years before collapse. The average connection strength oscillated greatly over time, and decreased more rapidly as fishing pressure increased (Fig. S2, Supporting Information). Occupancy in the sea urchin metapopulation did not show temporal oscillation before collapse like in the case of abalone metapopulation (Fig. S3, Supporting Information). These results indicate that sea fishing pressure weakens sea urchin's larval dispersal evenly across the SCB until the metapopulation collapses (Fig. 6).

Discussion

In the present study, we used network modularity to assess spatial structure of nearshore metapopulations and the impact of fishing mortality on their temporal and spatial dynamics. The modularity analysis showed a strong spatial signature for abalone and a weak one for sea urchin. Genetic research however shows some indication of spatial genetic structure for both species without geographic correlation (Kirby et al. 1998; Moberg and Burton 2000; Debenham et al. 2000; Gruenthal et al. 2007). The analysis also revealed stepwise drops in modularity and a rapid increase in the number of modules that abalone simulated metapopulations under exploitation experienced on the path to extinction. Weakening of within-module connections result in a fragmentation of large modules into small modules, followed by module extinction, and metapopulation extinction. In contrast, sea urchin simulated metapopulations showed great modularity variation, but collapsed abruptly under fishing pressure. We propose that abalone's lack of recovery in different areas of the SCB mainland might be due to diminished larval supply from regional ocean connections. In sum, these results emphasize the ability of modularity analysis to detect not only spatial structure in marine metapopulations, which varies among species, but also early changes in the spatial structure of metapopulations under exploitation.

However, there are notable caveats to modularity analysis especially that of resolution limit (Fortunato and Barthélemy 2007). Jacobi et al. (2012) suggests that modules identified from connectivity matrices are subpopulations. Therefore, the ability to detect small modules would be important to identify distinct subpopulations. Identifying modules would mean genetic and behavioral differences with consequences on its local dynamics (Sterner 2007), giving more


Year: 1996
Modules: 3
Modularity: 0.2325
Module 1
Module 2
Module 3
Year: 2000
Modules: 8
Modularity: 0.0273
Module 1
Module 2
Module 3
Module 4
Module 5
Module 6
Module 7
Module 8
Year: 1997
Modules: 5
Modularity: 0.1975
Module 1
Module 2
Module 3
Module 4
Module 5
Year: 2001
Modules: 3
Modularity: 0.1929
Module 1
Module 2
Module 3
Year: 1998
Modules: 3
Modularity: 0.1708
Module 1
Module 2
Module 3
Year: 2002
Modules: 6
Modularity: 0.1265
Module 1
Module 2
Module 3
Module 4
Module 5
Module 6
Year: 1999
Modules: 4
Modularity: 0.1500
Module 1
Module 2
Module 3
Module 4
Average 1996-2002
Modules: 4
Modularity: 0.1472

◀**Fig. 2** Modules and modularity indexes based on potential larval connectivity estimates (Mitarai et al. 2009; Watson et al. 2010) of sea urchin in the Southern California Bight for the period 1996–2002. To differentiate modules formed by distant locations, we used *different lines*

support for the use of metapopulation theory to study marine populations. Different within-module dynamics could also mean different harvest potential and a different management approach (Svedäng et al. 2010). On the other hand, the ability to detect small modules will depend on the spatial scale of subpopulations (which is often a choice by the investigator), as well as the metapopulation, and ultimately the network algorithms applied to identify modules. For instance, we used the walktrap algorithm (Pons and Latapy 2006), which is designed to detect modularity at both small and large networks. Other algorithms could have been used for the analysis, for example betweenness (Girvan and Newman 2002) and eigenvector (Newman 2006b) modularity, but several of these are limited in their ability to identify small modules (Fortunato and Barthélemy 2007). As a consequence, when attempting to identify subpopulations or modules within a metapopulation, for example for spatial management purposes, an exploration of results created by different algorithms is suggested.

