Paola Franzan Sanches

**Evaluation of Mangrove Connectivity using Biological Models with
different Larval Dispersal**

Tese apresentada ao Instituto Oceanográfico da
Universidade de São Paulo, como requisito para
obtenção do título de Doutora em Ciências, Programa
de Oceanografia, área de Oceanografia Biológica.

Orientador: Prof. Dr. Alexander Turra

Co-orientadores: Prof. Dr. Antonio Carlos Marques
Prof. Dr. Paulo Simionato Polito

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**UNIVERSIDADE DE SÃO PAULO
INSTITUTO OCEANOGRÁFICO**

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**Para Catharina,
o grande amor da minha vida,
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quem eu aprendo todos os dias a ser
mais feliz!**

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RESUMO

Redes de Áreas Marinhas Protegidas são uma estratégia chave para conservar a biodiversidade marinha contra as pressões antrópicas, devido à manutenção da conectividade entre as áreas. A conectividade garante o fluxo gênico e a resiliência. É afetada por processos oceanográficos, especialmente em manguezais, onde a descontinuidade espacial configura um aspecto insular e a variação da maré influencia a persistência e o recrutamento de juvenis. Considerando a vulnerabilidade dos manguezais devido à sua supressão que pode afetar o fluxo gênico, a compreensão de sua conectividade é essencial para sua conservação e seu manejo. Assim, os principais objetivos desta tese foram: 1) investigar o estado atual do conhecimento sobre conectividade ao longo da costa brasileira, bem como evidências do uso da conectividade no projeto e gestão de AMPs; 2) avaliar o fluxo gênico e as redes de conectividade na ZEE brasileira, a fim de verificar os extremos de distância em que a conectividade ainda ocorre para a costa brasileira; e 3) investigar a conectividade entre manguezais brasileiros com base na análise comparativa do marcador SNP de duas espécies com diferentes histórias de vida: o *Clibanarius vittatus*, com desenvolvimento larval indireto em contraste com o *Monokalliapseudes schubarti*, com desenvolvimento direto, com a hipótese de que existem diferenças na estrutura genética populacional de ambos, com populações mais estruturadas para *M. schubarti* devido ao seu desenvolvimento. Pretendíamos avaliar a extensão dos manguezais que atuam como stepping-stones, discutindo sua proteção sob as leis brasileiras. Entre os resultados, encontramos que: 1) peixes (52,2%) e ferramentas genéticas (69,3%) foram, respectivamente, os táxons e métodos mais comuns usados nos estudos, que foram realizados principalmente em escala regional (55,8%), cobrindo toda a costa brasileira. De todas as referências, 31% mencionaram espécies ou grupos taxonômicos e, apesar de quase 20% considerarem “conservação de áreas”, apenas 4,5% mencionaram explicitamente as AMP, como foco principal. Das 67 AMP brasileiras, apenas 7 mencionam a conectividade marinha em sua documentação. Identificamos dois aspectos-chave que são passos importantes para a operacionalização da conectividade na conservação marinha: a necessidade de pesquisa colaborativa e integrativa, em diferentes escalas espaço-temporais; 2) a maior distância com conectividade significativa é de 3.800 km. As distâncias mais altas têm apenas 1% de chance de ter maior conectividade e são predominantemente de força 1. Houve um baixo nível de conectividade entre as áreas no SE e S do Brasil e altos níveis de conectividade entre as áreas do NE e N. As ilhas têm principalmente baixos e intermediários níveis de conectividade com as áreas costeiras, mas o conhecimento sobre a conectividade das ilhas oceânicas é quase inexistente; 3) *C. vittatus* apresentou maior conectividade que *M. schubarti* e conseqüentemente a estrutura populacional é maior para *M. schubarti*, elevando a vulnerabilidade de *M. schubarti* em cenários de supressão de manguezais. Não há correlação significativa entre o fluxo gênico e a distância da população para ambas as espécies. Todos os mangues provaram ser importantes para outros manguezais, mas não foram identificados stepping-stones entre eles. Nossos resultados mostram que existe conectividade entre os manguezais preservados e não preservados. No entanto, a supressão de manguezais pode comprometer o fluxo gênico e um estudo com foco nos mangues como stepping-stones deve ser realizado. Ainda há tempo para recuperar os manguezais impactados, desde que as políticas mudem seu foco para a importância dos manguezais em relação ao fluxo gênico. Concluímos que há necessidade de estabelecer novas AMPs para atuar como stepping-stones em uma rede, bem como o aumento necessário em estudos de conectividade marinha, incluindo avaliações de conectividade entre AMPs e manguezais.

Palavras-chave: conectividade, AMP, conservação, Metas de Aichi, manguezais, fluxo gênico, SNP, *Clibanarius vittatus*, *Monokalliapseudes schubarti*, desenvolvimento larval

ABSTRACT

Networks of Marine Protected Areas are a key strategy to conserve marine biodiversity against anthropogenic pressures, due to the maintenance of connectivity among areas. Connectivity guarantees gene flow and resilience. It is affected by oceanographic processes, especially in mangroves, where spatial discontinuity configures an island aspect and tide variation influences the persistence and recruitment of juveniles. Considering mangrove vulnerability due to its suppression that can affect gene flow, the understanding of mangrove connectivity is essential to its conservation and management. Thus, the main goals of this thesis were: 1) to investigate the current state of knowledge about connectivity along the Brazilian coast as well as evidences of the use of connectivity in the design and management of MPAs; 2) to assess gene flow and networks of connectivity in the Brazilian EEZ, in order to verify extremes of distance in which connectivity still occurs for the Brazilian coast; and 3) to investigate connectivity among Brazilian mangroves based on a comparative analysis of SNP marker of two species with different life histories: the indirect larval development of *Clibanarius vittatus* contrasted with the direct development of *Monokalliapseudes schubarti*, with the hypothesis that there are differences in the genetic populational structure of both, with higher structured populations for *M. schubarti* due to its direct development. We intend to assess the extent of mangroves acting as stepping-stones, discussing its protection under Brazilian laws. Among results, we found that: 1) fish (52.2%) and genetic tools (69.3%) were, respectively, the most common taxa and method used in the studies, which were carried mostly at regional-scale (55.8%), but in combination covered all Brazilian coastline. From all references, 31% mentioned species or taxonomic groups and, although almost 20% considered “area conservation”, only four studies (4.5%) explicitly mentioned MPA, as its major focus. From the 67 Brazilian MPA, only 7 mention marine connectivity in documentation. We identified two key aspects that are important steps towards operationalizing connectivity in marine conservation: the need for collaborative and integrative research at different spatio-temporal scales; 2) the highest distance with significant connectivity is 3,800 km. Higher distances have only 1% of chance to have connectivity strength 3, and are predominantly strength 1. There was a low-level of connectivity among areas in SE and S Brazil and high levels of connectivity among areas in the NE and N Brazil. Islands had mostly low and intermediate levels of connectivity with coastal areas, but knowledge on the connectivity of oceanic islands is nearly nonexistent. 3) *C. vittatus* presented higher connectivity than *M. schubarti* and consequently population structure is higher for *M. schubarti*, elevating the vulnerability of *M. schubarti* in scenarios of mangrove suppression. There is no significant correlation between gene flow and population distance for both species. All mangroves have proved to be important to other mangroves, but no stepping-stones have been identified among mangrove sites. Our results show that connectivity exist among preserved and non-preserved mangroves. However, mangrove suppression can, compromise gene flow and a study focusing on mangroves as stepping-stones has to be undertaken. There is still time to recover impacted mangroves, as long as policies change their focus to mangroves’ importance concerning also gene flow. We conclude there is a need of establishing new MPAs to act as stepping-stones in a network, as well as the necessary increase in marine connectivity studies, including connectivity assessments among MPAs and mangroves.

Keywords: connectivity, MPA, conservation, Aichi Targets, mangroves, gene flow, SNP, *Clibanarius vittatus*, *Monokalliapseudes schubarti*, larval development

INTRODUCTION

Marine conservation efforts are fundamental to guarantee the maintenance of biodiversity and marine resources (OSD 14 – UN), considering the increasing of human-induced impacts and pressures such as climate change, overfishing, pollution, habitat loss, and fragmentation on coastal and marine environments (Halpern *et al.* 2008, 2015). Among strategies, protected areas are the most widely used tool to conserve biodiversity (Bensusan 2014), and the Aichi Targets presented in the 10th Convention of Parties at the Convention on Biological Diversity (CBD 2011), explicitly declared the need to conserve biodiversity and ecosystem services by keeping protected areas connected: by 2020, signatories of the convention must assure that “*10 percent of coastal and marine areas, [...] are conserved through effectively and equitably managed, ecologically representative and well connected systems of protected areas and other effective area-based conservation measures, and integrated into the wider landscapes and seascapes*” (Target 11, <https://www.cbd.int/sp/targets/>). However, until June 2018, only 3.6% of the global ocean was under protection (Sala *et al.* 2018).

Beyond the intrinsic values of marine protected areas (MPAs), it is expected that the MPAs acts as a network and synergistically maintain connectivity among marine ecosystems, and ensure the preservation of species and populations over time (Gaines *et al.* 2010; Grorud-Colvert *et al.* 2014; Magris *et al.* 2018). Connectivity is especially important in marine environments, where patchy distribution of populations with similar habitat (e.g. coral reefs) are connected via larval advection (Cowen & Spounagle 2009), or where species use more than one type of habitat along their life history (Olds *et al.* 2015). Connectivity also drives fundamental processes such as the displacement of species/populations across ecological/evolutionary time-scales (Kool *et al.* 2013), and biological responses to global change (Magris *et al.* 2014). Additionally, connectivity determines patterns in phylogeography (Bowen *et al.* 2016), metapopulation dynamics (Hastings & Bostford 2006), and provides recruitment subsidies to fished areas (Andrello *et al.*, 2017), a key management objective of MPA networks.

As a signatory of the CBD, Brazil complied to fulfill Aichi Targets, but until early 2018, only 1.57% of the total area of the Brazilian Economic Exclusive Zone (EEZ) was under some kind of protection (data available from the Brazilian Government). In March 2018, Brazil created four new MPAs, which increased the national’s MPA coverage to about 25%. However, although this number numerically complies with Aichi’s Goal 11, the spatial design of these MPAs did not contribute to the development of an ecological network of conservation areas (Magris & Pressey 2018), and did not comply with the necessary representation of the biota and community composition under biogeographic and ecological perspectives. Finally, these areas do not assure that Brazil is ready for the challenge to enforce and manage them, or just has created new paper parks.

worldwide (FAO 1985; Bosire et al. 2003, 2006, Kairo et al. 2008), focusing in health, productivity, biomass (Ong et al. 1995), nutrient cycles and ecological aspects, such as fauna re-colonization (Machintosh et al. 2002) (see a review of successful projects in Románach *et al.* 2018). Now, dispersal aspects and connectivity aspects are been considered in mangrove management (Binks et al. 2018, Stocken et al. 2018).

Considering Brazilian mangroves, until the year 2000, Brazil was one of the countries with higher mangrove areas (Valiela et al. 2001). However, Brazilian losses were of more than 50,000 ha (4% of the total mangrove cover) over the past three decades (Románach et al. 2018). This is curious, once mangroves are protected by the legislation (Permanent Protected Area, federal Law 12.651/2012), although surrounding areas and buffer zones are not considered by it (Románach *et al.* 2018). Thus, there is a clear need of studies concerning mangroves ecological, geological and physical aspects, but also connectivity aspects (Amaral et al. 2010).

This thesis is, thus, composed of three chapters conducted in order to understand the general perspective of connectivity knowledge concerning conservation, the gene flow regarding Brazilian EEZ and mangrove connectivity regarding genetic information. The first has as goal to investigate the current state of knowledge about biodiversity connectivity along the Brazilian coast as well as evidences of the use of connectivity in the design and management of MPAs. We hypothesized that there is a fragmented knowledge on this subject as well as a decoupling between the primary research studies on connectivity and their application in the conservation of the marine realm. Additionally, we hypothesized that design and management of the already existing Brazilian MPAs do not incorporate connectivity as a guiding principle. We also intended to address some challenges to improve the use of connectivity in decision-making.

The second chapter's goal is to assess gene flow and networks of connectivity in the Brazilian EEZ, considering a metanalysis of genetic data provided in chapter 1, in order to verify extremes of distance in which connectivity still occurs for the Brazilian coast.

The third has as goal to investigate connectivity among Brazilian mangroves based on a comparative analysis of two species with different life histories: the indirect larval development of *Clibanarius vittatus* contrasted with the direct development of *Monokalliapseudes schubarti*. We hypothesize differences in the genetic populational structure of *C. vittatus* and *M. schubarti*, with higher structured populations for *M. schubarti* due to its direct development. Finally, we intend to assess the extent of mangroves acting as stepping-stones, discussing its protection under Brazilian laws.

Chapter 1: Connectivity still is a challenge for marine conservation: evidences of science and policy gaps in the design of Marine Protected Areas in Brazil

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ABSTRACT

Connectivity plays a key role in the design of marine protected areas (MPAs) irrespective of their management goals. Although methods to design MPAs based on connectivity information have proliferated, its effective application in policy making is still rare. Because connectivity is a relatively recent issue in marine conservation, we hypothesized that there is a fragmented knowledge on this subject as well as a decoupling between the primary research studies on connectivity and their application in the conservation of the marine realm. To test the generality of this hypothesis, we reviewed the literature upon connectivity along the Brazilian coast, assessing key characteristics of these studies (taxa studied, methods of analysis, spatial extent, ecosystems surveyed, and conservation features considered such as species, taxonomic groups, habitats, and “MPA”), and explored some potential applications to inform conservation decisions. We found that fish (52.2%) and genetic tools (69.3%) were, respectively, the most common taxa and method used in the studies. Analyses were made mostly at regional-scale (55.8%), but in combination covered all Brazilian coastline. From all references, 31% mentioned species or taxonomic groups and, although almost 20% considered “area conservation”, only four studies (4.5%) explicitly mentioned MPA, as its major focus. By analyzing the documentation of the 67 Brazilian MPA, only 14 mention connectivity generically (7 marine environment). We identified two key aspects that are important steps towards operationalizing connectivity in marine conservation: the need for collaborative and integrative research at different spatio-temporal scales; and clear communication, buy-in, and coordination between scientists and policy makers when integrating scientific information into the decision process.

Keywords: connectivity tools, genetics, biophysical models, MPA, conservation, Aichi Targets

1. Introduction

Effects of human-induced impacts and pressures such as climate change, overfishing, pollution, habitat loss, and fragmentation on coastal and marine environments (Ma 2005, Lotze *et al.* 2006, Halpern *et al.* 2008, 2015) have exposed the challenges of designing conservation strategies to manage these dynamic ecosystems in a sustainable way (UNEP 2006). Among the strategies, protected areas are the most widely used tool to conserve biodiversity (Bensusan 2014), and the Aichi Targets presented in the 10th Convention of Parties at the Convention on Biological Diversity (CBD 2011), as the 2030 Agenda of Sustainable Development Goals (SDG)14.5, explicitly declared the need to conserve biodiversity and ecosystem services by keeping protected areas connected: by 2020, signatories of the convention must assure that “*10 percent of coastal and marine areas, [...] are conserved through effectively and equitably managed, ecologically representative and well connected systems of protected areas and other effective area-based conservation measures, and integrated into the wider landscapes and seascapes*” (Target 11, <https://www.cbd.int/sp/targets/>). However, until June 2018, only 3.6% of the global ocean was under protection (Sala *et al.* 2018).

Beyond the intrinsic values of marine protected areas (MPAs), it is expected that the MPAs acts as a network and synergistically maintain connectivity among marine ecosystems, and ensure the preservation of species and populations over time (Gaines *et al.* 2010; Grorud-Colvert *et al.* 2014; MAGRIS *et al.* 2018). Connectivity is especially important in marine environments, where patchy distribution of populations with similar habitat (e.g. coral reefs) are connected via larval advection (Cowen & Spounagle 2009), or where species use more than one type of habitat along their life history (Olds *et al.* 2015). Connectivity also drives fundamental processes such as the displacement of species/populations across ecological/evolutionary time-scales (Kool *et al.* 2013), and biological responses to global change (Magris *et al.* 2014). Additionally, connectivity determines patterns in phylogeography (Bowen *et al.* 2016), metapopulation dynamics (Hastings & Bostford 2006), and provides recruitment subsidies to fished areas (Andrello *et al.* 2017), a key management objective of MPA networks.

Connectivity can be accessed by different approaches, considering different levels of relationships, such as genetic, populational, community and ecosystemic level. (Carr *et al.* 2017). However, all these patterns are interconnected, once genetic patterns will determine population patterns, and community patterns, and so on By incorporating all these forms into conservation management, it is possible to predict more effectively the conditions under which MPAs will provide larger gains and improve management strategies.

Existing approaches to quantify or estimate connectivity vary from structural measures, such as the arrangement of landscape elements, to empirical measurements of movements, which provide

more reliable estimates of the actual connectivity among sites (Calabrese & Fagan 2004). An appropriate approach will depend on the objective, focal species, complexity of methods, and underlying data. For example, spatial depictions of connectivity can be provided by analyzing ecological data of presence and absence of organisms and tracking their movements (i.e. Mumby *et al.* 2004), by mapping habitats through remote sensing (i.e. Magris *et al.* 2013), by modeling larval dispersal (i.e. Treml *et al.* 2012, Wood *et al.* 2014 and Magris *et al.* 2016), or by analyzing gene flow (i.e. Brooker *et al.* 2000, Saenz-Agudelo *et al.* 2009, St-Onge *et al.* 2013). Although connectivity can be inferred using a suite of tools, operational challenges remain, and applications of connectivity to inform management decisions are still scarce.

As a signatory of the CBD, Brazil complied to fulfill Aichi Targets and SDG 14.5, but until early 2018, only 1.57% of the total area of the Brazilian Economic Exclusive Zone (EEZ) was under some kind of protection (data available from the Brazilian Government). In March 2018, Brazil created four new MPAs, which increased the national's MPA coverage to about 25%. However, although this number numerically complies with Aichi's Goal 11, the spatial design of these MPAs did not contribute to the development of an ecological network of conservation areas (Magris & Pressey 2018), and did not comply with the necessary representation of the biota and community composition under biogeographic and ecological perspectives. Finally, these areas do not assure that Brazil is ready for the challenge to enforce and manage them, or just has created new paper parks.

Due to the influence of connectivity on ocean biodiversity and marine ecosystems' health, especially concerning gene flow, this recent case in Brazil elicited a critical review on the current and potential incorporation of connectivity in the design of MPAs. This review investigated the current state of knowledge about biodiversity connectivity along the Brazilian coast as well as evidences of the use of connectivity in the design and management of MPAs. We hypothesized that there is a fragmented knowledge on this subject as well as a decoupling between the primary research studies on connectivity and their application in the conservation of the marine realm. Additionally, we hypothesized that design and management of the already existing Brazilian MPAs do not incorporate connectivity as a guiding principle. We also intended to address some challenges to improve the use of connectivity in decision-making.

2. Methods

We surveyed the studies concerning connectivity in the Brazilian coast, and whether they had recommendations for conservation management (e.g. MPA design). We searched the platforms Scielo and Web of Science to identify the studies, by using different combinations of the following

searching terms: 1: “(genetic diversity)”, “connectivity”, “genetic”, “geneflow”, “phylogenetic” and “dispersal”; 2: “(Brazilian coast)”, “Brazil” and “marine”; and 3: “larvae”, “marine invertebrates” and “marine vertebrates”. We extracted declarative arguments or statements about connectivity from the papers. We also checked by snowball any reference that should be considered in our survey but did not come out in the database search. We focused on the primary literature because we aimed to understand the current state of knowledge on marine connectivity in Brazil and identify research gaps in approaches that can inform conservation management.

We recorded the following additional information from each study: method or tool used to apply connectivity information, in order to understand how this topic is approached by Brazilian researchers;; year of publication, to understand when this kind of concern started in Brazilian research; taxa studied, to verify if there is any group of organisms, or group of research with higher interest in connectivity; ecosystem surveyed, to verify gaps among marine environments; and conservation feature considered (i.e., species, taxonomic groups, habitats, and “MPA”), to understand the focus of researches. Studies conducted on offshore islands were designated accordingly as: Fernando de Noronha, Atol das Rocas, São Pedro and São Paulo, and Trindade and Martim Vaz. If data was from fishery or aquaculture assays, we considered “fishery” and “farm” as the environment, because it was not possible to distinguish the exact environment, but these data are important to conservation management. We plotted the number of references per states or islands to evaluate the coverage of the Brazilian coast and because states have legal power to create Marine Protected Areas in their spheres. With these data we performed a Chi square test to verify if locations were equally represented, considering as expected the number of references in the location of the higher number of references. The literature search included studies made available up to May 2018. References from the search outside the scope of this paper were not considered.

Complementary, we surveyed the Brazilian decrees of creation of the MPAs and their management plans, when available, looking for connectivity in them, in order to know how and if the knowledge on connectivity has been applied in the design and/or management of the MPA.

3. Results

3.1 How is the knowledge on connectivity for the Brazilian coast?

We found 90 references that either analyzed or provided scientific data that could be incorporated into decision-making processes (see Supplementary Material; Table SM1). Four different methods/data were used to quantify or measure connectivity: community ecology data (10 references), genetic data (76), GIS/remote sensing (2), and oceanography dispersal models (2) (Table 1).

There is an increase in the number of papers using genetic tools over time, and new approaches arose with the availability of new technologies, such as satellites, whose first paper was published only in 2009 (Rudorff *et al.* 2009) (Figure 1).

Table1: Synthesis of the literature survey on connectivity along the Brazilian coast, with information on the method (community ecology, genetics, GIS, and oceanography dispersal models) used in the analyses; the spatial extent of the study (local or regional); whether the study focused on species/taxonomic groups, or on areas/habitats; and whether any recommendation on MPA design or management was mentioned.

Methodology	Number of studies	Goal: conservation of species or groups	Goal: conservation of areas/habitats	Mention MPA or inform MPA design
Genetics	76	28	10	1
Community ecology	10	0	8	2
GIS/remote sensing and spatial data	2	1	1	2
Dispersal modeling	2	0	0	1
TOTAL	90	29	19	6

Figure 1: Accumulation curve of (A) references on connectivity per year of publication, separated in the different approaches: community ecology (green); genetic (red); GIS/remote sensing (orange); dispersal modeling (blue); and (B) log (base 10) of references on connectivity per year of publication, separated in the different approaches (same colors used in A).

Taxa studied were fishe (n=58), crustacean (especially crabs, shrimps and lobsters; n=19), mollusc (n=7), cnidarian (n=4), mammal (n=4), ascidian (n=3), Porifera (n=3), bird (n=1), echinodermata (n=1), nemertea (n=1), and turtle (n=1) (Figure 2). Two studies did not specify the

taxa (“fauna”), and two others did not fit into such categories (“not applied”; viz. DIAS *et al.* 2012; MAGRIS *et al.* 2013).

Fifteen studies analyzed more than 3 species, all with genetic approaches (phylogeny studies, n=8) or with community ecology approaches (n=7, *e.g.*, community composition). Four studies were based on three species, while three studies on two species. The remaining five studies (n=5) used one species (Figure 2).

Figure 2: Number of references in relation to: (I) taxa (ascidian, bird, cnidaria, crustacean, porifera, fauna, fishes, mammals, mollusc, nemertea, sponges, turtle, and not applied) and approach as community ecology (green); genetic (red); GIS/remote sensing (orange); dispersal modeling (blue); (II) Number of species used and approach (same colors used in I).

Considering the ecosystem, the majority of studies mentioning connectivity were related to the nekton, basic for fisheries (n=19). The others were coastal pelagic environment (n=11), reef habitats (n=10), estuary (n=8), and mangrove ecosystems (n=6) (Figure 3). Some studies (n=13) did not mention the habitat or ecosystem where the organisms were sampled. There were no studies that explicitly mentioned to be held on beaches.

Although the studies seemed to be well distributed along the coast, there were significant differences between the number of investigations carried out on some states and offshore islands ($\chi^2_{\text{calc}} = 195.89$; $\chi^2_{\text{tab}} = 32.671$, DF= 21). For instance, Rio de Janeiro was the most studied location (29 references), 7 times more than the less studied Abrolhos and São Pedro and São Paulo islands (4 references each) (Figure 4). Overall, southeastern and southern regions (ES, RJ, SP, SC, RS) were the most studied (Figure 4). Moreover, there was no evidence that these studies subsidized creation or management of MPAs.

Figure 3: Number of references per type of habitat. (A): Based on the approach as community ecology (green); genetic (red); GIS/remote sensing (orange); dispersal modeling (blue).

Figure 4: Number of references for each locality in Brazilian EEZ (Amapá - AP, Pará - PA, Maranhão - MA, Piauí - PI, Ceará - CE, Rio Grande do Norte - RN, Paraíba - PB, Pernambuco - PE, Alagoas - AL, Sergipe - SE, Bahia - BA, Espírito Santo - ES, Rio de Janeiro - RJ, São Paulo - SP, Paraná - PR, Santa Catarina - SC, Rio Grande do Sul - RS) and islands (São Pedro and São Paulo - SPSP, Rocas Atoll - AR, Fernando de Noronha - FN, Abrolhos - AB, and Trindade and Martim Vaz - TR). