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Álvarez-Romero, JG, Munguía-Vega, A, Beger, M et al. (17 more authors) (2018) Designing connected marine reserves in the face of global warming. Global Change Biology, 24 (2). e671-e691. ISSN 1354-1013

https://doi.org/10.1111/gcb.13989

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Designing connected marine reserves in the face of global warming

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Keywords: marine conservation; systematic conservation planning; ecological network; larval dispersal; ocean warming; Gulf of California; marine reserve network; ecological process

Type of paper: Primary Research Article

Running head: Marine reserve networks and ocean warming

Citation: Álvarez-Romero, J. G., A. Munguía-Vega, M. Beger, M. Mancha-Cisneros, A. Suárez-Castillo, G. Gurney, R. Pressey, L. Gerber, H. Morzaria-Luna, H. Reyes-Bonilla, V. Adams, M. Kolb, E. Graham, J. VanDerWal, A. Castillo-López, G. Hinojosa-Arango, D. Petatán-Ramírez, M. Moreno-Baez, C. Godínez-Reyes, and J. Torre. 2017. Designing connected marine reserves in the face of global warming. *Global Change Biology*. DOI: 10.1111/gcb.13989

Abstract: Marine reserves are widely used to protect species important for conservation and fisheries and to help maintain ecological processes that sustain their populations, including recruitment and dispersal. Achieving these goals requires well-connected networks of marine reserves that maximize larval connectivity, thus allowing exchanges between populations and recolonization after local disturbances. However, global warming can disrupt connectivity by shortening potential dispersal pathways through changes in larval physiology. These changes can compromise the performance of marine reserve networks, thus requiring adjusting their design to account for ocean warming. To date, empirical approaches to marine prioritization have not considered larval connectivity as affected by global warming. Here, we develop a framework for designing marine reserve networks that integrates graph theory and changes in larval connectivity due to potential reductions in planktonic larval duration (PLD) associated with ocean warming, given current socioeconomic constraints. Using the Gulf of California as case study, we quantify the benefits and costs of adjusting networks to account for connectivity, with and without ocean warming. We compare reserve networks designed to achieve representation of species and ecosystems with networks designed to also maximize connectivity under current and future ocean-warming scenarios. Our results indicate that current larval connectivity could be reduced significantly under ocean warming because of shortened PLDs. Given the potential changes in connectivity, we show that our graph-theoretical approach based on centrality (eigenvector and distance-weighted fragmentation) of habitat patches can help design better-connected marine reserve networks for the future with equivalent costs. We found that maintaining dispersal connectivity incidentally through representation-only reserve design is unlikely, particularly in regions with strong asymmetric patterns of dispersal connectivity. Our results support previous studies suggesting that, given potential reductions in PLD due to ocean warming, future marine reserve networks would require more and/or larger reserves in closer proximity to maintain larval connectivity.

Introduction

Maintaining marine ecosystem services such as fisheries, recreation, and coastal protection is critical to safeguarding the livelihoods of coastal communities (Barbier *et al.*, 2010), particularly those highly dependent on marine resources (Sadovy, 2005). Marine reserves are widely used management tools to reduce fishing pressure and prevent habitat destruction (Allison *et al.*, 1998, Boonzaier & Pauly, 2016), with ecological and socioeconomic benefits (Gerber *et al.*, 2003, Lester *et al.*, 2009, Gurney *et al.*, 2014). Marine reserves can increase the resilience of marine ecosystems against impacts of climate change (Micheli *et al.*, 2012, Gurney *et al.*, 2013, Duffy *et al.*, 2016), particularly with respect to enhancing recovery processes after disturbance (Mellin *et al.*, 2016). Recovery through resettlement depends largely on maintaining the supply of larvae, underpinning the need for well-connected networks of marine reserves (Beger *et al.*, 2015). Consequently, linking marine reserves within networks is pivotal to the long-term persistence of marine populations (Almany *et al.*, 2009, Magris *et al.*, 2014), while also providing benefits to fisheries and conservation (Harrison *et al.*, 2012, Olds *et al.*, 2016). However, dispersal connectivity can be affected by climate change through reduced larval dispersal distances resulting from shortened planktonic larval duration (PLD), habitat loss, and reduction in reproductive output (O'Connor *et al.*, 2007, Munday *et al.*, 2009, Lett *et al.*, 2010), thus compromising the performance of marine reserve networks (Andrello *et al.*, 2015, Kleypas *et al.*, 2016).

Systematic conservation planning (SCP) is widely used to design marine reserves with conservation and socioeconomic objectives (Leslie, 2005, Ban *et al.*, 2013). Methods in marine SCP that incorporate spatially-explicit information on ecological connectivity (i.e., demographic links among populations via the dispersal of individuals as adults, juveniles, and larvae) are advancing rapidly (Magris *et al.*, 2014). Progress has been facilitated by development of new prioritization methods (Beger *et al.*, 2010, Engelhard *et al.*, 2017, Krueck *et al.*, 2017), improved oceanographic and connectivity modeling (Paris *et al.*, 2007, Treml *et al.*, 2008, Kool *et al.*, 2013), and better knowledge of ecological processes mediated by larval dispersal and adult movements (Gaines *et al.*, 2007, Cowen & Sponaugle, 2009, Green *et al.*, 2015). From the earliest and relatively simple marine SCP applications (e.g., Sala *et al.*, 2002) to the latest and more complex approaches (e.g., Bode *et al.*, 2016), several methods have been developed to design networks of marine reserves that consider connectivity, with varying levels of sophistication and data requirements (Magris *et al.*, 2014).

A common approach to planning for marine connectivity involves graph theory (Dale & Fortin, 2010) to represent and understand the structure of ecological networks, defined by links (i.e., ties or edges) between nodes (e.g., habitat patches) mediated through the exchange of organisms between nodes (e.g., larvae transported in ocean currents) (Treml *et al.*, 2008, Kool *et al.*, 2013). Under this approach, the centrality (Borgatti, 2005) of habitat patches (i.e., their relative importance based on their position within a network) can identify those contributing most to maintaining the overall connectivity of marine reserves (Beger *et al.*, 2010, Kininmonth *et al.*, 2011, Kool *et al.*, 2013). Graph-theoretical approaches vary in their conceptualization of centrality and level of sophistication, with most applications developing customized optimization algorithms given the limitations of existing planning software (e.g., Watson *et al.*, 2011, Jonsson *et al.*, 2016). Other graph-theoretical applications have used readily available and widely used conservation planning tools, such as Marxan (Ball *et al.*, 2009), to target self-persistent and highly central habitat patches. These studies have used habitat quality to adjust the potential contributions of habitat patches to connectivity (e.g., Magris *et al.*, 2016) and metapopulation models to assess the performance of marine reserve networks (e.g., White *et al.*, 2014). A common finding of these applications is that including spatially-explicitly information on connectivity can improve the design and performance of networks of marine reserves.

Despite recent advances in planning for marine connectivity, important research gaps remain. One major challenge is understanding how potential changes in connectivity patterns associated with climate change can affect existing marine reserves and how this information can be used to modify the configuration of marine reserve networks (Gerber *et al.*, 2014). Disregarding the effects of warming oceans on connectivity can significantly reduce the future performance of marine reserve networks because shorter larval dispersal distances mean that larval exchange and recruitment among reserves cease or are severely reduced (Andrello *et al.*, 2015).

Most marine SCP studies including climate change have focused on identifying areas that can act as thermal refugia or provide opportunities for adaptation under climate change (Levy & Ban, 2013, Magris *et al.*, 2015), but do not consider connectivity. To our knowledge, only three studies combine spatially-explicit connectivity and ecosystem responses to thermal stress to design marine reserve networks (i.e., Mumby *et al.*, 2011, Beger *et al.*, 2015, Magris *et al.*, 2017). However, none of these three studies adjust reserve location to account for potential changes in connectivity patterns due to climate change.

Based on current patterns of coral larval connectivity, Mumby *et al*. (2011) optimize reserve configuration to ensure that the flow of larvae between desired thermal regimes is maximized based on possible responses of corals in terms of adaptation or acclimation to thermal stress. Similarly, Magris *et al*. (2017) consider thermal-stress regimes to ensure reserve networks include coral reefs that are resilient to climate change through the inclusion of future thermal refugia and thermally-disturbed reefs, while simultaneously targeting highly central reef patches (e.g., sources, stepping stones); however, connectivity- and climate change-related objectives are set independently and, as the previous study, connectivity matrices do not reflect changes in larval dispersal. Finally, Beger *et al*. (2015) identify sites that maximize larval dispersal connectivity for two species (fish and sea cucumber) based on current connectivity and simultaneously target coral reefs based on their predicted distribution following dynamic growth trajectories of coral cover associated with future thermal stress.

A further limitation of existing planning studies that include connectivity is the paucity of empirical data regarding regional-scale dispersal patterns (e.g., Williamson *et al.*, 2016, Almany *et al.*, 2017), which is required to validate the results of modeled larval connectivity patterns (White *et al.*, 2010, Liggins *et al.*, 2013). Although readily available oceanographic tools can be parameterized for most regions to calculate connectivity matrices for multiple species (Cowen *et al.*, 2005, Treml *et al.*, 2008, Kool *et al.*, 2013), such modeling results are not typically corroborated before being used to inform marine reserve design.

Finally, a major oversight in this body of literature is the omission of socioeconomic considerations (but see: Beger *et al.*, 2015), which reflects a limitation of marine planning studies more generally (Leslie, 2005, Ban *et al.*, 2013). Simplifying planning studies by excluding conservation costs, or using unrealistic proxies, greatly limits the potential application and validity of findings (Klein *et al.*, 2008, Gurney *et al.*, 2015), and can result in social conflict or poor compliance with proposed marine reserves.

Our study proposes a novel approach to designing networks of marine reserves (i.e., no-fishing areas) that considers network design adjustments that account for changes in connectivity associated with shortened PLDs due to ocean warming, using validated patterns of larval dispersal and socioeconomic constraints. We use the Gulf of California as case study and address four questions: (1) Given predicted ocean warming, can we expect a significant reduction in larval dispersal connectivity? (2) Can we maintain connectivity over networks designed only for representation of species and ecosystems under current and ocean-warming scenarios, without significant increases in costs? (3) Given the potential reductions in larval dispersal due to ocean warming, what are implications of network designs that account (or not) for reduced future connectivity? (4) In the absence of information about larval dispersal connectivity (including under future ocean warming), can we achieve well-connected marine reserve networks incidentally through representation? Our paper thus provides the first SCP study to account for alterations in connectivity due to the potential shortening of PLD associated with future ocean warming, using validated patterns of larval dispersal and socioeconomic constraints.

Materials and methods

We first designed marine reserve networks based on both conventional (designed to represent only species and ecosystems) and graph-theoretical (designed to maximize connectivity under current and ocean-warming scenarios) approaches. We then compared the performance of networks in terms of overall ecological adequacy based on individual reserve size and home range of adults of focal species, whole-of-network larval connectivity, and opportunity costs of implementing the marine reserve networks (Figure S1 summarizes our planning steps).

Study area

Our study area is the Midriff Islands Region (hereafter 'RGI', acronym from Spanish '*Región de las Grandes Islas*') in the northern Gulf of California, Mexico (Fig. 1), an area of high conservation significance (Álvarez-Romero *et al.*, 2013), where marine ecosystems are threatened by overfishing, habitat destruction, and climate change (Lluch-Cota *et al.*, 2007). This region is also important for industrial, artisanal, and recreational fisheries (Erisman *et al.*, 2010, Moreno-Báez *et al.*, 2012). Marine protected areas are mainly restricted to the western coast of the Gulf of California and have very small no-fishing zones (Rife *et al.*, 2013), so overfishing remains a threat (Lluch-Cota *et al.*, 2007, Cinti *et al.*, 2014). Ocean warming poses a further threat to biodiversity and fisheries production in this region due to potential suppression of upwelling and reduction of primary productivity (Páez-Osuna *et al.*, 2016), changes in the distribution and abundance of species and habitats (Aburto-Oropeza *et al.*, 2010, Ayala-Bocos *et al.*, 2016), and – potentially – reduced larval connectivity.

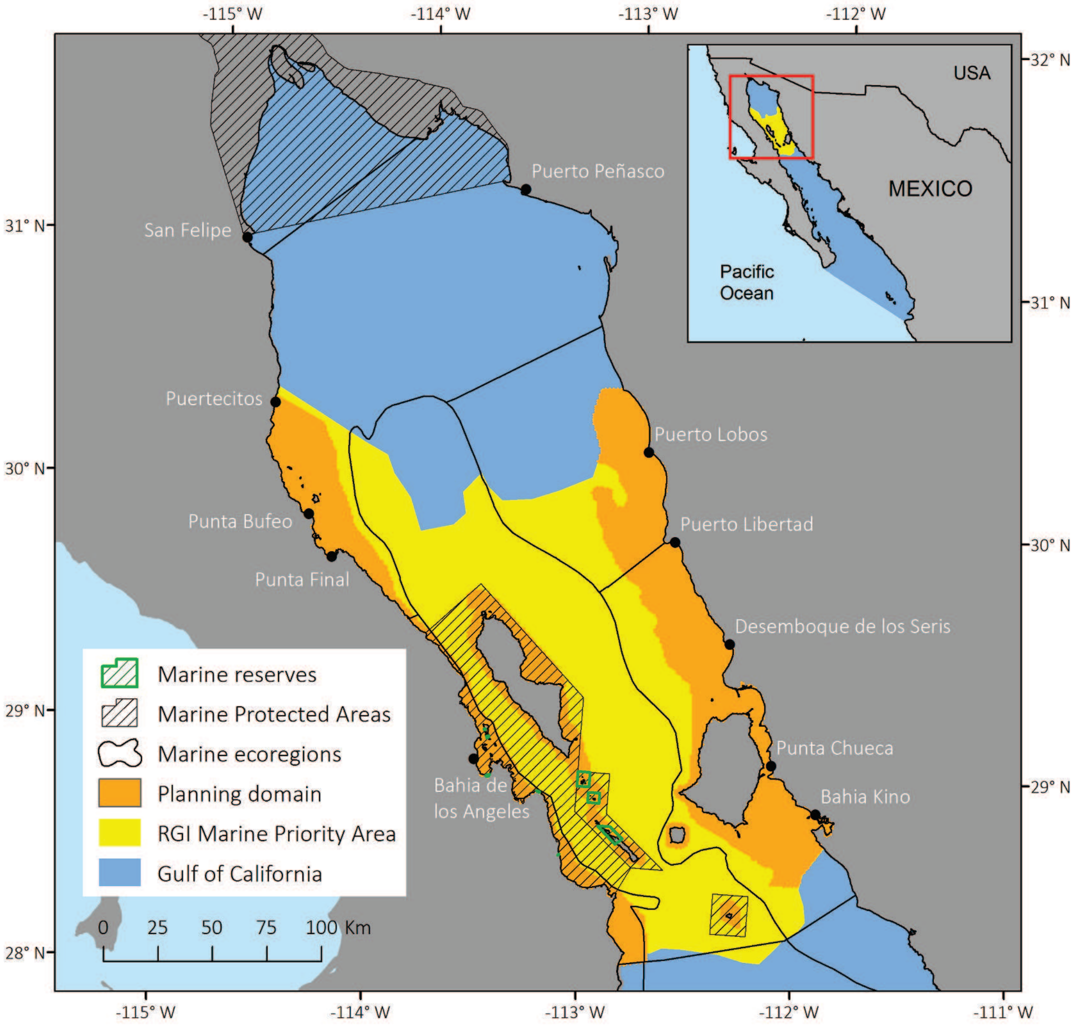

Fig. 1 - Planning domain boundaries within the Midriff Islands Region (RGI), Gulf of California. The planning domain was bounded by the Midriff Islands Marine Priority Area, an area of national significance (CONABIO *et al.*, 2007), but adjusted based on biophysical and socioeconomic considerations (Fig. S2). The map shows ecoregional boundaries used to stratify the planning domain, existing multiple-use marine protected areas with their corresponding no-fishing marine reserves, and coastal localities (2010 population in parenthesis): Puerto Peñasco (57,342), Puerto Lobos (90), Puerto Libertad (2,823), Desemboque de los Seris (300), Punta Chueca (520), Bahía Kino (7,000), San Felipe (16,702), Puertecitos (41), Punta Bufeo (<10), Punta Final (<10), and Bahía de Los Ángeles (800).

We focused primarily on rocky-reef ecosystems and associated species and habitats, which have outstanding biological and socioeconomic importance in the region. Rocky reefs sustain most of the biodiversity of macro-organisms in the Gulf of California compared to other ecosystems (Brusca, 2007). Species associated with rocky reefs are particularly important for small-scale fisheries and sustainable local livelihoods (Moreno-Báez *et al.*, 2012). Our analysis also included mangroves, *Sargassum* forests, and seagrass meadows because they provide important habitats for some life-history stages of reef-associated species and have local socioeconomic benefits (Sala *et al.*, 2002, Aburto-Oropeza *et al.*, 2008, Anadón *et al.*, 2011). We excluded mega-fauna (i.e., marine mammals, sea turtles, seabirds, pelagic fish) because they require different management strategies considered elsewhere (Anadón *et al.*, 2011).

The northern Gulf of California has unique oceanographic characteristics that result in strong asymmetric ocean circulation patterns. The area is characterized by a seasonally cyclonic (counter-clockwise) gyre during spring-summer causing a strong northward current along the eastern coast that reverses its direction to an anti-cyclonic (clockwise) gyre during fall-winter when a predominantly southward current is present in the eastern coast (Lavín & Marinone, 2003, Marinone, 2012). Consequently, larval dispersal is asymmetric and, depending on the phase of the gyre, areas located upstream relative to the predominant flow can act as 'sources' (i.e., sites supplying a large proportion of larvae and contributing significantly to recruitment), while sites located downstream act like 'sinks' (i.e., sites predominantly receiving larvae from multiple sources) and intermediate sites serve as 'stepping stones' (i.e., sites connecting areas otherwise disconnected) (Munguía-Vega *et al.*, 2014, Turk-Boyer *et al.*, 2014, Munguía-Vega *et al.*, 2015). Our study region is ideal to explore changes in connectivity due to ocean warming because the strong asymmetric current system means that changes in PLD will likely have stronger effects on larval connectivity than in more open ocean and symmetrical current systems (Selkoe *et al.*, 2016).

Targeted conservation features

The first step in the spatial prioritization process was determining where our target species occur, requiring spatially-consistent information about their distributions across the planning domain (Margules & Pressey, 2000). We used MaxEnt (Elith *et al.*, 2011) to generate species distribution models from species occurrence records of 98 fish and 87 invertebrates associated with rocky reefs (Supplementary Material, Tables S1-S3). We did not model species distributions under future ocean warming because these models require information not currently available (e.g., downscaled predictions of multiple environmental variables for future conditions) and reliability would be difficult to assess for most targeted species.

In addition to rocky reefs, we also targeted ecosystems that provide feeding, reproductive, and/or spawning habitat for reef-associated species during different life stages, and for which we had spatial data. We collated and refined existing distribution maps for six ecosystems: rocky reefs, mangroves, *Sargassum* beds, seagrass meadows, rhodolith beds, and coastal wetlands (Fig. S3). Maps were derived using spatial data available from existing planning exercises, previous studies, underwater censuses, satellite imagery, and localities provided by fishers (Table S4).

Finally, we targeted spawning aggregations (i.e., areas where individuals of marine species aggregate during the spawning season) because they are key to replenishing depleted populations (Sala *et al.*, 2003, Sadovy, 2005). We collated available information regarding the location of spawning aggregations for six invertebrates and four fish species (Table S2).

Socioeconomic considerations

We accounted for the socioeconomic impacts of marine reserves based on the potential economic loss associated with the exclusion of fishing. We used opportunity cost as a measure of loss, which is considered a best-practice approach when designing marine reserves (Ban & Klein, 2009, Ban *et al.*, 2013). Opportunity costs were estimated based on the biomass of targeted species, the potential catch of each species by different fisheries (26 fleets operate in the region), and the market value of fished species (Adams *et al.*, 2011) (Eqn 1). While climatic changes could also result in changes in socioeconomic variables considered in our study (e.g., fish catches: Kaplan *et al.*, 2013), exploring the simultaneous changes in fisheries catch, ecosystem function, and connectivity would require an integrated dynamic model to examine feedbacks between fish abundance, larval exchange, and fishing patterns, which was beyond our scope.

To calculate total opportunity cost per fleet, we used an end-to-end ecosystem model, based on the Atlantis framework for the northern Gulf of California (hereafter 'NGC Atlantis') (Ainsworth *et al.*, 2011). Atlantis is a spatially-explicit ecosystem model framework that simulates realistic ecosystem dynamics, including oceanography, biogeochemistry, food web interactions, and human activities, including fisheries (Fulton *et al.*, 2011). The NGC Atlantis model represents ecosystem structure and function. We used the model to simulate realistic system behavior, with predicted variables fitting observed data (Morzaria-Luna *et al.*, 2012). Fisheries in the model were represented by fleets, including small-scale, sport fishing, and industrial fisheries, whose simulated spatial use-patterns and catches reflected our best understanding of recent fishing activity in the region (Moreno-Báez *et al.*, 2010, Rábago-Quiroz *et al.*, 2011). We estimated opportunity cost per fleet based on a 1-yr forward simulation under modeled 2008 fishing mortality and predicted biomass per functional group and catch per fleet (Supplementary Material), and then summed all fleets for the total cost (Eqn 1).

Eqn 1

$$\boldsymbol{C_j = \sum_{i=1}^{n} p_{ji} \times b_i \times m_i}$$

C_j = opportunity cost for fleet j
n = number of species fished by fleet j
p_{ji} = percentage catch for fleet j of species i
b_i = predicted biomass of species i
m_i = average market value (MXN)of species i

The final opportunity cost (*C*) model (Fig. S4) was calculated by summing the individual opportunity costs (C_j) for each fleet. We applied a uniform weight (*w*) of 1 to all fleets (Eqn 2) because we lacked reliable information on the number of fishers per fleet (as suggested by Adams *et al.*, 2011) or the relative sensitivity of fleets to closure of fishing grounds.

Eqn 2

$$\boldsymbol{C = \sum_{j=1}^{J} w_j \times C_j}$$

C = total opportunity cost across the 26 fleets (MXN)
w_j = weight or relative importance of fleet j
C_j = opportunity cost for fleet j
J = number of fishing fleets (26)

Prioritizing the location of marine reserves

We generated alternative systems of marine reserves with the decision-support tool Marxan (Ball *et al.*, 2009) to achieve a set of conservation objectives while minimizing costs. In this case, we minimized opportunity costs to fishers affected by the exclusion of fishing within marine reserves. Our 1-km^2 hexagonal planning units (n = 11,097) covered coastal and marine areas. The size of the planning units matched the resolution of key input datasets (e.g., ecosystem maps, species distribution models). We used Marxan's functionality (i.e. adjusting the Boundary Length Modifier) to aggregate planning units to create larger marine reserves that are adequate to encompass the home range and territory of adults of targeted species (Green *et al.*, 2015). Given the applied nature of our study, clumping contributed to reducing the total number of reserves while maximizing individual reserve size and minimizing the overall boundary of marine reserve networks (Supplementary Material), which can improve their ecological adequacy and facilitate social compliance and enforcement (Fernandes *et al.*, 2005, Arias *et al.*, 2016).

Setting conservation goals and objectives

We defined four broad goals guided by previous planning exercises (Ulloa *et al.*, 2006, CONABIO *et al.*, 2007) and informed by consultation with relevant national government agencies and managers of marine protected areas (Table 1): (1) *Representation*: represent target species and ecosystems by protecting a percentage of their current distribution commensurate with their conservation requirements; (2) *Connectivity*: promote the long-term population viability of focal species by maintaining natural recruitment processes within the marine reserves network mediated by larval dispersal; (3) *Climate change*: design the network to maintain larval connectivity under future ocean-warming conditions; and (4) *Socioeconomic*: minimize costs to fishers affected by excluding fishing from marine reserves.

Table 1. Summary of prioritization scenarios. Our three scenarios aimed to minimize potential socioeconomic impacts to fishers based on the same opportunity costs data.

Scenario (solution)	Goal	Targeted features	Objectives
Representation, uniform connectivity (S1)	Protect areas important to safeguard ecosystems and species of conservation and commercial value	Rocky reef associated ecosystems (6 types), species (103 fishes, 87 invertebrates), and spawning aggregations (10 species)	Set individually for each ecosystem, species, and spawning aggregations considering rarity, vulnerability, and threats
Representation plus asymmetric connectivity (S2)	Same as S1, but network design adjusted to maximize larval connectivity between marine reserves	Same as S1, plus areas important to maintain ecological connectivity (hubs and stepping stones for larval exchange among reserves) of the three focal species	Same as S1, plus additional connectivity objectives set using centrality measures from dispersal models for the three focal species
Representation plus asymmetric connectivity under ocean warming (S3)	Same as S2, but network design adjusted to account for potential changes in larval connectivity patterns due to ocean warming	Same as S2, but the centrality of planning units was different due to modified larval dispersal patterns associated with shortened PLD given projected ocean warming	Same as S2, but connectivity objectives adjusted based on modified centrality under ocean warming

We calculated the target amount of each ecosystem and spawning aggregation to be represented in marine reserves based on information about rarity and exposure to threats (Pressey *et al.*, 2003). We set higher objectives (a.k.a. targets in some of the conservation science literature) for ecosystems that are relatively rare (i.e., occupy smaller areas within the region) and are subject to higher pressure from local stressors (e.g., coastal development, pollution, shipping), which we assessed based on models developed by Halpern *et al*. (2008) and Kolb *et al*. (2008). Our vulnerability assessment did not consider variable responses of species to threats, which was not possible given existing information, hence we calculated average ‘exposure’ to threats (Wilson *et al.*, 2005). For species, representation objectives also integrated rarity as well as indices for the heterogeneity of species distributions and exposure to threats (Supplementary Material). These indices allowed us to increase representation for species with smaller and patchier distributions, as well as for those more vulnerable to extinction and overfishing because they occupy higher trophic levels, use fewer ecosystems, have smaller depth ranges, and have narrower latitudinal distribution ranges.

Maximizing larval dispersal connectivity in marine reserve networks

We selected three focal species across three major taxa to plan for connectivity and ocean warming: Leopard grouper (*Mycteroperca rosacea*), Rock scallop (*Spondylus limbatus*), and Blue crab (*Callinectes bellicosus*). These are species of high conservation and commercial value in the region, and are well studied, including their patterns of larval connectivity (Munguía-Vega *et al.*, 2014); spatially-explicit information on their larval dispersal patterns is derived from coupled biological-oceanographic models that reliably predict genetic diversity and structure within these species in the northern Gulf of California (Turk-Boyer *et al.*, 2014, Munguía-Vega *et al.*, 2015, Lodeiros *et al.*, 2016). These three species spawn during spring-summer (cyclonic phase of the gyre), but have different larval dispersal pattern, i.e. slightly different peak spawning time and PLD (Table S5); thus, they represent a range of life histories and potentially distinct connectivity requirements. The habitats of the three focal species (Table S6) represent the range of ecosystems occupied by reef-associated and coastal species targeted in our prioritization analysis. We did not target species spawning during the anti-cyclonic phase because we did not have validated information to model their dispersal, but discuss this limitation below. Adult movements were considered through reserve size based on home range movements; however, our analysis of spatially-explicit connectivity focused on larval dispersal.