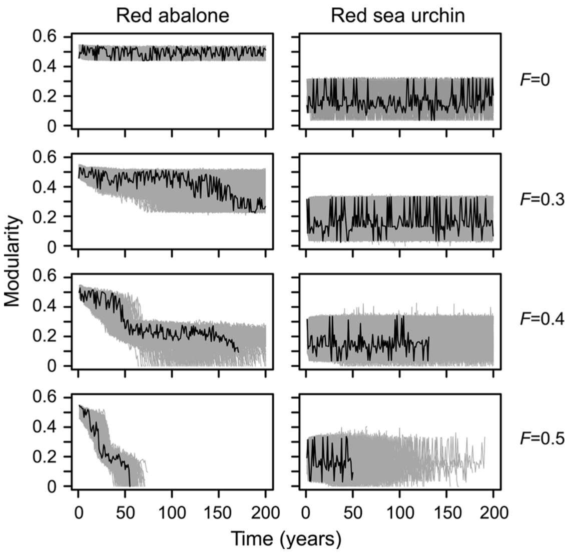


Fig. 3 Modularity time series obtained with the walktrap algorithm for simulations of abalone and sea urchin metapopulations with increasing fishing mortality. The figure depicts one simulation highlighted for illustration

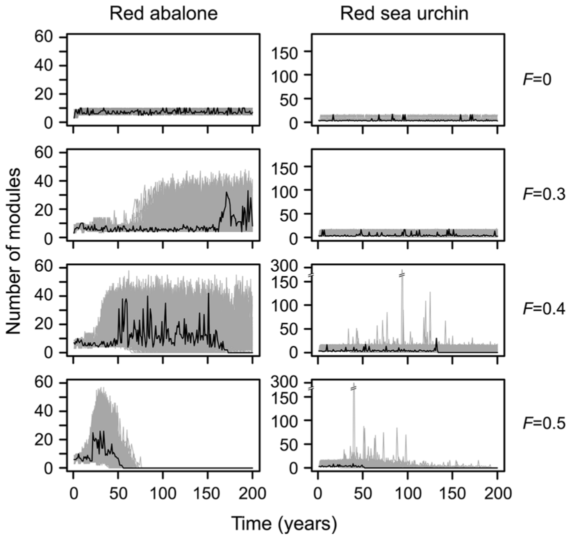


Fig. 4 Module-number time series found by the walktrap algorithm for simulations of abalone and sea urchin metapopulations with increasing fishing mortality. The figure depicts one simulation highlighted for illustration

Our results suggest that the abalone metapopulation in the SCB could have presented a spatial structure with distinct subpopulations (modules) with geographic correlation. Although genetic research on abalone show no geographic correlation along the coast of California, it does show some genetic differentiation (Kirby et al. 1998; Gruenthal et al. 2007). We also show the breakdown and extinction of modules under exploitation. This may be important for the application of metapopulation theory in the study of marine populations, which emphasizes connectivity dynamics, but downplays extinction and colonization (Kritzer and Sale 2004). Our study shows that under fishing pressure, these systems may behave as fragmented metapopulations, much like the terrestrial systems (Opdam 1991). Here, extinction rate would depend on the breakdown of large modules into small modules (within module connections), and recolonization rate of modules (between module connections).

The repeated divisions of modules identify a disruption in larval connectivity, revealing a sort of fragmentation without the disruption of the habitat. These dynamics however cannot be corroborated by genetic studies given that abalone has been depleted in most of the SCB (Karpov et al. 2000). Only some populations remain in the Northern Channel Islands, especially San Miguel Island. This distribution

