Dynamic connectivity patterns from an insular marine protected area in the Gulf of California

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1. Introduction

The Gulf of California (GC) is a semi-enclosed sea situated in Northwest Mexico with three marine faunal regions, the northern, central and southern (Brusca et al., 2005; Walker, 1960) (Fig. 1). Driven by low frequency currents and tides from the Pacific Ocean, and local winds, the circulation of the GC is seasonally-reversing; cyclonic in summer and anticyclonic in winter (Alvarez Borrego, 2010; Lavín et al., 2013). The cyclonic phase lasts from June to August and October, and the anticyclonic phase lasts from November to April, and entails the reversal of the northern Gulf eddy and the coastal current in the southern Gulf (Marinone, 2008). In addition to the seasonal circulation, there are meso-scale eddies in the southern Gulf, which have been modeled by Zamudio et al. (2008) and described in detail by Lavín et al. (2013).

We studied connectivity patterns from a small and isolated island in the Gulf of California (San Pedro Mártir Island Biosphere Reserve), as a source of propagules to surrounding Marine Protected Areas and fishing sites. We used a particle-tracking scheme based on the outputs of a three-dimensional numerical hydrodynamic model to assess the spatial domain to which the island exports larvae as well as larvae retention. We modeled the release of passive particles from locations around the island during the four release dates (May 15 and 31, and June 14 and 30), matching the lunar phases and the peak of the reproductive season for several commercial invertebrates and fish, at the time when currents in the Gulf typically reverse. For each simulation we analyzed the data at 15, 20 and 30 days after the release to represent different planktonic propagule durations. Particle dispersion was highly dynamic and spread over ~600 km along the coast over the study period. Overall, we observed potential ecological connectivity with a few key distant fishing sites that changed trough time, and potential genetic connectivity towards many near and distant sites, including all neighboring Marine Protected Areas, although not simultaneously. The percentages of particles remaining within the boundaries of the island tended to decline from May to June, and decreased with delayed planktonic propagule duration. The design of effective Marine Protected Areas should acknowledge the dynamic nature of connectivity patterns, for instance, by establishing adaptive network reserves to respond to changing ocean features that match reproductive patterns of target species and fisheries behavior.

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pathways for nutrients, food and propagules (eggs, larvae, and spores), and thus connecting marine species populations (Danell-Jiménez et al., 2009; Lavín and Marinone, 2003; Sánchez-Velasco et al., 2009). The MIR contains islands of different sizes, islets, basins, sills and straits which promote a unique seascape distinguished by its species richness and biodiversity largely supported by surrounding nutrient-rich waters brought to the upper layer throughout the year by tidal mixing and convergence-induced upwelling (Alvarez Borrego, 2010; López et al., 2006, 2008).

San Pedro Mártir Island (SPMI) is the most remote island in the GC (ca. 60 km from each coast) (Murphy et al., 2002) located in the southern limit of the MIR and positioned within a transition zone between the northern and central (Lavín and Marinone, 2003). This 2.9 km-diameter island harbors large colonies of cacti (Wilder and Fleger, 2010), and its surrounding waters are rich in fish, invertebrates, seabirds, marine mammals and sea-turtles, (CONANP-SEMARNAT, 2007). Given the unique characteristics of the island, including small size and isolation, it was decreed a Marine Protected Area (MPA) with the status of Biosphere Reserve (BR) in 2002 (DOF, 2002). In total, the reserve has an area of 302 km², including the island and two islets and 8 km² of coastal waters as core zone (no-take) and 291 km² of buffer zone where extractive activities are permitted (Fig. 1) (DOF, 2002). The island has long been used by sport fishers from continental Sonora targeting rocky reef and pelagic fishes (e.g., groupers, marlin, mahi-mahi) (Fujitani et al., 2012) and by small-scale commercial fishers from communities in both margins of the GC targeting mainly mollusk, lobsters, sea cucumbers and reef fishes (Erisman et al., 2011; Meza et al., 2008; Moreno-Báez et al., 2012). Currently, small-scale fishers within the buffer zone use three fishing gears: hookah diving, metallic traps, and hand lining. Although sport fishers are the most frequent visitors to the island, it is an important destination for small-scale commercial fisheries when fish abundances in remote fishing sites are depressed (Fujitani et al., 2012; Meza et al., 2008).

A distinctive attribute of many benthic invertebrate species (bivalves, crustaceans, echinoderms) and rocky reef fishes (sappers, groupers) is that they are structured as metapopulations: an assemblage of geographically separate subpopulations of sedentary organisms that are interconnected by the exchange of planktonic propagules (Lipcius et al., 2005). The extent to which these subpopulations are linked by the exchange of planktonic propagules is termed connectivity and can have multiple and different patterns, and implications (Lowe and Allendorf, 2010; Palumbi, 2003; Soria et al., 2012). The design of management strategies that explicitly acknowledge the complexity and dynamics of metapopulation connectivity would be most appropriate. In this sense, MPA networks, including fully protected marine reserves or no-take zones, are a tool to overcome the loss of biodiversity and the over-exploitation of fisheries that can integrate the spatial structure of marine populations in the design of management strategies (Gaines et al., 2010). The process of selecting an area or several areas to be set as MPAs is inherently a challenging assignment that involves the consideration of biophysical and human dimensions (Pollnac et al., 2010; Soria et al., 2012; Ulloa et al., 2006). As for the design of effective MPAs in general, the determination of the geographical scale, direction and magnitude of propagule dispersal, for instance through the use of oceanographic models, and its demographic and genetic impacts on distant populations is a critical area of research (Cowen and Sponaugle, 2009; Lowe and Allendorf, 2010; Palumbi, 2003; Soria et al., 2012). On one hand, demographic connectivity is characterized by relatively large amounts of propagules that have measurable effects in fishing activities over ecological timescales, while genetic connectivity usually involves fewer propagules that are, however, key for biodiversity conservation over evolutionary time scales,
including genetic diversity and structure that affect the evolutionary potential for adaptation (Lowe and Allendorf, 2010; Steneck et al., 2009). Since connectivity is usually assumed to decline with distance (Almany et al., 2009; Steneck et al., 2009), demographic connectivity is thought to occur only among nearby sites, while genetic connectivity could be more prevalent among distant sites. In the presence of strong directional currents, such as in the GC the importance of MPA location increases (Crowder et al., 2000; Gaines et al., 2003; Soria et al., 2012), compared to places where currents are mainly stochastic (Siegel et al., 2008).

Small, isolated MPAs as SPMI are common around the world (Mora and Sale, 2011), but are generally assumed to have low connectivity and thus low resiliency (Almany et al., 2009; Bell and Okamura, 2005). In general, small islands are deemed less important compared to big reserves because small reserves tend to be less self-sufficient and protect relatively smaller populations that produce fewer propagules (Almany et al., 2009; Claudet et al., 2008). However, contrary to this view, small islands could be completely self-sufficient for small-island endemic species (Robertson, 2001). To be self-sufficient, a MPA needs at least 10% self-recruitment (Cowen and Sponaugle, 2009). Thus, the importance of small isolated MPAs for fisheries and conservation is unclear. The peculiar location of SPMI near the limits of the northern and central GC might suggest that the island could be influenced by multiple oceanographic conditions, acting as a significant source of propagules towards different populations in the GC and thus contribute to regional fisheries and conservation.

Many benthic invertebrate species show annual reproductive cycles with intense activity throughout spring and summer, but varying in their timing, intensity and peaks, and thus entailing distinct breeding patterns (Erisman et al., 2010; Giese and Pearse, 1974). Marine currents may disperse planktonic propagules over long distances in relatively short time, but process driving patterns of connectivity might vary temporally and spatially. Changes in connectivity through the year are rarely taken into account for MPA designs, even when they have the potential to drastically change the efficacy of MPAs for meeting conservation and fishery goals. This is particularly true if spawning of marine invertebrates varies within and between species simultaneously with drastic changes in strong seasonal patterns such as winds and ocean current speed and direction (Ledesma-Vazquez et al., 2009; Marinone, 2012) that could potentially alter metapopulation connectivity over a scale of a few hundred kilometers (Amoroso et al., 2011; Becker et al., 2007; Marinone et al., 2011). As a result, patterns of connectivity can vary according to population breeding dynamics and oceanographic factors, entailing different management implications (Becker et al., 2007; Cowen and Sponaugle, 2009; Palumbi, 2003; Soria et al., 2012).

The goal of this study was to estimate connectivity patterns from SPMI as a potential source of propagules to surrounding MPAs and fishing sites. For this, we used a particle-tracking scheme based on the outputs of a three-dimensional numerical hydrodynamic model to identify the areas, including self-replenishment, to which the island, and to delimit and select key fishing sites from which to release simulated particles. Information on fishing zones was collected through a rapid appraisal (Beebe, 1995) conducted in 2005–2006, designed to develop a preliminary, region-wide overview of the socioeconomic and demographic patterns of small-scale fisheries in the northern GC. We identified 17 benthic rocky reef species, including invertebrates and fish, currently fished in the SPMI BR by the two closest fishing communities, Bahía de Kino and El Barril, showing various planktonic propagule durations centered between two weeks and one month (Table 1).

2.2. Spatial units of connectivity

To evaluate connectivity we defined spatial units of analysis by combining physical and political domains, as well as fishers’ and scholars’ knowledge about biophysical attributes of the region as described in detail in Soria et al. (2012). The physical domain of the study area was defined using the coast line developed by the Instituto Nacional de Estadística, Geografía e Informática, México (www.inegi.org.mx) and incorporated political boundaries, such as MPAs (CONANP, 2009) and the 100 m isobaths (Fig. 2).

2.3. Particle-tracking from a three-dimensional hydrodynamic model

We used the three-dimensional baroclinic numerical Hamburg Shelf Ocean Model (Backhaus, 1985) adapted to the GC by Marinone (2008) to estimate the velocity field of the study area. This Eulerian model has a mesh size of ~1.31 × 1.54 km in the horizontal, and 12 layers in the vertical with the lower levels fixed at 10, 20, 30, 60, 100, 150, 200, 250, 350, 600, 1000, and 4000 m (Marinone et al., 2011). Physical forcing in the open boundary includes the main tidal components (M2, S2, N2, K1, O1, P1, Ssa, and the Sα), and climatological hydrographic historical data. We also used sea surface climatological heat and fresh water fluxes. Wind forcing was based on a horizontally homogeneous seasonal climatology constructed from QuikSCAT data. The model equations are solved semi-implicitly with fully prognostic temperature and salinity fields, which allow time-dependent baroclinic motions (Marinone, 2008). Therefore the model is climatological except for the tides, with the consequence that the seasonal signal of the currents are the same every year, but the phase of the springs–neaps cycle changes from year to year. At the seasonal scale, the most important forcing mechanism is due to the Pacific, followed by the local wind (Marinone, 2003; Ripa, 1997).

We estimated particle trajectories following the advection/diffusion scheme described in Proehl et al. (2005) and Visser (2008). The Lagrangian trajectories are due to the Eulerian velocity field plus a random–walk contribution related to turbulent eddy diffusion processes. The model has advection in all directions (x, y, z, t) and adequately reproduces the main seasonal and tidal circulation for the GC (Marinone, 2008).

We released 4000 passive particles (i.e., virtual propagules) from five locations around SPMI (Fig. 1b) as proxies to represent relevant reproductive/spawning sites of commercial coastal benthic species. These sites included Punta Rabijunco (28°38′ S–112°28′W) and Los Morritos (28°37′ S–112°28′W) inside the core zone; and inside
the buffer zone Arroyo Cartelón (28°38′N–112°29′W), La Cueva (28°38′N–112°31′W), and Barra Baya (28°37′N–112°31′W) in the N, NW and SW of the island, respectively. Particle trajectories were integrated for the five sites and results expressed as total export values. We conducted simulations for four release dates (May 15 and 31, and June 14 and 30 of 2007; the year was chosen arbitrarily) matching new and full moon lunar phases each month, for a total 5 sites × 4000 particles × 4 dates = 80,000 particles. Release dates were selected to match the spawning time of most benthic rocky reef species (Table 1).

We tracked particle positions (latitude, longitude, and depth) every hour after release and queried the data by means of ArcGIS 9.3 (ESRI) to obtain the number and origin of the modeled particles reaching each specific coastal unit. For analysis, we selected the data at 15, 20, and 30 days after the release, respectively, as a proxy to represent different maximum planktonic propagule durations among benthic rocky reef species (Castellanos-Martínez, 2008; Hamel et al., 2003; Herrero-Perezrl et al., 1999; Soria et al., 2010) (Table 1). We estimated the percentages of particles that settled at each coastal spatial unit relative to the total number of particles released from SPMI. Local retention was estimated as the percentages of particles that remained within the buffer zone of the SPMI over the total particles released (Botsford et al., 2009). We conducted surface drifter-tracking experiments around SPMI to investigate the near-field circulation. From May 11 to May 15, 2009, we made daily deployment of five Pacific Gyre MicroStar drifters with a Tristar drogue at 1 m depth within the core zone (Fig. 1), and tracked them for 8 h. These drifters transmitted their GPS location via GlobalStar satellite telephone every 10 min (Cabrera-Ramos et al., 2010).

### 3. Results

#### 3.1. Connectivity patterns

Overall, the output of the dispersion model could be characterized by four distinctive patterns, which are present, to a degree, in all simulations. First, one group of particles showed a north-east pathway dispersing along the west coast of Tiburón Island (Fig. 2A–D) and could eventually extend to the mainland coast, reaching the main fishing grounds of Puerto Libertad, Puerto Lobos and Bahía San Jorge and eventually the Alto Golfo de California & Delta del Rio Colorado BR located ~400 km to the north from the release site. Second, another cluster of particles was dispersed south-west towards the east coast of the Baja California Peninsula, covering a wide-range including El Barril, El Vizcaíno BR, Santa Rosalía and reaching Bahía Concepción located ~200 km from the release site (Fig. 2A–D). Third, the MIR also benefited from particles exported from the Island, including San Esteban Island, San Lorenzo Archipelago NP, and Bahía de los Angeles Canal de Ballenas y Salsipuedes BR (Fig. 2A–D). The model also predicted a significant trapping of particles in the release area for each simulation, most evident for May (Fig. 2A, B).

We observed that patterns of connectivity from SPMI BR to other coastal sites were highly dynamic over the 30 days simulated, driven by changes in ocean current speed and direction (Fig. 2). These changes were consistent among propagule durations and included a steady increase in the spatial scale of connectivity from May 15th to June 30th, particularly towards northern sites (Fig. 3, for 30 days of planktonic propagule duration). Also, we observed drastic shifts along time in the coastal areas that received the largest amounts of particles (between ~15 and 25%) released in SPMI. For example, at 30 days, the most important site receiving particles in May 15th was an isolated island (Tortuga) located 110 km to the southwest of the release site. Although the importance of this remote island was maintained later, in May 31st the site receiving most particles was now Puerto Libertad, located ~150 km to the northeast. In June, we observed that the most important sites receiving particles from ISPIM continued shifting towards the north, and on June 30th this corresponded to Bahía San Jorge located ~325 km (linear distance) to the north of the island (Fig. 3).

#### 3.2. Mean lineal distance and frequency distributions

Particles released in mid-May showed a unimodal distance distribution where most of the particles dispersed ≤100 km, while in late June showed a multimodal distribution related to groups of particles going to the north and south, respectively, where most particles...
dispersed ≤ 300 km (Fig. 4). On average, the spatial scale of particle dispersal showed a tendency to be higher with longer planktonic propagule duration and it was about twice as large for particles going towards the north compared to the south (Figs. 2 and 4). Overall, we observed a trend where the velocity of particles (Fig. 4) and the spatial scale of dispersal increased from May 14th to June 30th (Table 2, Fig. 4). The estimated mean linear distance of particle dispersal in May ranged between 29.7 and 103.2 km with maximum values between 87.9 and 228.3 km according to their planktonic propagule duration (Table 2) and particles concentrated within the

Fig. 2. Spatial units of analysis and model outputs of particles at 15, 20, and 30 days of planktonic propagule duration. Modeled propagules where released in five sites around SPMI BR and advection started in A) 15 May, B) 31 May, C) 14 June, and D) 30 June.
ration was 30 days. Note that only coastal areas with habitat for settlement of benthic invertebrates and reef fish are included.

3.3. Self-recruitment

On average, the proportion of particles remaining within the boundaries of SPMI (~10 km width) tended to decrease with increasing planktonic propagule duration (Fig. 5). The buffer and core zones of the reserve showed an abrupt decrease of particles within the first week [not shown]; afterwards particle percentages remained around 15% within the island area. Local trapping across planktonic propagule durations showed values ≥ 10% in May to lower values in June (Fig. 5). For example, about 10% of particles remained in the boundaries of the BR after having been released on May 15th and advected for 30 days, while this value decreased to ~2.5% for particles released in June 30th (Fig. 5).

3.4. Surface drifters

The surface current pattern close to the island measured with the drifters (Fig. 6a) shows that in May 2009 the island was immersed in a fast current to the NW. The drifter data also suggest the potential for trapping (stagnation points) on the windward side of the island (SE) where currents hit it and also in the opposite leeward side (NW) (Fig. 6a). Although the drifter data cannot be used to validate the model because of the difference in space and times scales, Fig. 6b shows agreement in the far-field direction of the currents (to the NW), but the model speeds are lower, which is reasonable, considering that they are averages.

4. Discussion

4.1. Dynamics of temporal and geographical scales of connectivity

Our oceanographic model stressed that highly dynamic patterns of connectivity across short temporal but large spatial scales, could characterize a small and isolated island with MPA status. Our findings suggest the multifaceted aspect of the benefits provided by SPMI BR for propagules export and self-recruitment. Contrary to the view that small and isolated MPAs show low connectivity, we observed high potential connectivity (i.e., demographic) with a few key but distant fishing sites, and lower potential connectivity (i.e., genetic) with many nearby and distant fishing sites, and with all the other four coastal neighboring MPAs, albeit not simultaneously. In addition we observed conditions for self-recruitment of the populations within SPMI BR. However, the most significant observation was that the role of the island in each of these important aspects changed dramatically over a relatively short-medium period (two months), encompassing the peak of spawning for multiple species. This highlights the dynamic nature of marine connectivity and suggests that the design of effective MPAs and MPA networks should acknowledge the spatial and temporal complexity and dynamics of patterns of connectivity and should not be designed or implemented as static entities based upon connectivity observed on a single snapshot in time or using fixed rules of the kind "one size fits all".

The SPMI BR might have an influence on propagule dispersal involving a very large spatial scale (over 600 km along the coast). The export of particles from the island up to 400 km towards the north is on average of four times larger than previously reported results for the mainland coast of the GC (Soria et al., 2012). Although our study did not include larval behavior and thus we could be over estimating dispersal distances (Cowen and Sponaugle, 2009; Levin, 2006; Soria et al., 2012), the large influence of SPMI BR could be partly explained by its particular location. The island borders the northern limit of the Central GC that shows cyclonic circulation, where it bifurcates and allows some particles to disperse south toward the peninsula, while others reach the mainland shelf of the northern GC across the MIR channels. Thus, the geographic proximity to distinct oceanographic regions showing unique faunal affinities suggests relevant biological connectivity of the island. Also contributing is the timing of spawning coinciding with the reversal and intensification of currents from May to July, particularly of the northward coastal current along the mainland coast of Sonora, driven by an increase of southerly winds (Ledesma-Vazquez et al., 2009). We also confirmed that under the strong directional currents, connectivity in the GC commonly does not decrease with distance, and that the links between
sites that may be connected via propagule dispersal at ecological and evolutionary time scales might be not intuitive and are highly time-sensitive.

Although our study points to the importance of a small and isolated reserve as an important source in metapopulation dynamics of some fishing sites, in MPA network resilience and in the conservation of biodiversity for multiple sites, we caution that being a hub also has the down-side of a larger likelihood of spreading risk (Watson et al., 2011). Risk could be due to natural processes (e.g., disease) or induced by anthropogenic causes (e.g., poisons used to eradicate exotic species such as rats on isolated islands) (Samaniego-Herrera et al., 2011), or possible oil-spills by cargo ships passing near the island.

Propagule exports might benefit, at different points in time, important fishing sites, such as Puerto Libertad, Puerto Lobos and Bahía San Jorge along the Sonoran Coast, and western locations along the Baja California Peninsula (El Barril, Santa Rosalía, and Bahía Concepción). Other important findings are connectivity pathways conducive to localized propagules export within the MIR. For instance, cumulative percentages of particles that have been dispersed up to 50 km (the minimum distance to reach the southern boundaries of the San Lorenzo Archipelago BR, San Esteban and Tiburón islands) fall between 23 and 90% depending on planktonic propagule duration and release date. A higher percentage of particles

<table>
<thead>
<tr>
<th>Date</th>
<th>Planktonic propagule duration (days)</th>
<th>15 days</th>
<th>20 days</th>
<th>30 days</th>
</tr>
</thead>
<tbody>
<tr>
<td>May 15</td>
<td>Mean</td>
<td>29.7</td>
<td>37.5</td>
<td>52.7</td>
</tr>
<tr>
<td></td>
<td>SD</td>
<td>16.4</td>
<td>20.6</td>
<td>33.2</td>
</tr>
<tr>
<td></td>
<td>Maximum</td>
<td>87.9</td>
<td>116.7</td>
<td>147.1</td>
</tr>
<tr>
<td>May 31</td>
<td>Mean</td>
<td>44.7</td>
<td>66.8</td>
<td>103.2</td>
</tr>
<tr>
<td></td>
<td>SD</td>
<td>28.9</td>
<td>44.3</td>
<td>72.1</td>
</tr>
<tr>
<td></td>
<td>Maximum</td>
<td>100.5</td>
<td>143.4</td>
<td>228.2</td>
</tr>
<tr>
<td>June 14</td>
<td>Mean</td>
<td>64.6</td>
<td>86.2</td>
<td>119.7</td>
</tr>
<tr>
<td></td>
<td>SD</td>
<td>51.7</td>
<td>68.8</td>
<td>89.8</td>
</tr>
<tr>
<td></td>
<td>Maximum</td>
<td>163.5</td>
<td>226.4</td>
<td>307.0</td>
</tr>
<tr>
<td>June 30</td>
<td>Mean</td>
<td>98.5</td>
<td>124.9</td>
<td>162.4</td>
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<tr>
<td></td>
<td>SD</td>
<td>80.3</td>
<td>94.0</td>
<td>112.4</td>
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<tr>
<td></td>
<td>Maximum</td>
<td>235.5</td>
<td>297.4</td>
<td>393.9</td>
</tr>
</tbody>
</table>
are expected to be dispersed less than 50 km in May in comparison with values observed throughout June, which reflects the rapid change in the range distance of connectivity patterns. Overall, the model reveals the oceanographic complexity of the study area and provides the basis for the development of ecological and evolutionary hypothesis to be tested in the field, with potential to contribute to the management and conservation of marine resources in the region.

4.2. Self-replenishment

The horizontal resolution of the numerical model does not adequately represent oceanographic processes occurring at small and medium scales (Werner et al., 2007) around the island. The size of SPMI BR is just twice the mesh size resolution of the model, indicating a much higher resolution that is needed to model local retention and highlighting the value of empirical surfer drifter data.

The circulation in the area of SPMI BR contains a quasi-permanent anticyclonic eddy (Mateos et al., 2006) and some retention can be expected in the area in general and in the island shores, especially during May. Despite the species’ planktonic propagule durations (max. 30 days), the island could benefit from the retention of a fraction of propagules (less than 10%) trapped within reserve boundaries, thus contributing to self-sufficiency, which is key for a successful MPA. For instance, at least 10% of recruits should be locally produced in order to promote self-replenishment (Largier, 2003). However, according to our models the island changed from being self-sufficient in mid-May to being mainly dependent upon external sources at the end of June, albeit the drifter data suggested some retention on the windward side of the island, coincidently near the core-zone of the reserve, which was not captured by the models. However, measurements of marine currents closer to shore are needed to assess near-field local retention in coastline bays and coves that characterize the island in more detail.

Whether self-recruitment would suffice self-replenishment demands requires further investigation in order to understand the relevance of locally produced propagules relative to distant sources that might be also contributing to local populations. The rationale underlying reserves is that they protect local populations, contributing to repopulate unprotected localities. The effectiveness of a given reserve will be influenced by the extent that local populations are able to recover, either by self-recruitment or by propagules imports from distant resources (Shanks, 2009; Shanks et al., 2003). Also, for local populations inhabiting isolated reserves to persist, the size (e.g., diameter) of the reserve should be at least twice the mean dispersal distance (Botsford et al., 2003; Crowder et al., 2000; Halpern, 2003; Hastings and Botsford, 2003). The implementation of such measure would be technically difficult in the study area given its biophysical and social characteristics and the estimated geographical scale of propagule dispersal, which may vary over short-medium temporal scales. The purpose of this study was to understand the connectivity patterns of the reserve as a source of propagules, but further studies should be undertaken to test the biological connectivity of the island,
for instance with population genetics or genomic data. Future work is also needed to determine the role of self-replenishment and to incorporate biological traits and oceanographic features not addressed in this study that might affect connectivity patterns.

4.3. Potential implications for conservation and fisheries management

Effective conservation and fisheries management require understanding the spatial and temporal scales at which fishing activities and ecosystem processes take place (Fogarty and Botsford, 2007; Lipcius et al., 2005; Moreno-Báez et al., 2010). Our study shed some light on the likely geographical scale of connectivity between the SPMI BR and distant areas, suggesting an influence on multiple and diverse areas, but also on the dynamic nature of the influence radius of propagules export. This information provides support for spatial-based planning processes such as siting of MPAs, which are being internationally promoted as a useful ecosystem management tool (Douvere, 2008). For instance, the island might contribute with propagules to fishing grounds along the mainland coast and the MIR in general, and also to all existing MPAs within a certain radius and the spatial influence could vary considerably over short temporal scales. Propagule dispersal has a strong effect on population dynamics of sessile/benthic invertebrates and rocky fish species, including those whose juvenile and adult movements are negligible relative to the geographical scale of realized propagule dispersal, affecting demographic and genetic connectivity (Cowen and Sponaugle, 2009; Fogarty and Botsford, 2007; Lowe and Allendorf, 2010). We hypothesize that even though impact on fisheries stocks might be limited to a few locations, the export of propagules would at least contribute to the conservation of biodiversity, such as subpopulation viability and evolutionary adaptation.

Considering the multiple dispersal pathways associated to the island, including self-recruitment, would add more complexity and challenges to fisheries management and conservation of marine resources around the island, compared to other systems (Alberto et al., 2011; White et al., 2010). Conversely, understanding such complexity by identifying connectivity pathways might clarify where populations interact with human activities. Marine reserves have gained special consideration because of the positive effects that they have on exploited resources, as has been recently documented for the conservation of biodiversity, such as subpopulation viability and evolutionary adaptation.

In conclusion, our study stresses the importance that a small and isolated island MPA might have when located at the boundary of distinct oceanographic systems as source of propagules for multiple regions and as potential stepping-stones. Our data indicates that this MPA is likely not self sufficient particularly for species with planktonic propagule durations larger than 15 days. Future studies should establish the origin of propagules that arrive to the island and that support fisheries for species with long planktonic propagule durations that used to be common in the island but are currently over-exploited (e.g., lobsters like Panulirus spp. and Scyllarides spp.). Moreover, patterns of connectivity might be highly dynamic covering a wide range of spatial scales (tents to hundreds of kilometers) that could change across short temporal scales within a single reproductive season. Even though their contribution to fisheries stocks might be limited to few locations, the island would at least contribute to the conservation of biodiversity on a very large scale. The dynamic nature of marine connectivity might influence demographic and genetic connectivity and such complexity should be acknowledged when designing tools for fisheries management and conservation of marine resources like MPA networks in the region and elsewhere.

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References


Other limitations of the model are that it does not include mesoscale or inter-annual variability. The most important inter-annual variability in the GC is produced by the ENSO phenomenon, and it consists of an intensified influx of tropical surface water during summer (Lavin et al., 2003; Lavin and Marinone, 2003), which would carry the particles that entered the northern GC further north. There are few studies of the effect of meso-scale structures on propagule dispersal in the GC (Lavin et al., 2013; Sánchez-Velasco et al., 2013; Zamudio et al., 2008).

4.4. Conclusion

In conclusion, our study stresses the importance that a small and isolated island MPA might have when located at the boundary of distinct oceanographic systems as source of propagules for multiple regions and as potential stepping-stones. Our data indicates that this MPA is likely not self sufficient particularly for species with planktonic propagule durations larger than 15 days. Future studies should establish the origin of propagules that arrive to the island and that support fisheries for species with long planktonic propagule durations that used to be common in the island but are currently over-exploited (e.g., lobsters like Panulirus spp. and Scyllarides spp.). Moreover, patterns of connectivity might be highly dynamic covering a wide range of spatial scales (tents to hundreds of kilometers) that could change across short temporal scales within a single reproductive season. Even though their contribution to fisheries stocks might be limited to few locations, the island would at least contribute to the conservation of biodiversity on a very large scale. The dynamic nature of marine connectivity might influence demographic and genetic connectivity and such complexity should be acknowledged when designing tools for fisheries management and conservation of marine resources like MPA networks in the region and elsewhere.