We applied a graph-theoretical approach to account for larval connectivity patterns in the design of marine reserve networks. This required mapping potential spawning and recruitment habitats of focal species and characterizing planning units by their potential contribution to the overall connectivity of networks during spring-summer (e.g., White *et al.*, 2014, Magris *et al.*, 2016). We used the ecosystems inhabited by each focal species (Table S6) to represent their spawning and/or recruitment habitats, and assumed they all have, potentially, equal per unit area contributions of larvae. We did not distinguish between spawning and recruitment habitats because for our targeted species both are mainly areas within rocky reef systems (Aburto-Oropeza *et al.*, 2007, Soria *et al.*, 2012).

We set representation objectives for spawning and recruitment habitats to preferentially include units that are important '*hubs*' (i.e., units strongly connected both upstream and downstream and potentially important for metapopulation robustness) or '*stepping stones*' (i.e., units that, if lost, would strongly reduce the connectivity of the reserve network). We characterized hub and stepping-stone units based on selected centrality metrics (described below), and weighted the contribution of each unit to maintaining whole-of-network larval connectivity by its amount of spawning and recruitment habitat (Watson *et al.*, 2011, White *et al.*, 2014). We lacked the necessary information to compare the resulting networks with reliable metapopulation models and test population viability of focal species. Our study thus aimed to maximize connectivity given socioeconomic constraints. We assumed that creating better connected (e.g., denser) networks of marine reserves can help support populations that can recover faster from disturbance and maintain fish biomass.

Our approach to planning for connectivity comprised five steps: (1) estimate ecological connectivity at coarse spatial scale using a larval dispersal model; (2) downscale connectivity from coarse connectivity units to planning-unit scale; (3) calculate centrality of planning units based on downscaled connectivity matrices and available habitat per planning unit; (4) map connectivity features that represent the potential contribution of habitat patches to act as hubs or stepping stones; and (5) set representation objectives for connectivity features under socioeconomic constraints.

In **step 1**, we parameterized a dynamic larval dispersal model with corresponding spawning times and PLDs to calculate connectivity matrices describing the probability of larvae being transported between broad connectivity units (Fig. S6) and the direction of larval flow for the three focal species. We used the velocity field from the three-dimensional baroclinic Hamburg Shelf Ocean Model (HAMSOM) for the Gulf of California (Backhaus, 1985) to calculate the particle trajectories of passive larvae released from points representing potential spawning habitat in the northern Gulf (Marinone, 2003, Marinone, 2008). We predicted larval dispersal from the converged oceanographic model that adequately reflected the main seasonal signals of surface temperature, heat balance, tidal elevation, currents, and surface circulation (Lavin *et al.*, 1997, Marinone, 2003). The model represents an average year based on a climatology spanning historic databases. Given the lack of reliable downscaled projections of physical variables that force the model, our dispersal model did not explicitly include potential changes in currents due to ocean warming (e.g., Andrello *et al.*, 2015), which is an area of active research. Further details of the oceanographic modeling can be found in previous studies (Soria *et al.*, 2012, Munguía-Vega *et al.*, 2014, Munguía-Vega *et al.*, 2015) and are summarized in the Supplementary Material.

Initially, we conducted this analysis for parameters representing current climatic conditions, followed by an analysis with adjusted values representing a predicted increase in average ocean temperature of 3°C across the region. Although the mean increase in sea-surface temperature across the Gulf of California is predicted to be ~0.63 °C by 2050, this increase varies by sub-region and up to 3°C (Ayala-Bocos *et al.*, 2016). Therefore, we chose to model a 3°C increase in ocean temperature, based on the highest Representative Concentration Pathway (RCP 8.5), to illustrate extreme (but possible) changes in functional connectivity (i.e., based on direct effects on the biology of dispersing individuals, including their dispersal potential based on the planktonic larval duration; Gerber *et al.*, 2014); current emissions are tracking just above that pathway (Sanford *et al.*, 2014). Outcomes from intermediate RCPs would thus likely be included within the range of variation observed in our results.

We estimated the potential changes in larval connectivity due to ocean warming following a functional connectivity framework (Gerber *et al.*, 2014), which relates empirically demonstrated relationships between increases in ocean temperatures and changes in PLD (Gillooly *et al.*, 2002, O'Connor *et al.*, 2007) to reduced potential dispersal distances and connectivity. We predicted reductions in PLD under a 3° C increment in temperature with a population-averaged exponential-quadratic model (Eqn 3), which best describes the general temperature dependence of PLD for 69 fish and invertebrate species (O'Connor *et al.*, 2007).

Eqn 3

$$\ln(\mathrm{PLD}) = \beta_0 - \beta_1 \times \ln(\mathrm{T}/T_c) - \beta_2 \times (\ln(\mathrm{T}/T_c))^2$$

$\beta_0 = 3.17;$ value of $\ln(\mathrm{PLD})$ at $15^o\mathrm{C}$
$\beta_1 = -1.34;$ parameter adequately describing 69 species of fish and invertebrates
$\beta_2 = -0.28;$ parameter adequately describing 69 species of fish and invertebrates
$T_c = 15^o\mathrm{C}$

In **step 2**, we downscaled the larval connectivity matrix estimated for connectivity units to the planning-unit scale based on three factors (Eqns 4-5): probability that two planning units are connected at coarse spatial scale; probability that focal species occur; and amount of potential spawning and/or recruitment habitat for each species. Effectively, the likelihood and magnitude of the connection between any given pair of planning units depends on large-scale connectivity patterns and their potential to produce and/or receive larvae.

Eqn 4

$$\boldsymbol{S_{a\to b} = C_a \times C_b \times P_{A\to B}}$$

$S_{a\to b}$ = asymmetric tie strength between planing unit a and b
$P_{A\to B}$ = probability of larvae going from connectivity unit A to connectivity unit B
C_a = relative contribution of planning unit a to provide habitat (Eqn 5)
C_b = relative contribution of planning unit b to provide habitat (Eqn 5)

Eqn 5

$$\boldsymbol{C_i = p_i \times h_i}$$

C_i = relative contribution of planning unit i to provide spawning or recruitment habitat
p_i = probability that the focal species occurs in planning unit i
h_i = proportion of planning unit i with spawning and/or recruitment habitat

In **step 3**, we used UCINET software (Borgatti *et al.*, 2002) to calculate the centrality of planning units with downscaled connectivity matrices to quantify their potential role as hubs or stepping stones. We selected two centrality measures that take into account the direction and strength of the connections, and provide information about the importance of planning units (nodes) as hubs or stepping stones (Supplementary Material). We measured the potential of planning units acting as hubs using eigenvector centrality (Bonacich, 1972), which reflects the importance of a node within the overall structure of the network (nodes are more central if they are connected to many other highly connected nodes), which has proven useful to identify subpopulations that are critical to metapopulation robustness (Watson *et al.*, 2011). Our measure of the value of planning units as stepping stones was distance-weighted fragmentation (Borgatti *et al.*, 2002), which calculates the effect of removing a node on the overall connectivity of the network (Table S7).

Given our aim was to maximize whole-of-network connectivity, and that only very few previously identified locations within our planning region showed modeled and empirical evidence of high self-recruitment (Soria *et al.*, 2012, Munguía-Vega *et al.*, 2014), we did not target areas for self-recruitment. In fact, the location of sites showing high local larval retention in the region are unique, and our larval dispersal model shows they are few (Table S8) and associated to small eddies that form near the northern pointy ends of large islands or coastlines.

The overall centrality of each planning unit was then calculated as the normalized sum of the two centrality measures (Eqn 6), which represents its importance as hub and/or stepping stone. This assumed equal importance of the two measures in determining overall larval connectivity. In our case, we had no evidence to set independent and differing objectives because it is unclear which property is more important to achieve population persistence.

Eqn 6

$$\boldsymbol{k_i} = \frac{(\boldsymbol{E_i} + \boldsymbol{dwF_i})}{\mathbf{max}(\boldsymbol{k})}$$

k_i = normalized centrality of planning unit i
E_i = eigenvector centrality of planning unit i
dwF_i = distance weighted fragmentation centrality of planning unit i

In **step 4**, we mapped connectivity features adjusted by the amount of spawning and/or recruitment habitat and the normalized centrality to depict planning units' connectivity potential for the three focal species under current and future ocean-warming scenarios. Because empirical data on size-specific fecundity, larval production, larval survival, and settlement patterns were not available for our system, we approximated the number of larvae produced with the amount of spawning and/or recruitment habitat present in each planning unit to scale centrality values according to the reasonable assumption that units with larger amounts of habitat will produce more larvae (Watson *et al.*, 2011, White *et al.*, 2014). We then multiplied the normalized centrality of each planning unit ($\boldsymbol{k_i}$) by the amount of spawning and/or recruitment habitat within each unit (Eqn 7).

Eqn 7

$$\boldsymbol{A_i} = \boldsymbol{k_i} \times \boldsymbol{a_i}$$

A_i = contribution of planning unit i to connectivity
k_i = normalized centrality of planning unit i
a_i = amount of spawning and/or recruitment habitat within planning unit i (m^2)

To compare the performance of reserve networks generated considering connectivity with those that considered only representation of species and ecosystems we mapped and targeted (see **step 5**) a dummy connectivity feature with uniform connectivity ($\boldsymbol{k_i} = 1$) that represented only the amount of spawning and/or recruitment habitat. We constrained our maps of connectivity features to units with recorded connections (Fig. S6).

In **step 5**, we followed the method proposed by Magris *et al*. (2016) to calculate representation objectives for connectivity features. We identified subsets of planning units with the highest contributions to connectivity, and used their summed values across all planning units to set representation objectives expressed as percentages of totals. Following discussions with local managers, we decided that a 5% reduction of opportunity cost across all fleets would be an acceptable loss. We found that setting objectives for representing connectivity features based on the top 67th percentile roughly corresponded to a 5% loss in opportunity cost. This analysis resulted in varying sets of connectivity objectives across species and scenarios (Table S9).

Performance of resulting marine reserve networks

We assessed the performance of marine reserve networks in terms of ecological adequacy (based on reserve size and home range of adults of focal species) and whole-of-network larval connectivity. First, we explored the dimensions of individual marine reserves because recent studies indicate that their potential to protect a range of species depends on the length of marine reserves, which should encompass at least twice the adult home range of a particular species (Green *et al.*, 2015). The minimum reserve sizes were calculated using a multiple linear regression model including total length and trophic level as explanatory variables (Munguía-Vega *et al.*, in prep). We focused this analysis on fish because the adults of targeted invertebrates generally display low mobility.

Second, we assessed and compared whole-of-network connectivity of reserve networks generated considering centrality of planning units (**S2** and **S3**, i.e., variable $\boldsymbol{k}$) against networks generated assuming uniform connectivity (**S1**, i.e., **k = 1**). We used UCINET software (Borgatti *et al.*, 2002) to (a) calculate selected network cohesion measures (e.g., density, degree, compactness) and (b) test for statistical significance of differences in density (main proxy for whole-of-network connectivity) between the three solutions (under both assumptions related to the effects of ocean warming; Fig. 2) by creating a bootstrapped distribution. We sampled the network with replacement from the nodes (assuming nodes are interchangeable) and estimated average density, z-score, and p-value (Snijders & Borgatti, 1999). Further, we calculated the 'maximum flow' (Ford & Fulkerson, 1956), which in our case is a proxy for the potential flow of larvae between marine reserves given different network configurations (i.e. S1, S2 or S3); see Table 2.

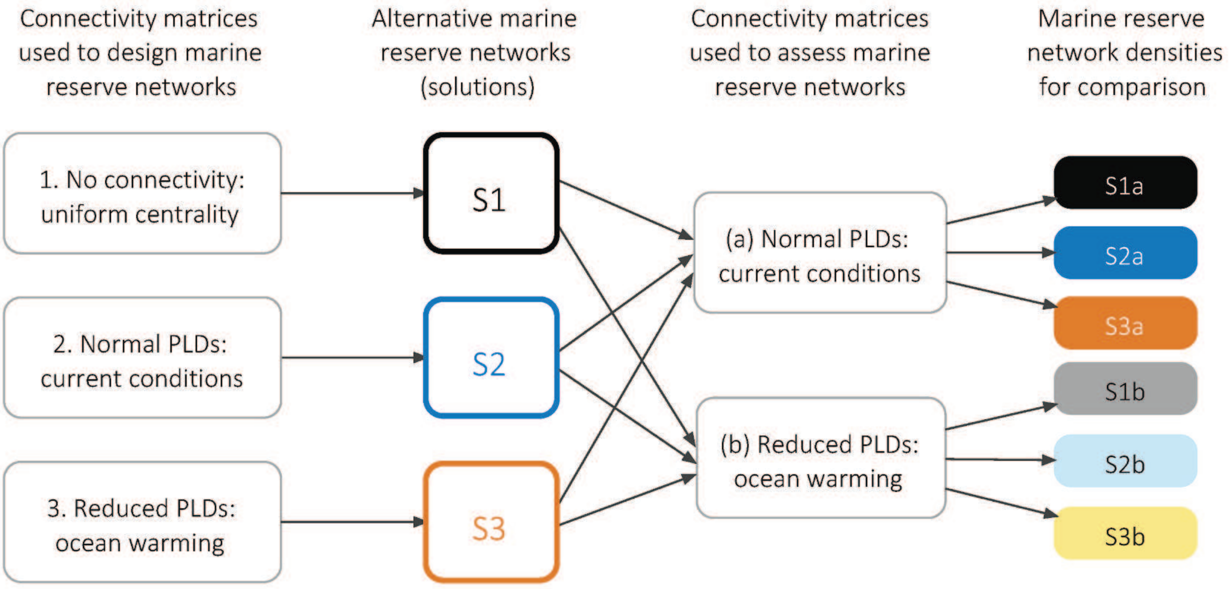

Fig. 2 Performance assessment of alternative marine reserve networks under two assumptions regarding changes in PLDs. We assessed the performance of the three marine reserve networks solutions (**S1**, **S2** and **S3**; **Table 1**) under the assumption that: (a) the effect of ocean warming on PLDs is negligible (larval connectivity patterns and PLDs remain the same); or (b) ocean warming will significantly reduce PLDs (major changes in larval connectivity patterns occur).

Finally, we used Conefor 2.6 software (Saura & Torné, 2009) to calculate the Integral Index of Connectivity (IIC), which considers connectivity within the wider context of habitat availability. The index integrates the amount of habitat within each patch and connectivity among individual reserves into graph structure as a binary variable, where connectivity is either present or absent (Pascual-Hortal & Saura, 2006). The value of IIC ranges from 0 to 1 (increasing with improved connectivity) and is broadly defined as the probability that two individuals randomly placed within the landscape fall into habitat areas that are connected given the set of habitat patches and the connections among them. Calculations were based on the downscaled connectivity matrices under normal or reduced PLD for *Mycteroperca rosacea*, the amount of recruitment habitat within each reserve for the species, and the total area present in each reserve network as the denominator.

Reduced dispersal connectivity due to ocean warming is likely to be significant, but the predicted magnitude of future increases in temperature (and resulting shortening of PLD) is highly uncertain (IPCC, 2014). Therefore, we explored the consequences of designing networks that account for reduced future connectivity or that disregard these changes under two alternative assumptions: (**a**) changes in dispersal connectivity due to ocean warming are negligible (i.e., PLDs remain unaffected) or (**b**) changes are significant and reduction of PLDs occur as expected. To achieve this, we compared the density of networks for each solution under the assumptions that PLDs remained the same or were shortened (Fig. 2). Effectively, we compared six scenarios that explore the extremes of what could happen (nothing or major changes) and thus expect the potential variation in functional connectivity would likely be contained within these extremes.

Results

Changes in larval connectivity due to ocean warming

Our analysis of connectivity based on the larval dispersal model indicated that ecological connectivity patterns differed notably between the current and future warmer ocean scenarios (Fig. 3). Across the three focal species, the ecological networks become less connected because some areas previously connected by larval dispersal were predicted to be unreachable due to estimated reduction in PLD under warmer ocean conditions. Reduction in density was significant only for the Leopard grouper (*Mycteroperca rosacea*), almost 30% less dense (p-value = 0.0038) (Table S10). The low densities of networks for both the Rock scallop (*Spondylus limbatus*) and the Blue crab (*Callinectes bellicosus*) under current conditions (Fig. 3c) meant that reduced density under ocean warming was too low to be detected statistically.

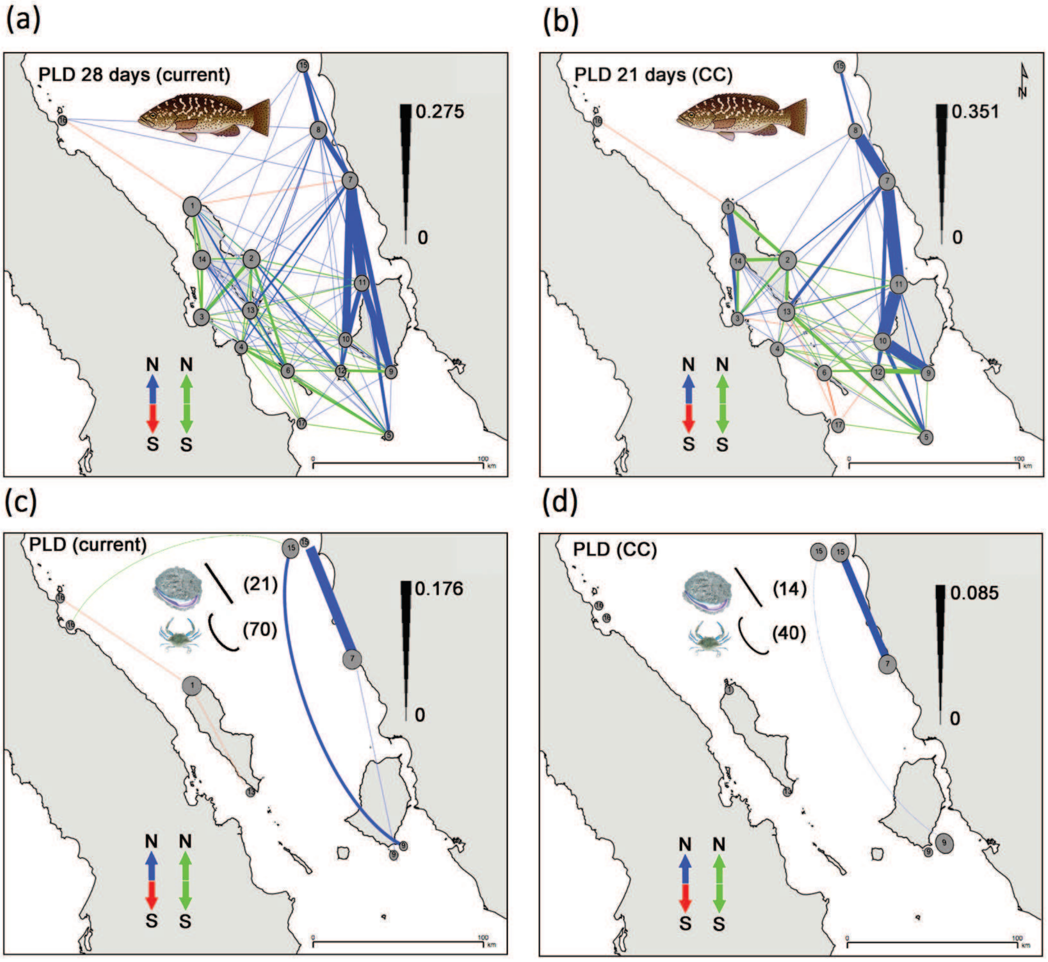

Fig. 3 Regional patterns of larval connectivity under current and 3°C ocean-warming (CC) scenarios. The maps show the connectivity patterns for the three focal species estimated using the larval dispersal model: Leopard grouper (*Mycteroperca rosacea*) under **(a)** current conditions (PLD: 28 days) and **(b)** ocean warming (PLD: 21 days); **(c)** Rock scallop (*Spondylus limbatus*) and Blue crab (*Callinectes bellicosus*) under current conditions and PLDs of 21 days and 70 days, respectively; and **(d)** *S. limbatus* and *C. bellicosus* under ocean warming and PLDs of 14 days and 40 days, respectively. Node size is scaled according to eigenvector centrality to visually represent the relative importance of different areas to act as 'hubs' to maintain the overall connectivity in the region (i.e., larger nodes are more important). Line thickness represents the strength of connections between areas (i.e., probability of larvae moving from one area to another), while color indicates the main direction of larval movement; green lines indicate bidirectional flow.

Moreover, symmetric (bidirectional) connectivity currently occurring among some sites (e.g., between the Midriff Islands and the Baja California Peninsula, Fig. 3), was predicted to change to more asymmetric (unidirectional) connectivity under ocean warming (i.e., from nodes in Baja California towards the Midriff Islands only). Consequently, under ocean warming, some links between closer habitat patches were predicted to become stronger and the relative importance (centrality) to maintain overall connectivity changed notably (Fig. 3). For instance, the future network for the Leopard grouper (*M. rosacea*) under the ocean-warming scenario had fewer links across the region from west to east in the northern area of the RGI and relatively stronger directed links among certain areas (e.g., among habitat patches on the west coast). While some areas maintained the same overall flow of larvae within the system (e.g., nodes 2, 4, 6, 7, 9, 15), other areas located upstream of the anti-clockwise flow became less central (e.g., 1, 3, 14), while those in the southern portion of the RGI increased their centrality (e.g., 5, 10-13, 17).

The ecological networks for *C. bellicosus* and *S. limbatus* were notably less dense than the network for *M. rosacea* in both climatic scenarios (Fig. 3c-d, Table S10) because they inhabit either fewer ecosystems (Table S6) and/or ecosystems are present in lower frequency in the RGI (Fig. S3). We observed that most sites that were connected by larval dispersal for *C. bellicosus* and *S. limbatus* on the western coast of the RGI under current temperatures became completely isolated under ocean warming, while connections on the eastern coast of the RGI became weaker. The species with the shortest PLD (*S. limbatus*) overall seemed to show more loss of connectivity under ocean warming than the species with longer PLD (*C. bellicosus*), given the increase in isolation even when its habitat patches were located comparatively closer to each other. Effectively, larval dispersal networks for these two species were a subset of the network of the grouper (*M. rosacea*), in part because they were all subject to the same cyclonic phase of the oceanographic gyre. For the above reasons, in the following sections we present the results only for *M. rosacea*.

Cost-effectiveness of marine reserve networks designed using connectivity information

Our prioritization analysis showed that targeting connectivity following a graph-theoretical approach based on current centrality of habitat patches (S2) can help design more connected networks than solutions assuming uniform connectivity (S1) for equivalent costs (in our case set at 5% of the total opportunity cost). The benefits of the S2 approach are evident in the slower increase in the opportunity cost of marine reserve networks considering connectivity with increasing representation objectives for spawning and recruitment habitat (Fig. 4).

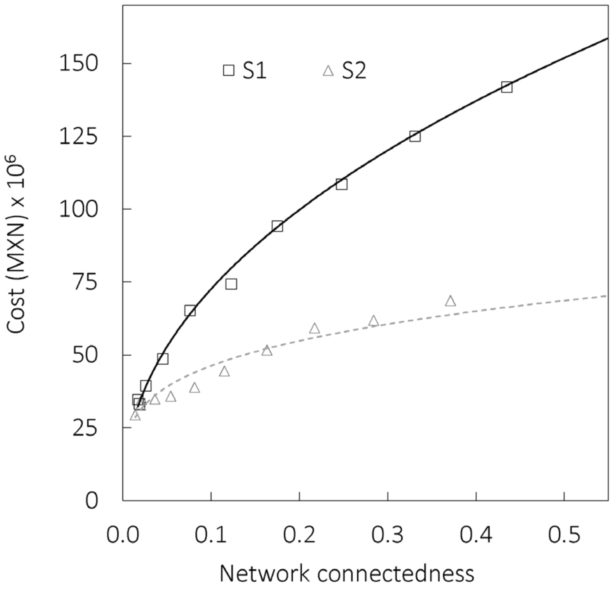

Fig. 4 Comparison of whole-of-network connectedness of solutions generated under alternative connectivity scenarios. The lines represent fitted power functions ($R^2 \geq 0.934$) based on two sets of points (i.e., marine reserve network solutions): (**S1**) solutions generated assuming uniform connectivity, i.e. $\boldsymbol{k = 1}$ (black line) and (**S2**) solutions generated targeting connectivity features based on eigenvector centrality and distance-weighted fragmentation (grey dashed line). Tradeoff curves were generated by gradually increasing the representation objectives for connectivity features (including the dummy connectivity feature for S1, where **k** = 1), plotted against the total opportunity cost in Mexican Pesos (MXN) for each network under each set of objectives.

In the RGI, opportunity costs were highly biased towards the north-western and eastern regions (Fig. S4), which is in part mediated by human settlements (i.e., more fishers nearby). The downstream position of the eastern section of the RGI in the summer-fall phase of the gyre could translate to more prosperous fishing activities because of a regionally increased availability of many commercial species that are summer spawners (Moreno-Báez *et al.*, 2012, Munguía-Vega *et al.*, 2015). By including connectivity in our prioritization analyses, we were able to prioritize upstream sources on the western and southern sections of the RGI (Fig. 5b-c). In turn, this resulted in more cost-efficient networks that reduced the amount of protection at downstream sites with small contributions to the connectivity of the overall network but higher opportunity costs.

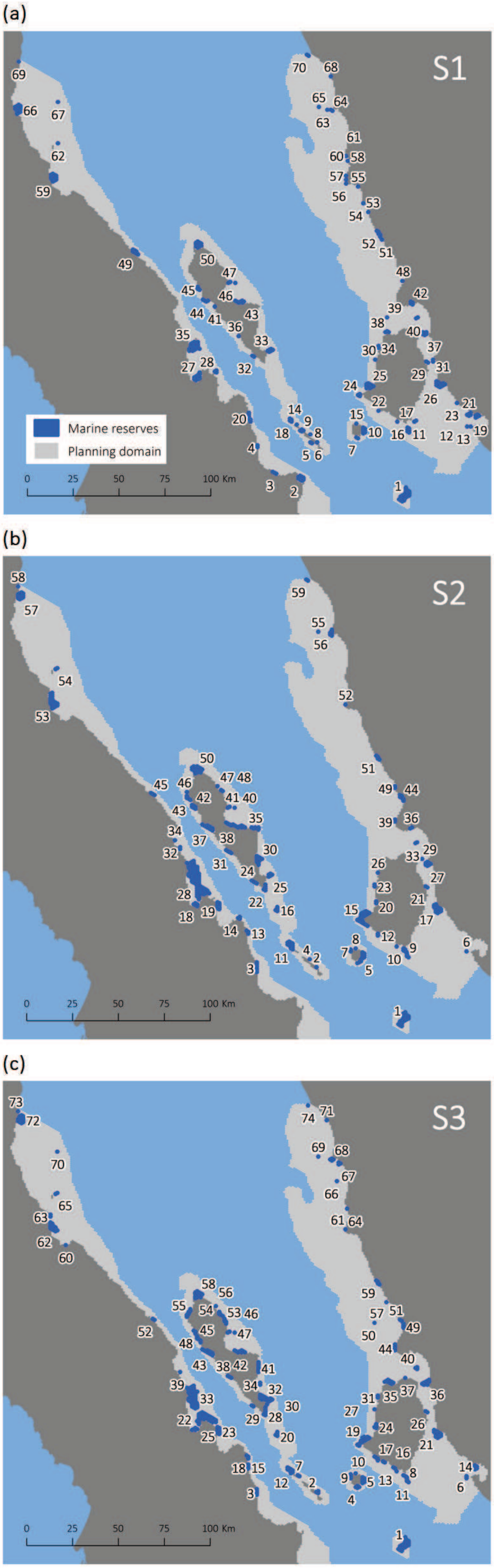

Fig. 5 Alternative marine reserve networks for the current and future ocean-warming scenarios. Marxan's lowest-cost configuration for each of the three final solutions (**Table 1**): (**a**) S1, representation of species distributions and ecosystems assuming uniform connectivity (70 reserves, mean size: 4.1 km^2, mean separation: 6.9 km); (**b**) S2, representation considering larval connectivity under present conditions (59 reserves, mean size: 7.0 km^2, mean separation: 6.9 km); and (**c**) S3, representation considering connectivity under a 3°C ocean-warming scenario (74 reserves, mean size: 5.6 km^2, mean separation: 5.4 km); see **Tables S11-12**. Marine reserves under the ocean-warming scenario (S3) are 22% closer to each other on average (but up to 42%) when compared to the connectivity-only scenario (S2); see **Table S13**. Each solution represents one potential spatial configuration of a network of marine reserves that can achieve the corresponding set of objectives (i.e., best configuration out of 100 Marxan runs) with comparable socioeconomic impacts on fisheries (~5% opportunity cost). Numbers indicate individual marine reserves and correspond with numbered nodes in **Fig. 6**.

Performance of marine reserve networks under current and future ocean warming

Marine reserves designed under the three scenarios (S1 to S3) have comparable dimensions with those in the region, but are generally larger (Tables S11-12). The average length of marine reserves was 2.7 km for S1, 4.0 km for S2, and 3.6 km for S3, which based on the regression model derived from Green et al. (2015) could protect most of the 99 targeted fishes (S1: 74%, S2: 81%, and S3: 79%), except for species >100 cm with larger home ranges (Table S14). While we did not have enough information to estimate reserve size requirements for invertebrates, we consider that marine reserves under all scenarios will likely protect most species of invertebrates, which generally display low mobility, including *Callinectes bellicosus* and *Spondylus limbatus*.

The networks of the three alternative solutions showed notable differences in terms of connectivity under both current and future ocean-warming scenarios for *M. rosacea* (Fig. 6). Overall, reserves designed following a graph-theoretic approach (S2 and S3) had more connections with and were closer to other reserves in the network (Table 2). Marine reserves under our ocean-warming scenario were 22% closer to each other (but up to 42% in some cases) and the number of reserves increased from 59 to 74 (25%) when compared to the connectivity-only scenario (Tables S11-13). Our results indicate that S2 and S3 networks outperformed the network designed following the representation-only approach (S1) in terms of their potential to maintain larval dispersal connectivity for the same cost.

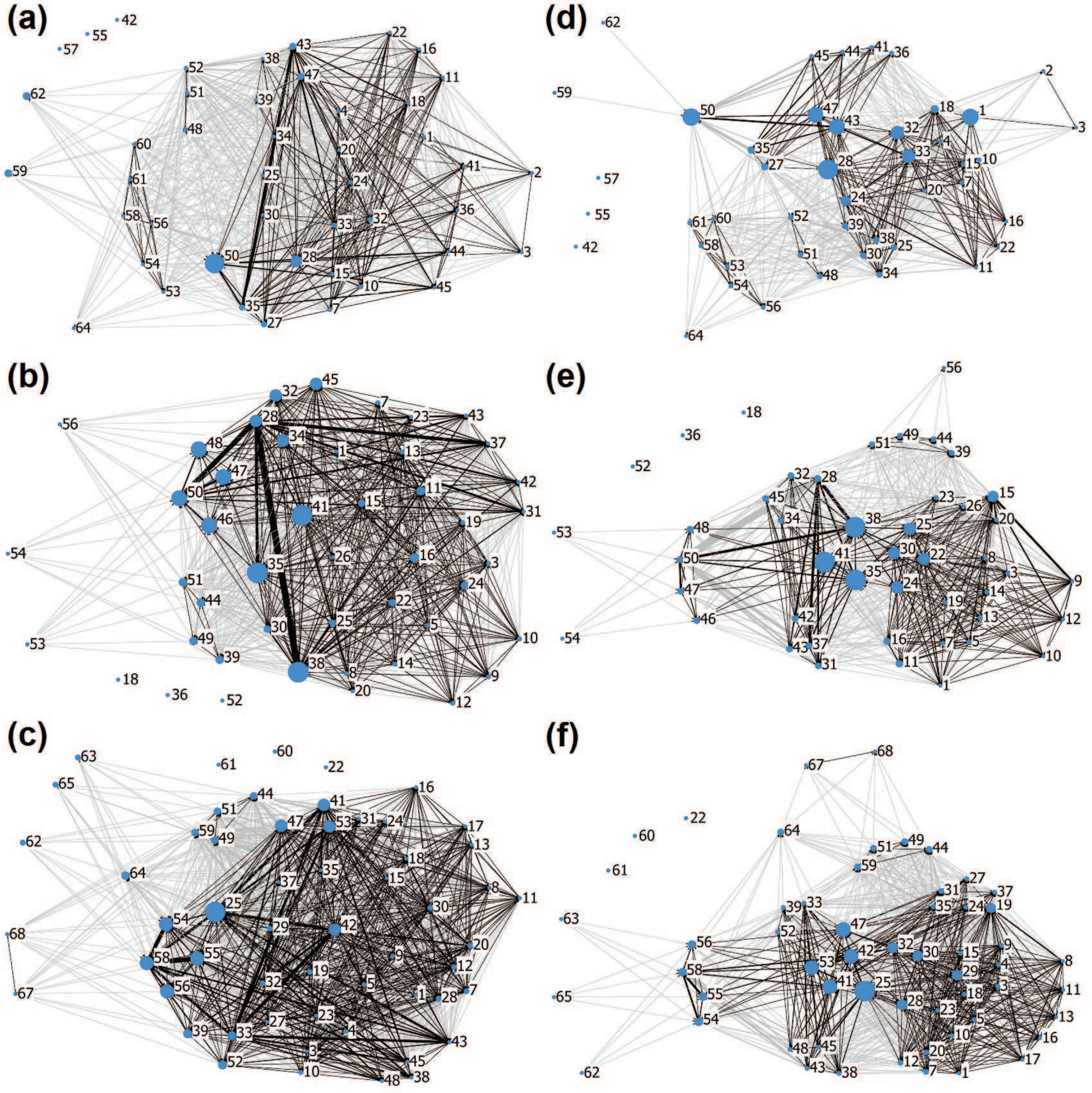

Fig. 6 Estimated larval connectivity patterns for the Leopard grouper (*Mycteroperca rosacea*) based on alternative marine reserve networks for the current and future ocean-warming scenarios. Network correspond to our three solutions: S1 (representation only), S2 (representation plus connectivity), and S3 (S2 under ocean warming), under current conditions, based on connectivity matrix using normal PLD: S1 (**a**), S2 (**b**), and S3 (**c**); and under ocean warming, using shortened PLD: S1 (**d**), S2 (**e**), and S3 (**f**). Size of nodes (marine reserves) is scaled according to flow betweenness to visually represent their potential importance as stepping stones to maintain the overall connectivity in the RGI (larger nodes are more important). We used NetDraw (Borgatti, 2002) to represent reserves in non-geographic space (numbers correspond with marine reserves in **Fig. 5**) using the spring-embedding algorithm (Gower scaling) and proximity based on geodesic distances.

From a whole-of-network perspective, S2 and S3 networks were not only better connected, but also more compact, and less centralized (Table 2). In both of these solutions, network connectedness relied less on only few reserves (Fig. 6), thereby increasing the resilience of networks to impacts on or loss of individual reserves. Given these structural characteristics, S2 and S3 networks were denser than S1, particularly when connectivity was calculated using normal (p-value ≤ 0.066), compared to shortened (p-value ≤ 0.099) PLDs (Table S15).

Also worth noting, are the differences in network structure resulting from estimated PLD reductions due to ocean warming, particularly: reduction in density; decrease in reciprocal ties; loss of alternative dispersal routes among reserves; and presence of clusters of reserves connected by a relatively small number of reserves acting as stepping stones (Fig. 6).

Table 2. Differences in dispersal connectivity for the Leopard grouper (*Mycteroperca rosacea*) between the three marine reserve network solutions. The table presents selected network cohesion measures indicative of whole-of-network connectivity, calculated using the connectivity matrices based on PLDs for current conditions(subindex ‘a’) or shortened PLDs under ocean-warming (subindex ‘b’) (Fig. 2). Maximum values for each combination of measure and climate condition are in bold.

		Assessment for current conditions			Assessment for 3°C ocean warming		
Measure	Definition	$S1_a$	$S2_a$	$S3_a$	$S1_b$	$S2_b$	$S3_b$
Average degree	Average number of links between pairs of marine reserves within the network	20	25	**29**	15	18	**23**
H-Index	Largest number X such that there are X nodes with degree ≥ X in the network	22	27	**31**	18	20	**25**
Centralization	Extent to which there is a small number of highly central nodes	**0.436**	0.336	0.354	**0.483**	0.292	0.443
Density	Number of ties divided by the maximum number possible; matrix diagonal is ignored	0.450	**0.552**	0.538	0.337	**0.417**	0.414
Connectedness	One minus fragmentation (proportion of pairs of vertices that are unreachable)	0.849	0.852	**0.862**	0.663	**0.743**	0.742
Average distance	Average geodesic distance (number of links in a shortest path) amongst reachable pairs of marine reserves	**1.754**	1.481	1.502	**1.609**	1.596	1.567
Compactness	Average of all the reciprocal geodesic distances	0.615	**0.683**	0.681	0.487	0.559	**0.562**
Max flow	Median value of maximum possible flow between any two vertices for each network configuration	4.5E+05	2.3E+06	**3.6E+06**	9.1E+05	**4.1E+06**	3.8E+06

We found that designing networks considering connectivity (S2 and S3) consistently outperformed networks in terms of higher densities (Fig. 7a, Tables 2 and S14) and larval flow between reserves (Fig. 7b), regardless of whether effect of ocean warming on PLDs is significant (i.e., major changes in larval connectivity patterns occur) or not. Differences between solutions S2 and S3 were small (and not significant) irrespective of the climate scenario used to assess the networks (Fig. 2). Moreover, in agreement with predicted reduced connectivity due to ocean warming (Fig. 3), all three solutions (networks) under future climatic conditions were less dense (Fig. 6), effectively representing a subset of expected connections under present climatic conditions. While planning for reduced connectivity under ocean warming (S3) had similar connectivity as the network designed using normal PLDs (**S2**), it outperformed the network designed without connectivity information (**S1**).

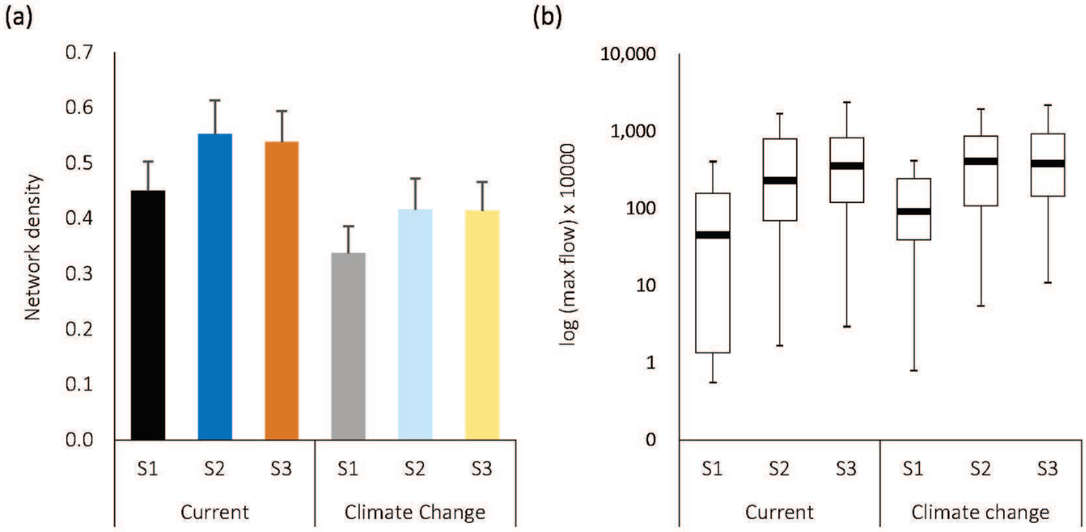

Fig. 7 Comparison of dispersal connectivity of marine reserve networks. **(a)** Comparison of networks in terms of their density for the current and climate change (3°C ocean warming) scenarios; error bars depict the bootstrapped standard error, illustrating the higher density of scenarios that considered connectivity, and the overall reduction in density across all solutions under future ocean warming. **(b)** Variability in the maximum flow between marine reserves for each solution, indicating the larger flow of larvae expected to occur among reserves of networks designed using connectivity information (including those under ocean warming). See **Fig. 2** for an explanation of how we assessed the three alternative marine reserve networks under two assumptions regarding changes in PLDs.

The ecologically-relevant connectivity index (IIC) confirmed that networks considering connectivity (S2 and S3) had considerably more links and were more connected than the network based only on representation objectives (S1), under both current and ocean-warming scenarios (Table S16). These results were robust regardless of differences between networks in terms of number of reserves and total area, which were used to calculate the index. The networks considering connectivity had more total area (45-46% more) and recruitment habitat (19-20% more). The index also indicated that S3 was slightly more connected than S2 under both assumptions, but particularly (as expected) under the ocean-warming scenario. This analysis indicates that designing networks under the assumption of shortened PLDs perform better in terms of maintaining connectivity irrespective of the magnitude of PLD changes. Yet, given potential changes in larval connectivity, it might not be possible to maintain the current levels of larval flow among individual reserves in the future.

Discussion

With imminent and ongoing changes to our oceans, our study pioneers the globally important challenge of maintaining the connectedness and thus improving the potential performance of marine reserve networks, despite changes in larval physiology and resulting connectivity associated with ocean warming. We propose a novel framework for designing marine reserve networks that integrates graph theory and changes in larval connectivity due to potential reductions in PLD associated with ocean warming, given socioeconomic constraints. Previous studies have combined spatially-explicit connectivity and ecosystem responses to thermal stress to design marine reserve networks (i.e., Mumby *et al.*, 2011, Beger *et al.*, 2015, Magris *et al.*, 2017), but ours is the first to show the benefits (in terms of maintaining larval connectivity) of adjusting the design of marine reserve networks to account for the potential reductions in connectivity associated with ocean warming due to PLD shortening and to quantify the costs of these adjustments.

We show that ecological connectivity patterns can change significantly with estimated ocean warming, resulting in less connected larval dispersal networks. These findings emphasize the need to consider the potential impact of climate change on species with variable dispersal patterns (Andrello *et al.*, 2015, Beger *et al.*, 2015) and indicate that important changes in marine reserve network design may be needed to maintain connectivity under future climatic conditions (Gerber *et al.*, 2014, Kleypas *et al.*, 2016). However, if distances among habitat patches are shorter, ocean warming could increase connectivity at smaller spatial scales because more larvae would be exchanged between nearby sites (Munday *et al.*, 2009).

In general, we found reduced connectivity between sites and shifts in centrality to sites located downstream in the direction of the flow due to future ocean warming; these patterns are probably exacerbated in the strongly asymmetric current system from the RGI, where PLD is positively related to distance traveled by larvae (Munguía-Vega *et al.*, 2014, Soria *et al.*, 2014). Under these conditions, species that show a patchy distribution with large distances between habitat patches could be heavily affected. Yet, mobility of some species during the adult phase (TinHan *et al.*, 2014) could buffer some of the effects of a reduction in connectivity during the larval phase due to ocean warming, compared to species with sedentary adults (e.g., corals, bivalves).

The effects of ocean warming on connectivity will likely vary significantly among species with diverse physiologies and life-histories (O'Connor *et al.*, 2007), which calls for further studies to explore the potential effects of including additional focal species. In our case, we expect variations will not be as severe for marine reserves located in more open ocean with symmetrical current systems, where larval connectivity is not as sensitive to PLD (Selkoe *et al.*, 2016). Our focal species represented a range of taxa with varying life histories and potentially distinct connectivity requirements, but did not include species spawning in winter (anti-cyclonic phase of the gyre). While various species of commercial importance are summer spawners (cyclonic phase of the gyre) (Soria *et al.*, 2014), many others are winter spawners and were not explicitly targeted in our analysis. Future research will help to assess whether including connectivity data on winter spawners could require changes in the configuration of marine reserve networks in the region.

Changes in connectivity due to ocean warming beyond PLD reductions could further change the design of marine reserve networks. Our analyses were adequate given the information available, but we recommend further research to explore changes in connectivity due to altered current speed and direction based on the predicted shifts of biophysical variables using oceanographic models (e.g., Andrello *et al.*, 2015). Improvements could add variations due to ocean acidification, spawning timing, larval survival, and larval behavior (Treml *et al.*, 2012, Gerber *et al.*, 2014), which – in some cases – could require further adjustments to the configuration of marine reserves. Furthermore, there is evidence that regions to the north and south are influencing connectivity patterns in the RGI (Marinone, 2012), which would require parameterizing the dispersal model for potential input and export of larvae beyond our study area.

Potential changes in the distribution and abundance of species (Perry *et al.*, 2005, Ayala-Bocos *et al.*, 2016) and their larval recruitment habitats (Aburto-Oropeza *et al.*, 2010) can also affect dispersal kernels (Gerber *et al.*, 2014), which could require further adjustments to networks. However, available data suggests the geographic range of focal species (e.g., *Mycteroperca rosacea* and *Sargassum* beds, an important recruitment habitat) in the RGI will remain relatively stable under climate change (Precoma de la Mora, 2015, Ayala-Bocos *et al.*, 2016, Munguía-Vega *et al.*, in prep). Further work on developing distribution and abundance models for species and habitats, as well as on their potential effects on connectivity are thus potential areas of further research.

Here, we demonstrate that following a graph-theoretical approach (based on centrality of habitat patches) can help to design more connected marine reserve networks for costs equivalent to an approach that does not account for connectivity. We show that maintaining dispersal connectivity incidentally through representation-only reserve design approaches is unlikely, particularly in regions with strong asymmetric dispersal connectivity patterns, such as the RGI. Previous studies have found similar results (White *et al.*, 2014, Magris *et al.*, 2016), but ours is the first to show benefits (in terms of maintaining larval connectivity) and potential costs of this approach under future ocean warming. Adjusting network designs to maintain connectivity assuming shorter PLDs prove effective to maximize connectivity under current and ocean-warming scenarios. However, given likely changes in larval connectivity due to ocean warming these adjustments may not be sufficient to maintain the current levels of larval connectivity among reserves in the future.

Our study emphasizes the importance of considering spatially-explicit connectivity patterns of a region to adjust the design of marine reserve networks accordingly. In our case, the study area is characterized by highly-asymmetric currents (Marinone, 2012), where connectivity heavily depends on PLD and reductions in PLD directly translate into less connectivity among distant habitat patches and centrality shifting to downstream areas. In other systems (i.e., where currents are more symmetric or multi-directional) connectivity may not be as sensitive to PLD (Selkoe *et al.*, 2016) and we should not expect the same magnitude of the effects in connectivity or centrality, or at least not due to the same mechanism.

Our results suggest that, given potential reductions in PLD and connectivity due to ocean warming, future networks of marine reserves would require more and/or larger reserves in closer proximity to maintain connectivity. Incorporating connectivity resulted in networks characterized by a better distribution of centrality among reserves (i.e., network connectedness relied less on few highly central reserves). We argue this characteristic could increase the resilience of networks to impacts on or loss of individual reserves (Bodin & Saura, 2010), effectively spreading risk and improving the chances of success of the network to maintain connectivity under future climates and multiple threats (Green *et al.*, 2014). Further, creating better-connected (e.g., denser) networks (Green *et al.*, 2015) could contribute to faster recovery and more sustainable fish biomass.

We found that further adjusting the design of marine reserve networks to account for ocean warming will not necessarily incur significant changes in costs. Here, the increase in size and number of reserves did not significantly increase costs through shifting reserves to lower cost areas that nonetheless were key for larval connectivity because of their upstream location relative to the direction of the predominant flow. However, our socioeconomic model did not account for potential changes in fish distribution and catches following ocean warming (Kaplan *et al.*, 2013), which could require further adjustments in the configuration of marine reserves. Further, our study shares the common limitation of prioritization approaches based on summed opportunity cost layers because it can mask potential inequalities in the distribution of costs to different stakeholders (Gurney *et al.*, 2015). Adding a weighting factor based on the number of fishers by fleet (Adams *et al.*, 2011) or reflecting the relative sensitivity of different fleets to fishery closures (Cinner *et al.*, 2012) could minimize this problem. Other options include using optimization software that allows the use of multiple cost layers (Klein *et al.*, 2009) or customizing optimization to include socioeconomic objectives for different stakeholder groups (Halpern *et al.*, 2013).

Further, our exploration of marine reserve size allowed us to assess the adequacy of alternative marine reserve networks to protect targeted species (Green *et al.*, 2015, Munguía-Vega *et al.*, in prep). The dimensions of marine reserves under the three prioritization scenarios are adequate to protect most targeted species. Yet, accounting for larval connectivity and ocean warming resulted in relatively larger reserves, when compared to the representation-only approach. This means that these networks are not only better connected, but can also protect a wider range of species. While we recognize that the size of the smaller reserves in our networks will not be adequate to protect highly mobile species, we argue that larger pelagic fish require different management strategies considered elsewhere (see: Anadón *et al.*, 2011).

While the protection of hubs and stepping stones significantly improved overall connectivity (including under future warmer conditions), adding the protection of self-sustaining populations could be necessary in some cases (White *et al.*, 2014, Magris *et al.*, 2016). While we did not target high self-recruitment areas, our analysis indicated that these areas were incidentally included in solutions (e.g., within modeling units 1, 8, 11; Fig. 3), yet we suggest SCP applications should consider identifying and explicitly targeting self-recruitment areas (Zamborain-Mason *et al.*, 2017). Further, assigning higher objectives to upstream sites showing high centrality makes sense from a metapopulation point of view, yet the relation of centrality with genetic diversity is inverse in the RGI, at least for some species (Lodeiros *et al.*, 2016). Thus this approach would be favoring protection of sites with relatively lower genetic diversity and potentially reduced evolutionary capacity to adapt. Future studies aiming to follow a similar approach to ours would benefit from exploring the above-mentioned considerations.

Our results were influenced by the relatively coarse resolution of both the larval dispersal model and the end-to-end ecosystem model used to derive cost data. While both models are robust and have been validated (Morzaria-Luna *et al.*, 2012, Munguía-Vega *et al.*, 2014), testing the effectiveness of downscaling techniques was beyond our scope. Further modeling (Lett *et al.*, 2010) and sensitivity analyses (Richardson *et al.*, 2006, Cheok *et al.*, 2016) to explore different methods to address these data limitations are needed. Additionally, our larval dispersal model could be improved using smaller units, more release sites, modeling major inter-annual variability (e.g., ENSO events), and adjusting larval output based on habitat suitability. Likewise, our cost layer could be improved using abundance/biomass models at finer resolutions (Adams *et al.*, 2011), or Atlantis outputs could be coupled with a bioeconomic model, such as input-output models of the study region that account for costs to both fisheries and supporting industries (Kaplan & Leonard, 2012). Finally, the threat model used to assess exposure to threats and adjust representation targets can be improved using higher resolution threat data and include variable responses of species and habitats to different threats (e.g., Halpern *et al.*, 2007).

Our approach focuses on maximizing larval connectivity to promote the persistence of populations within a network of marine reserves, but their impacts can certainly go beyond their boundaries. Previous studies demonstrate that the benefits of marine reserves can extend into fished areas through spillover of adults (Goñi et al., 2010), enhanced larval dispersal (Cudney-Bueno et al., 2009) or both (Kerwath et al., 2013). Studying the off-reserve effects of the proposed networks can thus help us understand their wider ecological and socioeconomic impacts across the region.

Further, while marine reserves can play an important role in the management of marine ecosystems, they can be more effective when implemented along other management strategies following an ecosystem-based management (EBM) approach (Ainsworth et al., 2012) and within a marine spatial planning framework (Agardy et al., 2011, Moreno-Báez et al., 2012). Ongoing efforts in the region, including those of organizations contributing to this study (e.g., Comunidad y Biodiversidad: cobi.org.mx), consider the participatory design and implementation of marine reserves as a key component of EBM in the RGI (Turk-Boyer et al., 2014, Munguía-Vega et al., 2015). Ongoing management strategies include programs to reduce bycatch of threatened species (e.g. vaquita and marine turtles), environmental impact assessments, Territorial Use Rights in Fisheries (TURFs) programs, catch share systems, fisheries refuges, certification of industrial fisheries, and other sustainable fisheries management strategies (e.g., size and seasonal limits) designed in collaboration with fishers (Poon & Bonzon, 2013, Turk-Boyer et al., 2014, Munguía-Vega et al., 2015, Aburto-Oropeza et al., 2017). Exploring the role of networks of marine reserves in the broader context of current and future EBM programs is an important research avenue in the region and beyond.

In summary, our study offers a novel approach to inform real-world marine planning initiatives in the region and beyond. We demonstrate that marine reserve design can be improved to account for larval connectivity without a significant increase in opportunity costs to fishers. Adjusting the design to account for future reduced connectivity due to ocean warming did not result in further improvements in connectivity, but achieved better results than reserve designs assuming uniform connectivity. Considering current patterns of connectivity could help to buffer against ocean warming effects, even if the reduction in PLD is not explicitly included during the network design process.

Acknowledgements

We thank the editor and three anonymous reviewers for their valuable comments and suggestions, which greatly improved the paper. We thank the following people for providing information, technical support and/or participating in the planning process and workshops: Ana Luisa Figueroa, Griselda Franco, Imelda Amador, José Anadón, Mario Rojo, and Ollin González-Cuellar. We also thank the support of Comisión Nacional de Acuacultura y Pesca, Comisión Nacional de Áreas Naturales Protegidas, Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, David and Lucile Packard Foundation (DLPF), Fondo Mexicano para la Conservación de la Naturaleza, Marisla Foundation, Sandler Family Supporting Foundation, The Nature Conservancy, United Nations Development Program, Walton Family Foundation, and World Wildlife Fund-Carlos Slim Foundation Alliance. A special thank you to fishers for providing information and participating in ongoing research activities. JGAR, GGG, and RLP acknowledge the support of the Australian Research Council (ARC) Center of Excellence for Coral Reef Studies. AMV was supported by grants from DLPF to the PANGAS Science Coordination (2013-39400, 2015-62798). MB was supported by the ARC Centre of Excellence for Environmental Decisions with an Early Career Travel Grant and Discovery Early Career Research Award (CE110001014).

References

Aburto-Oropeza O, Ezcurra E, Danemann G, Valdez V, Murray J, Sala E (2008) Mangroves in the Gulf of California increase fishery yields. Proceedings of the National Academy of Sciences of the United States of America*,* **105**, 10456-10459.

Aburto-Oropeza O, Leslie HM, Mack-Crane A, Nagavarapu S, Reddy SMW, Sievanen L (2017) Property Rights for Fishing Cooperatives: How (and How Well) Do They Work? The World Bank Economic Review*,* **31**, 295-328.

Aburto-Oropeza O, Paredes G, Mascareñas-Osorio I, Sala E (2010) Climatic influence on reef fish recruitment and fisheries. Marine Ecology Progress Series*,* **410**, 283–287.

Aburto-Oropeza O, Sala E, Paredes G, Mendoza A, Ballesteros E (2007) Predictability of reef fish recruitment in a highly variable nursery habitat. Ecology*,* **88**, 2220-2228.

Adams VM, Mills M, Jupiter SD, Pressey RL (2011) Improving social acceptability of marine protected area networks: A method for estimating opportunity costs to multiple gear types in both fished and currently unfished areas. Biological Conservation*,* **144**, 350-361.

Agardy T, Di Sciara GN, Christie P (2011) Mind the gap: addressing the shortcomings of marine protected areas through large scale marine spatial planning. Marine Policy*,* **35**, 226-232.

Ainsworth CH, Kaplan IC, Levin PS *et al.* (2011) Atlantis model development for the Northern Gulf of California. U.S. Dept. Commer., NOAA Tech. Memo. NMFS-NWFSC-110. pp Page, Seattle, WA, USA, Northwest Fisheries Science Center (NWFSC), National Marine Fisheries Service (NMFS), National Oceanic and Atmospheric Administration (NOAA).

Ainsworth CH, Morzaria-Luna H, Kaplan IC *et al.* (2012) Effective ecosystem-based management must encourage regulatory compliance: A Gulf of California case study. Marine Policy*,* **36**, 1275-1283.

Allison GW, Lubchenco J, Carr MH (1998) Marine reserves are necessary but not sufficient for marine conservation. Ecological Applications*,* **8**, S79-S92.

Almany G, Connolly S, Heath D *et al.* (2009) Connectivity, biodiversity conservation and the design of marine reserve networks for coral reefs. Coral Reefs*,* **28**, 339-351.

Almany GR, Planes S, Thorrold SR *et al.* (2017) Larval fish dispersal in a coral-reef seascape. Nature Ecology & Evolution*,* **1**, 0148.

Álvarez-Romero JG, Pressey RL, Ban NC, Torre-Cosío J, Aburto-Oropeza O (2013) Marine conservation planning in practice: lessons learned from the Gulf of California. Aquatic Conservation: Marine and Freshwater Ecosystems*,* **23**, 483-505.

Anadón JD, D'agrosa C, Gondor A, Gerber LR (2011) Quantifying the spatial ecology of wide-ranging marine species in the Gulf of California: implications for marine conservation planning. PLoS ONE*,* **6**, e28400.

Andrello M, Mouillot D, Somot S, Thuiller W, Manel S (2015) Additive effects of climate change on connectivity between marine protected areas and larval supply to fished areas. Diversity and Distributions*,* **21**, 139-150.

Arias A, Pressey RL, Jones RE, Álvarez-Romero JG, Cinner JE (2016) Optimizing enforcement and compliance in offshore marine protected areas: a case study from Cocos Island, Costa Rica. Oryx*,* **50**, 18-26.

Ayala-Bocos A, Reyes-Bonilla H, Calderón-Aguilera LE, Herrero-Perezrul MD, González-Espinosa PC (2016) Forecasting changes in sea surface temperature in the Gulf of California and their effects on abundance and distribution of reef species. Revista Ciencias Marinas y Costeras*,* **8**, 29-40.

Backhaus JO (1985) A three-dimensional model for the simulation of the shelf sea dynamics. Dtsch Hydrogr*,* **38**, 165-187.

Ball I, Possingham H, Watts DJ (2009) Marxan and relatives: software for spatial conservation prioritization. In: *Spatial Conservation Prioritization Quantitative Methods and Computational Tools.* (eds Moilanen A, Wilson K, Possingham H) pp Page. Oxford, UK, Oxford University Press.

Ban NC, Januchowski-Hartley SR, Álvarez-Romero JG, Mills M, Pressey RL, Linke S, De Freitas DM (2013) Marine and freshwater conservation planning: from representation to persistence. In: *Conservation Planning: Shaping the Future.* (eds Craighead L, Convis C) pp Page. Redlands, CA, Esri Press.

Ban NC, Klein CJ (2009) Spatial socioeconomic data as a cost in systematic marine conservation planning. Conservation Letters*,* **2**, 206-215.

Barbier EB, Hacker SD, Kennedy C, Koch EW, Stier AC, Silliman BR (2010) The value of estuarine and coastal ecosystem services. Ecological Monographs*,* **81**, 169-193.

Beger M, Linke S, Watts M, Game E, Treml E, Ball I, Possingham HP (2010) Incorporating asymmetric connectivity into spatial decision making for conservation. Conservation Letters*,* **3**, 359-368.

Beger M, Mcgowan J, Treml EA *et al.* (2015) Integrating regional conservation priorities for multiple objectives into national policy. Nature communications*,* **6**.

Bode M, Williamson DH, Weeks R *et al.* (2016) Planning marine reserve networks for both feature representation and demographic persistence using connectivity patterns. PLoS ONE*,* **11**, e0154272.

Bodin Ö, Saura S (2010) Ranking individual habitat patches as connectivity providers: Integrating network analysis and patch removal experiments. Ecological Modelling*,* **221**, 2393-2405.

Bonacich P (1972) Factoring and weighting approaches to status scores and clique identification. The Journal of Mathematical Sociology*,* **2**, 113-120.

Boonzaier L, Pauly D (2016) Marine protection targets: an updated assessment of global progress. Oryx*,* **50**, 27-35.

Borgatti S (2002) NetDraw: Graph Visualization Software. pp Page, Harvard, MA, USA, Analytic Technologies.

Borgatti S, Everett M, Freeman L (2002) UCINET 6 for Windows: Software for social network analysis (Version 6.102). Harvard, MA: Analytic Technologies.

Borgatti SP (2005) Centrality and network flow. Social Networks*,* **27**, 55-71.

Brusca RC (2007) Invertebrate biodiversity in the northern Gulf of California In: *Dry borders. Great natural reserves of the Sonoran Desert.* (eds Felger RS, Broyles B) pp Page. Salt Lake city, The University of Utah press.

Cheok J, Pressey RL, Weeks R, Andréfouët S, Moloney J (2016) Sympathy for the devil: detailing the effects of planning-unit size, thematic resolution of reef classes, and socioeconomic costs on spatial priorities for marine conservation. PLoS ONE*,* **11**, e0164869.

Cinner JE, Mcclanahan TR, Graham NaJ *et al.* (2012) Vulnerability of coastal communities to key impacts of climate change on coral reef fisheries. Global Environmental Change*,* **22**, 12-20.

Cinti A, Duberstein JN, Torreblanca E, Moreno-Báez M (2014) Overfishing Drivers and Opportunities for Recovery in Small-Scale Fisheries of the Midriff Islands Region, Gulf of California, Mexico: the Roles of Land and Sea Institutions in Fisheries Sustainability. Ecology and Society*,* **19**.

Conabio, Conanp, Tnc, Pronatura (2007) *Analisis de vacios y omisiones en conservacion de la biodiversidad marina de Mexico: oceanos, costas e islas,* Mexico, D.F., Comision Nacional para el Conocimiento y Uso de la Biodiversidad (CONABIO), Comision Nacional de Areas Naturales Protegidas (CONANP), The Nature Conservancy (TNC), Pronatura A.C.

Cowen RK, Paris CB, Srinivasan A (2005) Scaling of connectivity in marine populations. Science, 1122039.

Cowen RK, Sponaugle S (2009) Larval dispersal and marine population connectivity. Annual Review of Marine Science*,* **1**, 443-466.

Cudney-Bueno R, Lavín MF, Marinone SG, Raimondi PT, Shaw WW (2009) Rapid effects of marine reserves via larval dispersal. PLoS ONE*,* **4**, e4140.

Dale MRT, Fortin MJ (2010) From Graphs to Spatial Graphs. Annual Review of Ecology, Evolution, and Systematics*,* **41**, 21-38.

Duffy JE, Lefcheck JS, Stuart-Smith RD, Navarrete SA, Edgar GJ (2016) Biodiversity enhances reef fish biomass and resistance to climate change. Proceedings of the National Academy of Sciences*,* **113**, 6230-6235.

Elith J, Phillips SJ, Hastie T, Dudík M, Chee YE, Yates CJ (2011) A statistical explanation of MaxEnt for ecologists. Diversity and Distributions*,* **17**, 43-57.

Engelhard SL, Huijbers CM, Stewart-Koster B, Olds AD, Schlacher TA, Connolly RM (2017) Prioritizing seascape connectivity in conservation using network analysis. Journal of Applied Ecology*,* **54**, 1130-1141.

Erisman B, Mascarenas I, Paredes G, De Mitcheson YS, Aburto-Oropeza O, Hastings P (2010) Seasonal, annual, and long-term trends in commercial fisheries for aggregating reef fishes in the Gulf of California, Mexico. Fisheries Research*,* **106**, 279-288.

Fernandes L, Day J, Lewis A *et al.* (2005) Establishing representative no-take areas in the Great Barrier Reef: large-scale implementation of theory on marine protected areas. Conservation Biology*,* **19**, 1733-1744.

Ford LR, Fulkerson DR (1956) Maximal flow through a network. Canadian journal of Mathematics*,* **8**, 399-404.

Fulton EA, Link JS, Kaplan IC *et al.* (2011) Lessons in modelling and management of marine ecosystems: the Atlantis experience. Fish and Fisheries*,* **12**, 171-188.

Gaines SD, Gaylord B, Gerber L, Hastings A, Kinlan BP (2007) Connecting places: the ecological consequences of dispersal in the sea. Oceanography*,* **20**, 90-99.

Gerber LR, Botsford LW, Hastings A, Possingham HP, Gaines SD, Palumbi SR, Andelman S (2003) Population models for marine reserve design: a retrospective and prospective synthesis. Ecological Applications*,* **13**, S47-S64.

Gerber LR, Mancha-Cisneros MDM, O'connor MI, Selig ER (2014) Climate change impacts on connectivity in the ocean: implications for conservation. Ecosphere*,* **5**, 1-18.

Gillooly JF, Charnov EL, West GB, Savage VM, Brown JH (2002) Effects of size and temperature on developmental time. Nature*,* **417**, 70-73.

Goñi R, Hilborn R, Díaz D, Mallol S, Adlerstein S (2010) Net contribution of spillover from a marine reserve to fishery catches. Marine Ecology Progress Series*,* **400**, 233-243.

Green AL, Fernandes L, Almany G *et al.* (2014) Designing marine reserves for fisheries management, biodiversity conservation, and climate change adaptation. Coastal Management, **42**, 143-159.

Green AL, Maypa AP, Almany GR *et al.* (2015) Larval dispersal and movement patterns of coral reef fishes, and implications for marine reserve network design. Biological Reviews, **90**, 1215-1247.

Gurney GG, Cinner J, Ban NC *et al.* (2014) Poverty and protected areas: An evaluation of a marine integrated conservation and development project in Indonesia. Global Environmental Change, **26**, 98-107.

Gurney GG, Melbourne-Thomas J, Geronimo RC, Aliño PM, Johnson CR (2013) Modelling coral reef futures to inform management: can reducing local-scale stressors conserve reefs under climate change? PLoS ONE, **8**, e80137.

Gurney GG, Pressey RL, Ban NC, Álvarez-Romero JG, Jupiter S, Adams VM (2015) Efficient and equitable design of marine protected areas in Fiji through inclusion of stakeholder-specific objectives in conservation planning. Conservation Biology, **29**, 1378–1389.

Halpern BS, Klein CJ, Brown CJ *et al.* (2013) Achieving the triple bottom line in the face of inherent trade-offs among social equity, economic return, and conservation. Proceedings of the National Academy of Sciences, **110**, 6229-6234.

Halpern BS, Selkoe KA, Micheli F, Kappel CV (2007) Evaluating and Ranking the Vulnerability of Global Marine Ecosystems to Anthropogenic Threats. Conservation Biology, **21**, 1301-1315.

Halpern BS, Walbridge S, Selkoe KA *et al.* (2008) A global map of human impact on marine ecosystems. Science, **319**, 948-952.

Harrison HB, Williamson DH, Evans RD *et al.* (2012) Larval Export from Marine Reserves and the Recruitment Benefit for Fish and Fisheries. Current Biology, **22**, 1023-1028.

Ipcc (2014) Climate Change 2014: Synthesis Report. pp Page, Geneva, Switzerland, Intergovernmental Panel on Climate Change (IPCC).

Jonsson PR, Nilsson Jacobi M, Moksnes P-O (2016) How to select networks of marine protected areas for multiple species with different dispersal strategies. Diversity and Distributions, **22**, 161-173.

Kaplan IC, Gray IA, Levin PS (2013) Cumulative impacts of fisheries in the California Current. Fish and Fisheries, **14**, 515-527.

Kaplan IC, Leonard J (2012) From krill to convenience stores: Forecasting the economic and ecological effects of fisheries management on the US West Coast. Marine Policy, **36**, 947-954.

Kerwath SE, Winker H, Götz A, Attwood CG (2013) Marine protected area improves yield without disadvantaging fishers. Nat Commun, **4**.

Kininmonth S, Beger M, Bode M *et al.* (2011) Dispersal connectivity and reserve selection for marine conservation. Ecological Modelling, **222**, 1272-1282.

Klein CJ, Chan A, Kircher L *et al.* (2008) Striking a balance between biodiversity conservation and socioeconomic viability in the design of marine protected areas. Conservation Biology, **22**, 691-700.

Klein CJ, Steinback C, Watts M, Scholz AJ, Possingham HP (2009) Spatial marine zoning for fisheries and conservation. Frontiers in Ecology and the Environment, **8**, 349-353.

Kleypas JA, Thompson DM, Castruccio FS, Curchitser EN, Pinsky M, Watson JR (2016) Larval connectivity across temperature gradients and its potential effect on heat tolerance in coral populations. Global Change Biology, **22**, 3539-3549.

Kolb M (2008) Tecnical report MEXBIO-CLUEbase Mexico. pp Page, Mexico, D.F., Mexico, Comision Nacional para el Conocimiento y Uso de la Biodiversidad (CONABIO).

Kool JT, Moilanen A, Treml EA (2013) Population connectivity: recent advances and new perspectives. Landscape Ecology, **28**, 165-185.

Krueck NC, Ahmadia GN, Green A *et al.* (2017) Incorporating larval dispersal into MPA design for both conservation and fisheries. Ecological Applications, **27**, 925-941.

Lavín M, Marinone S (2003) An overview of the physical oceanography of the Gulf of California. In: *Nonlinear processes in geophysical fluid dynamics.* (eds Velasco OU, Sheinbaum J, Ochoa J) pp Page. Dordrecht, Holanda, Kluwer Academia Publishers.

Lavin MF, Durazo R, Palacios E, Argote ML, Carrillo L (1997) Lagrangian observations of the circulation in the northern Gulf of California. Journal of Physical Oceanography, **27**, 2298-2305.

Leslie HM (2005) Synthesis of marine conservation planning approaches. Conservation Biology, **19**, 1701-1713.

Lester SE, Halpern BS, Grorud-Colvert K *et al.* (2009) Biological effects within no-take marine reserves: a global synthesis. Marine Ecology-Progress Series, **384**, 33-46.

Lett C, Ayata S-D, Huret M, Irisson J-O (2010) Biophysical modelling to investigate the effects of climate change on marine population dispersal and connectivity. Progress in Oceanography, **87**, 106-113.

Levy JS, Ban NC (2013) A method for incorporating climate change modelling into marine conservation planning: An Indo-west Pacific example. Marine Policy, **38**, 16-24.

Liggins L, Treml EA, Riginos C (2013) Taking the plunge: an introduction to undertaking seascape genetic studies and using biophysical models. Geography Compass, **7**, 173-196.

Lluch-Cota SE, Aragon-Noriega EA, Arreguin-Sanchez F *et al.* (2007) The Gulf of California: Review of ecosystem status and sustainability challenges. Progress in Oceanography, **73**, 1-26.

Lodeiros C, Soria G, Valentich-Scott P *et al.* (2016) Spondylids of Eastern Pacific Ocean. Journal of Shellfish Research, **35**, 279-293.

Magris RA, Heron SF, Pressey RL (2015) Conservation planning for coral reefs accounting for climate warming disturbances. PLoS ONE, **10**, e0140828.

Magris RA, Pressey RL, Mills M, Vila-Nova DA, Floeter S (2017) Integrated conservation planning for coral reefs: Designing conservation zones for multiple conservation objectives in spatial prioritisation. Global Ecology and Conservation, **11**, 53-68.

Magris RA, Pressey RL, Weeks R, Ban NC (2014) Integrating connectivity and climate change into marine conservation planning. Biological Conservation, **170**, 207-221.

Magris RA, Treml EA, Pressey RL, Weeks R (2016) Integrating multiple species connectivity and habitat quality into conservation planning for coral reefs. Ecography, **39**, 649-664.

Margules CR, Pressey RL (2000) Systematic conservation planning. Nature, **405**, 243-253.

Marinone SG (2003) A three-dimensional model of the mean and seasonal circulation of the Gulf of California. Journal of Geophysical Research, **108**, 1-27.

Marinone SG (2008) On the three-dimensional numerical modeling of the deep circulation around Ángel de la Guarda Island in the Gulf of California. Estuarine, Coastal and Shelf Science, **80**, 430-434.

Marinone SG (2012) Seasonal surface connectivity in the Gulf of California. Estuarine, Coastal and Shelf Science, **100**, 133-141.

Mellin C, Aaron Macneil M, Cheal AJ, Emslie MJ, Julian Caley M (2016) Marine protected areas increase resilience among coral reef communities. Ecology Letters, **19**, 629-637.

Micheli F, Saenz-Arroyo A, Greenley A, Vazquez L, Espinoza Montes JA, Rossetto M, De Leo GA (2012) Evidence that marine reserves enhance resilience to climatic impacts. PLoS ONE, **7**, e40832.

Moreno-Báez M, Cudney-Bueno R, Orr BJ *et al.* (2012) Integrating the spatial and temporal dimensions of fishing activities for management in the Northern Gulf of California, Mexico. Ocean & Coastal Management, **55**, 111-127.

Moreno-Báez M, Orr BJ, Cudney-Bueno R, Shaw WW (2010) Using fishers' local knowledge to aid management at regional scales: spatial distribution of small-scale fisheries in the northern Gulf of California, Mexico. Bulletin of Marine Science, **86**, 339-353.

Morzaria-Luna HN, Ainsworth CH, Kaplan IC, Levin PS, Fulton EA (2012) Exploring trade-offs between fisheries and conservation of the vaquita porpoise (Phocoena sinus) using an Atlantis ecosystem model. PLoS ONE, **7**, e42917.

Mumby PJ, Elliott IA, Eakin CM *et al.* (2011) Reserve design for uncertain responses of coral reefs to climate change. Ecology Letters, **14**, 132-140.

Munday PL, Leis JM, Lough JM, Paris CB, Kingsford MJ, Berumen ML, Lambrechts J (2009) Climate change and coral reef connectivity. Coral Reefs, **28**, 379-395.

Munguía-Vega A, Jackson A, Marinone SG *et al.* (2014) Asymmetric connectivity of spawning aggregations of a commercially important marine fish using a multidisciplinary approach. PeerJ, **2:e511; DOI 10.7717/peerj.511**.

Munguía-Vega A, Morzaria-Luna HN, Suarez-Castillo AN *et al.* (in prep) Ecological guidelines for designing a network of marine reserves in the unique biophysical environment of the Gulf of California. Ecological Applications.

Munguía-Vega A, Torre J, Turk-Boyer P *et al.* (2015) PANGAS: an interdisciplinary ecosystem-based research framework for small-scale fisheries in the northern Gulf of California. Journal of the Southwest, **57**, 337-390.

O'connor MI, Bruno JF, Gaines SD, Halpern BS, Lester SE, Kinlan BP, Weiss JM (2007) Temperature control of larval dispersal and the implications for marine ecology, evolution, and conservation. Proceedings of the National Academy of Sciences, **104**, 1266-1271.

Olds AD, Connolly RM, Pitt KA *et al.* (2016) Quantifying the conservation value of seascape connectivity: a global synthesis. Global Ecology and Biogeography*,* **25**, 3-15.

Páez-Osuna F, Sanchez-Cabeza JA, Ruiz-Fernández AC *et al.* (2016) Environmental status of the Gulf of California: a review of responses to climate change and climate variability. Earth-Science Reviews*,* **162**, 253-268.

Paris CB, Cherubin LM, Cowen RK (2007) Surfing, spinning, or diving from reef to reef: effects on population connectivity. Marine Ecology Progress Series*,* **347**, 285-300.

Pascual-Hortal L, Saura S (2006) Comparison and development of new graph-based landscape connectivity indices: towards the priorization of habitat patches and corridors for conservation. Landscape Ecology*,* **21**, 959-967.

Perry AL, Low PJ, Ellis JR, Reynolds JD (2005) Climate change and distribution shifts in marine fishes. Science*,* **308**, 1912-1915.

Poon SE, Bonzon K (2013) *Catch Share Design Manual Vol. 3: Territorial Use Rights for Fishing,* New York, NY, USA, Environmental Defense Fund.

Precoma De La Mora M (2015) Distribucion potencial de peces de importancia comercial en el norte del Golfo de California: Inlfuencia del cambio climatico sobre las principales areas de pesca de la zona. Unpublished MSc Centro de Investigacion Cientifica y de Educacion Superior de Ensenada (CICESE), Ensenada, BC, Mexico, 89 pp.

Pressey RL, Cowling RM, Rouget M (2003) Formulating conservation targets for biodiversity pattern and process in the Cape Floristic Region, South Africa. Biological Conservation*,* **112**, 99-127.

Rábago-Quiroz CH, López-Martínez J, Valdez-Holguín JE, Nevárez Martínez MO (2011) Distribución latitudinal y batimétrica de las especies más abundantes y frecuentes en la fauna acompañante del camarón del Golfo de California, México. Revista de Biología Tropical*,* **59**, 255-267.

Richardson EA, Kaiser MJ, Edwards-Jones G, Possingham HP (2006) Sensitivity of marine-reserve design to the spatial resolution of socioeconomic data. Conservation Biology*,* **20**, 1191-1202.

Rife AN, Erisman B, Sanchez A, Aburto-Oropeza O (2013) When good intentions are not enough: insights on networks of "paper park" marine protected areas. Conservation Letters*,* **6**, 200-212.

Sadovy Y (2005) Trouble on the reef: the imperative for managing vulnerable and valuable fisheries. Fish and Fisheries*,* **6**, 167-185.

Sala E, Aburto-Oropeza O, Paredes G, Parra I, Barrera JC, Dayton PK (2002) A general model for designing networks of marine reserves. Science*,* **298**, 1991-1993.

Sala E, Aburto-Oropeza O, Paredes G, Thompson G (2003) Spawning aggregations and reproductive behavior of reef fishes in the Gulf of California. Bulletin of Marine Science*,* **72**, 103-121.

Sanford T, Frumhoff PC, Luers A, Gulledge J (2014) The climate policy narrative for a dangerously warming world. Nature Clim. Change*,* **4**, 164-166.

Saura S, Torné J (2009) Conefor Sensinode 2.2: A software package for quantifying the importance of habitat patches for landscape connectivity. Environmental Modelling & Software*,* **24**, 135-139.

Selkoe KA, Gaggiotti OE, Treml EA, Wren JLK, Donovan MK, Toonen RJ (2016) The DNA of coral reef biodiversity: predicting and protecting genetic diversity of reef assemblages. Proceedings of the Royal Society B: Biological Sciences*,* **283**.

Snijders TaB, Borgatti SP (1999) Non-parametric standard errors and tests for network statistics. Connections*,* **22**, 1-11.

Soria G, Munguía-Vega A, Marinone SG, Moreno-Báez M, Martínez-Tovar I, Cudney-Bueno R (2012) Linking bio-oceanography and population genetics to assess larval connectivity. Marine Ecology Progress Series*,* **463**, 159-175.

Soria G, Torre-Cosio J, Munguía-Vega A, Marinone SG, Lavín MF, Cinti A, Moreno-Báez M (2014) Dynamic connectivity patterns from an insular marine protected area in the Gulf of California. Journal of Marine Systems*,* **129**, 248-258.

Tinhan T, Erisman B, Aburto-Oropeza O, Weaver A, Vázquez-Arce D, Lowe CG (2014) Residency and seasonal movements in Lutjanus argentiventris and Mycteroperca rosacea at Los Islotes Reserve, Gulf of California. Marine Ecology Progress Series*,* **501**, 191-206.

Treml E, Halpin P, Urban D, Pratson L (2008) Modeling population connectivity by ocean currents, a graph-theoretic approach for marine conservation. Landscape Ecology*,* **23**, 19-36.

Treml EA, Roberts JJ, Chao Y, Halpin PN, Possingham HP, Riginos C (2012) Reproductive output and duration of the pelagic larval stage determine seascape-wide connectivity of marine populations. Integrative and Comparative Biology, **52**, 525-537.

Turk-Boyer P, Morzaria-Luna HN, Martinez-Tovar I, Downton-Hoffmann C, Munguía-Vega A (2014) Ecosystem-based fisheries management of a biological corridor along the Northern Sonora coastline (NE Gulf of California). In: *Fisheries Management of Mexican and Central American Estuaries.* (eds Amezcua F, Bellgraph B) pp Page. Dordrecht, Netherlands, Springer.

Ulloa R, Torre J, Bourillón L, Gondor A, Alcantar N (2006) Planeación ecorregional para la conservación marina: Golfo de California y costa occidental de Baja California Sur. Informe final a The Nature Conservancy. pp Page, Guaymas, Mexico, Comunidad y Biodiversidad, A.C.

Watson JR, Siegel DA, Kendall BE, Mitarai S, Rassweiller A, Gaines SD (2011) Identifying critical regions in small-world marine metapopulations. Proceedings of the National Academy of Sciences, **108**, E907–E913.

White C, Selkoe KA, Watson J, Siegel DA, Zacherl DC, Toonen RJ (2010) Ocean currents help explain population genetic structure. Proceedings of the Royal Society B: Biological Sciences.

White JW, Schroeger J, Drake PT, Edwards CA (2014) The value of larval connectivity information in the static optimization of marine reserve design. Conservation Letters, **7**, 533-544.

Williamson DH, Harrison HB, Almany GR *et al.* (2016) Large-scale, multi-directional larval connectivity among coral reef fish populations in the Great Barrier Reef Marine Park. Molecular Ecology, n/a-n/a.

Wilson K, Pressey RL, Newton A, Burgman M, Possingham H, Weston C (2005) Measuring and incorporating vulnerability into conservation planning. Environmental Management, **35**, 527-543.

Zamborain-Mason J, Russ GR, Abesamis RA, Bucol AA, Connolly SR (2017) Network theory and metapopulation persistence: incorporating node self-connections. Ecology Letters, **20**, 815-831.