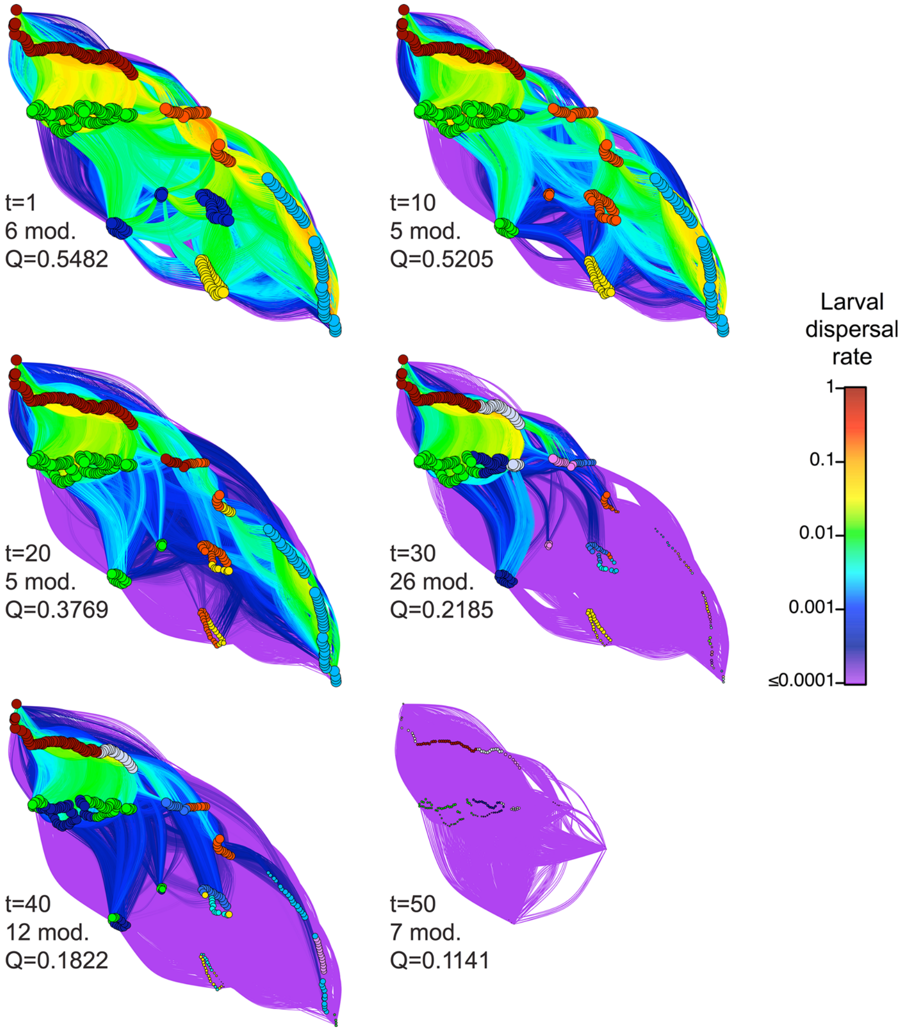


Fig. 5 Network of the abalone metapopulation in the SCB under intense fishing pressure ($F = 0.5$) at years 1, 10, 20, 30, 40 and 50. Vertex size is proportional to the logarithm of the local density, and vertex color defines a module. Edge color is proportional to the logarithm of larval dispersal rates

matches patterns that we saw in our simulations, where the Northern Channel Islands stayed longer. We hypothesize that historical abalone collapse in the SCB may have been influenced not only by exploitation patterns (Karpov et al. 2000 show proportional landings from the mainland and the islands), but also by slow deterioration of region-wide larval connectivity pathways. In general, these qualitative similarities between our simulations and real-world events indicate that connectivity is an important factor when trying to understand extirpation events and region-wide collapses of fish stocks, relative to other possible contributing factors such as habitat fragmentation.

Sea urchin has shown a weak spatial structure with modules grouping distant nodes. This pattern has also been found in previous genetic research (Moberg and Burton 2000). However, our results also reveal great variation in modularity values, where high modularity could indicate years of low mixing. This variation most likely depends on temporal variability of ocean currents (Treml et al. 2008). Nevertheless, years of low mixing could be reflected in greater genetic differentiation among recruits without great effect on the adults (Moberg and Burton 2000). These results could have implications on the management of sea urchin. Fishing has already begun to decline densities in the SCB, and it has been hypothesized that juvenile recruitment has mitigated fishing pressure so far (Leet et al. 2001). It is likely that high variation in their modularity also reflects years of high mixing that favor replenishment of fished areas. However, this effect may only be masking the road to regional collapse,

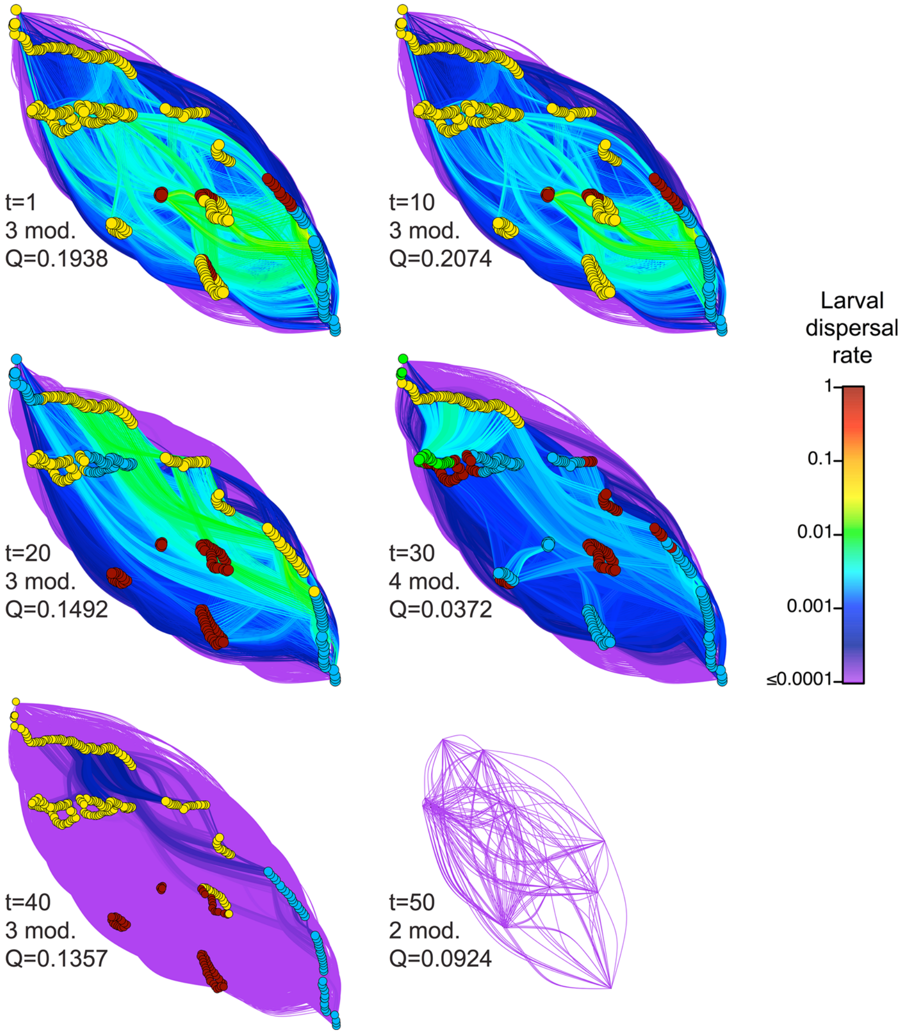


Fig. 6 Network of the sea urchin metapopulation in the SCB under intense fishing pressure ($F = 0.5$) at years 1, 10, 20, 30, 40 and 50. Vertex size is proportional to the logarithm of local density, and vertex color defines a module. Edge color is proportional to the logarithm of larval dispersal rates

which could be a point of no return for sea urchin in the SCB.

Highly connected networks can show resistance to change, but collapse abruptly when a critical stress level is reached, while modular networks are expected to adjust gradually to stress (Dunne et al. 2002; van Nes and Scheffer 2005; Scheffer et al. 2012). As seen above, this may be true for the weakly modular sea urchin metapopulation. However, as fishing continues and mortality increases, modularity shows step-wise changes for the abalone metapopulation. Borthagaray et al. (2014) proposes modularity as an early-warning tool that measures distance to tipping points considering its gradual response to dispersal ability. Our study, which analyzes both spatial and temporal dynamics, shows that modularity could also capture early changes in the spatial structure of exploited systems. Therefore, the modularity index might be used as an early warning signal (Scheffer et al. 2009) for tipping points in metapopulation connectivity. These tipping points are not critical transitions, in the dynamical systems sense, but an important change in the spatial structure that can affect the overall state of the system. In that sense, modularity of metapopulations could be used as an early warning signal of region-wide collapse, but only under certain ecological conditions (e.g. short PLD).

Metapopulation modularity is also useful when designing spatial forms of marine policy, such as marine protected areas, because it suggests the presence of distinct subpopulations divided by dispersal barriers (Jacobi et al. 2012). For instance, managing fish stocks as single large entities can lead to overestimates of growth and harvest potential (Sterner 2007). Therefore, in order to improve upon this, spatial management should acknowledge the spatial structure and presence of distinct subpopulations (modules) within metapopulations. Abalone in northern California still holds an important abalone fishery (California Department of Fish and Game 2005) and a previous study has shown genetic differentiation between subpopulations there (Gruenthal et al. 2007). However, abalone in this region is managed as one single stock and the results presented here suggest that more spatially nuanced management in this region would lead to a healthier stock (California Department of Fish and Game 2005; Svedäng et al. 2010). Past experience in cod have demonstrated that ignoring subpopulations for management can lead to stock collapse and slow recovery (Sterner 2007).

In conclusion, when analyzing the modularity of nearshore metapopulations we detected a relationship between spatial and temporal dynamics. The analysis of potential connectivity showed us a strong spatial structure in the abalone metapopulation and a weak one in the sea urchin metapopulation of the SCB. The analysis of realized connectivity showed us a stepwise decline of modularity, a serial fragmentation and ultimate collapse for abalone, whereas sea urchin showed great modularity variation and an abrupt collapse of the metapopulation. These results could indicate a pattern of subpopulation collapse for abalone, driven by heavy exploitation over several decades that reduced within- and between-module larval dispersal rates. We propose that the observed patterns of collapse could be a factor determining its current distribution. These differences highlight previously unappreciated nuance to metapopulation modularity, which has been simply hypothesized to (always) increase the resilience of metapopulations to perturbation (Kashtan et al. 2009; Fletcher et al. 2013). Last, abalone and sea urchin have similar distribution, and as a consequence they might be considered similar in terms of their management requirements. However, as we have shown, they show dramatic differences in their spatial metapopulation structure and temporal dynamics in response to exploitation. As a consequence they actually demand very different approaches to spatial marine management. This will be true of other marine species with similar life history strategies, e.g. purple sea urchin, (Rogers-Bennett 2013), other abalone species (Leet et al. 2001), and other benthic species. Ultimately, modularity analyses can be used to group species based on their potential spatial response to exploitation. In doing so, approaches to spatial management like marine protected areas, can be designed more effectively.

Acknowledgements This work was supported by NSF Grants OCE-0410439 as part of the Project "Linking Human and Biophysical Processes in the Coastal Marine Ecosystem of Baja California", and GEO-1211972 as part of the CNH Project "Complexity and Adaptation in Marine Social-ecological Systems". We also thank Satoshi Mitarai and David Siegel for creating the connectivity data, Laura Rogers-Bennett and Cynthia Catton for the useful information of red abalone and red sea urchin, and the Pisco Project for the abalone and sea urchin data made available in their website (http://www.piscoweb.org).

References

Bell SS, Brooks RA, Robbins BD, Fonseca MS, Hall MO (2001) Faunal response to fragmentation in seagrass habitats: implications for seagrass conservation. Biol Conserv 100:115–123. doi:10.1016/S0006-3207(00)00212-3

Berec L, Angulo E, Courchamp F (2007) Multiple Allee effects and population management. Trends Ecol Evol 22:185–191

Bonin MC, Almany GR, Jones GP (2011) Contrasting effects of habitat loss and fragmentation on coral-associated reef fishes. Ecology 92:1503–1512

Borthagaray AI, Barreneche JM, Abades S, Arim M (2014) Modularity along organism dispersal gradients challenges a prevailing view of abrupt transitions in animal landscape perception. Ecography 37:564–571

Caley MJ, Carr MH, Hixon MA, Hughes TP, Jones GP, Menge BA (1996) Recruitment and the local dynamics of open marine populations. Annu Rev Ecol Syst 27:477–500. doi:10.1146/annurev.ecolsys.27.1.477

California Department of Fish and Game (2005) Abalone recovery and management plan. The Resources Agency, Sacramento

Carlisle J (1962) Spawning and early life history of *Haliotis rufescens*. Nautilus 76:44–48

Cavanaugh KC, Siegel DA, Raimondi PT, Alberto F (2014) Patch definition in metapopulation analysis: a graph theory approach to solve the mega-patch problem. Ecology 95:316–328

Ciannelli L, Fisher JAD, Skern-Mauritzen M, Hunsicker ME, Hidalgo M, Frank KT, Bailey KM (2013) Theory, consequences and evidence of eroding population spatial structure in harvested marine fishes: a review. Mar Ecol Prog Ser 480:227–243. doi:10.3354/meps10067

Cowen RK, Paris CB, Srinivasan A (2006) Scaling of connectivity in marine populations. Science 311:522–527

Crandall ED, Treml EA, Liggins L, Gleeson L, Yasuda N, Barber PH, Wörheide G, Riginos C (2014) Return of the ghosts of dispersal past: historical spread and contemporary gene flow in the blue sea star *Linckia laevigata*. Bull Mar Sci 90:399–425. doi:10.5343/bms.2013.1052

Csardi G, Nepusz T (2006) The igraph software package for complex network research. InterJ Complex Syst, 1695. http://igraph.orgwhere journal=InterJournal, volume=Complex Systems, pages=1695

De Wit P, Palumbi SR (2013) Transcriptome-wide polymorphisms of red abalone (*Haliotis rufescens*) reveal patterns of gene flow and local adaptation. Mol Ecol 22:2884–2897

Debenham P, Brzezinski M, Foltz K, Gaines S (2000) Genetic structure of populations of the red sea urchin, *Strongylocentrotus franciscanus*. J Exp Mar Biol Ecol 253:49–62

Denny MW, Shibata MF (1989) Consequences of surf-zone turbulence for settlement and external fertilization. Am Nat 134:859–889

Deza AA, Anderson TW (2010) Habitat fragmentation, patch size, and the recruitment and abundance of kelp forest fishes. Mar Ecol Prog Ser 416:229–240

Dong C, McWilliams JC (2007) A numerical study of island wakes in the Southern California Bight. Cont Shelf Res 27:1233–1248

Dong C, McWilliams JC, Shchepetkin AF (2007) Island wakes in deep water. J Phys Oceanogr 37:962–981

Dong C, Idica EY, McWilliams JC (2009) Circulation and multiple-scale variability in the Southern California Bight. Prog Oceanogr 82:168–190

Dunne JA, Williams RJ, Martinez ND (2002) Network structure and biodiversity loss in food webs: robustness increases with connectance. Ecol Lett 5:558–567

FAO (2012) The state of the world fisheries and aquaculture 2012. Rome

Fletcher Jr RJ, Revell A, Reichert BE, Kitchens WM, Dixon JD, Austin JD (2013) Network modularity reveals critical scales for connectivity in ecology and evolution. Nat Commun. doi:10.1038/ncomms3572

Fortunato S (2010) Community detection in graphs. Phys Rep 486:75–174

Fortunato S, Barthélemy M (2007) Resolution limit in community detection. Proc Natl Acad Sci 104:36–41

Gascoigne J, Lipcius RN (2004) Allee effects in marine systems. Mar Ecol Prog Ser 269:49–59

Girvan M, Newman MEJ (2002) Community structure in social and biological networks. Proc Natl Acad Sci 99:7821–7826

Goodsell PJ, Connell SD (2002) Can habitat loss be treated independently of habitat configuration? Implications for rare and common taxa in fragmented landscapes. Mar Ecol Prog Ser 239:37–44

Gruenthal KM, Acheson LK, Burton RS (2007) Genetic structure of natural populations of California red abalone (*Haliotis rufescens*) using multiple genetic markers. Mar Biol 152:1237–1248

Halpern BS, Walbridge S, Selkoe KA, Kappel CV, Micheli F, D'Agrosa C, Bruno JF, Casey KS, Ebert C, Fox HE, Fujita R, Heinemann D, Lenihan HS, Madin EMP, Perry MT, Selig ER, Spalding M, Steneck R, Watson R (2008) A global map of human impact on marine ecosystems. Science 319:948–952. doi:10.1126/science.1149345

Harrold C, Reed DC (1985) Food availability, sea urchin grazing, and kelp forest community structure. Ecology 66:1160–1169

Jackson JBC, Kirby MX, Berger WH, Bjorndal KA, Botsford LW, Bourque BJ, Bradbury RH, Cooke R, Erlandson J, Estes JA, Hughes TP, Kidwell S, Lange CB, Lenihan HS, Pandolfi JM, Peterson CH, Steneck RS, Tegner MJ, Warner RR (2001) Historical overfishing and the recent collapse of coastal ecosystems. Science 293:629–637. doi:10.1126/science.1059199

Jacobi MN, André C, Döös K, Jonsson PR (2012) Identification of subpopulations from connectivity matrices. Ecography 35:1004–1016

Johnson SY, Dartnell P, Cochrane GR, Golden NE, Phillips EL, Ritchie AC, Greene HG, Krigsman LM, Kvitek RG, Dieter BE, Endris CA, Seitz GG, Sliter RW, Erdey MD, Gutierrez CI, Wong FL, Yoklavich MM, Draut AE, Hart PE, Conrad JE (2013) California state waters map series: offshore of Santa Barbara, California. United States Geological Survey, Reston, VA

Kaplan DM, Botsford LW, O'Farrell MR, Gaines SD, Jorgensen S (2009) Model-based assessment of persistence in proposed marine protected area designs. Ecol Appl 19:433–448. doi:10.1890/07-1705.1

Karpov KA, Haaker PL, Taniguchi IK, Rogers-Bennett L (2000) Serial depletion and the collapse of the California abalone (*Haliotis* spp.) fishery. In: Campbell A (ed) Workshop on rebuilding abalone stocks in British Columbia. NRC Research Press, Ottawa, pp 11–24

Kashtan N, Parter M, Dekel E, Mayo AE, Alon U (2009) Extinctions in heterogeneous environments and the evolution of modularity. Evolution 63:1964–1975. doi:10.1111/j.1558-5646.2009.00684.x

Kato S, Schroeter SC (1985) Biology of the red sea urchin, *Strongylocentrotus franciscanus*, and its fishery in California. Mar Fish Rev 47:1–20

Keitt TH, Urban DL, Milne BT (1997) Detecting critical scales in fragmented landscapes. Conserv Ecol 1:4

Kikuchi S, Uki N (1974) Technical study on artificial spawning of abalone, genus *Haliotis* III. Reasonable sperm density for fertilization. Bull Tohoku Reg Fish Res Lab 34:67–71

Kinlan BP, Gaines SD (2003) Propagule dispersal in marine and terrestrial environments: a community perspective. Ecology 84:2007–2020

Kirby VL, Villa R, Powers DA (1998) Identification of microsatellites in the California red abalone, *Haliotis rufescens*. J Shellfish Res 17:801–804

Kritzer JP, Sale PF (2004) Metapopulation ecology in the sea: from Levins' model to marine ecology and fisheries science. Fish Fish 5:131–140

Leaf RT, Andrews AH, Cailliet GM, Brown TA (2008) The feasibility of bomb radiocarbon analysis to support an age-at-length relationship for red abalone, *Haliotis rufescens* Swainson in Northern California. J Shellfish Res 27:1177–1182

Leet WS, Dewees CM, Klingbeil R, Larson EJ (2001) California's living marine resources: a status report. UCANR Publications, Sacramento

Leighton DL (1966) Studies of food preference in algivorous invertebrates of Southern California kelp beds. Pac Sci 20:104–113

Leighton DL (1974) The influence of temperature on larval and juvenile growth in three species of Southern California abalones. Fish Bull 72:1137–1145

Levitan DR (2002) Density-dependent selection on gamete traits in three congeneric sea urchins. Ecology 83:464–479

Miller KJ, Maynard BT, Mundy CN (2008) Genetic diversity and gene flow in collapsed and healthy abalone fisheries. Mol Ecol 18:200–211

Minor ES, Urban DL (2007) Graph theory as a proxy for spatially explicit population models in conservation planning. Ecol Appl 17:1771–1782

Mitarai S, Siegel DA, Watson JR, Dong C, McWilliams JC (2009) Quantifying connectivity in the coastal ocean with application to the Southern California Bight. J Geophys Res Oceans 114:C10026. doi:10.1029/2008JC005166

Moberg PE, Burton RS (2000) Genetic heterogeneity among adult and recruit red sea urchins, *Strongylocentrotus franciscanus*. Mar Biol 136:773–784

Myers RA, Barrowman NJ, Hutchings JA, Rosenberg AA (1995) Population dynamics of exploited fish stocks at low population levels. Science 269:1106–1108

Newman MEJ (2006a) Modularity and community structure in networks. Proc Natl Acad Sci 103:8577–8582

Newman MEJ (2006b) Finding community structure in networks using the eigenvectors of matrices. Phys Rev E 74:36104

Opdam P (1991) Metapopulation theory and habitat fragmentation: a review of holarctic breeding bird studies. Landscape Ecol 5:93–106

Paris CB, Helgers J, van Sebille E, Srinivasan A (2013) Connectivity modeling system: a probabilistic modeling tool for the multi-scale tracking of biotic and abiotic variability in the ocean. Environ Model Softw 42:47–54

Pauly D (2009) Beyond duplicity and ignorance in global fisheries. Sci Mar. 73:215–224

Planes S, Jones GP, Thorrold SR (2009) Larval dispersal connects fish populations in a network of marine protected areas. Proc Natl Acad Sci 106:5693–5697

Pons P, Latapy M (2006) Computing communities in large networks using random walks. J Graph Algorithms Appl 10:191–218

Rogers-Bennett L (2013) *Strongylocentrotus franciscanus* and *Strongylocentrotus purpuratus*. In: Lawrence John M (ed) Sea urchins: biology and ecology. Elsevier, Amsterdam, pp 413–435

Rogers-Bennett L, Dondanville RF, Kashiwada J (2004) Size specific fecundity of red abalone (*Haliotis rufescens*): evidence for reproductive senescence? J Shellfish Res 23:553–560

Scheffer M, Bascompte J, Brock WA, Brovkin V, Carpenter SR, Dakos V, Held H, van Nes EH, Rietkerk M, Sugihara G (2009) Early-warning signals for critical transitions. Nat 461:53–59. doi:10.1038/nature08227

Scheffer M, Carpenter SR, Lenton TM, Bascompte J, Brock W, Dakos V, van de Koppel J, van de Leemput I, Levin SA, van Nes EH, Pascual M, Vandermeer J (2012) Anticipating critical transitions. Science 338:344–348. doi:10.1126/science.1225244

Shchepetkin AF, McWilliams JC (2005) The regional oceanic modeling system (ROMS): a split-explicit, free-surface, topography-following-coordinate oceanic model. Ocean Model 9:347–404

Steinhaeuser K, Chawla NV (2010) Identifying and evaluating community structure in complex networks. Pattern Recognit Lett 31:413–421

Sterner T (2007) Unobserved diversity, depletion and irreversibility. The importance of subpopulations for management of cod stocks. Ecol Econ 61:566–574

Svedäng H, Stål J, Sterner T, Cardinale M (2010) Consequences of subpopulation structure on fisheries management: cod (*Gadus morhua*) in the Kattegat and Öresund (North Sea). Rev Fish Sci 18:139–150

Treml EA, Halpin PN, Urban DL, Pratson LF (2008) Modeling population connectivity by ocean currents, a graph-theoretic approach for marine conservation. Landscape Ecol 23:19–36

van Nes EH, Scheffer M (2005) Implications of spatial heterogeneity for catastrophic regime shifts in ecosystems. Ecology 86:1797–1807

Watson JR, Mitarai S, Siegel DA, Caselle JE, Dong C, McWilliams JC (2010) Realized and potential larval connectivity in the Southern California Bight. Mar Ecol Prog Ser 401:31–48. doi:10.3354/meps08376

Watson JR, Siegel DA, Kendall BE, Mitarai S, Rassweiller A, Gaines SD (2011) Identifying critical regions in small-world marine metapopulations. Proc Natl Acad Sci 108:E907–E913. doi:10.1073/pnas.1111461108

White JW, Botsford LW, Moffitt EA, Fischer DT (2010) Decision analysis for designing marine protected areas for multiple species with uncertain fishery status. Ecol Appl 20:1523–1541

Yang Z, Algesheimer R, Tessone CJ (2016) A comparative analysis of community detection algorithms on artificial networks. Sci Rep 6:30750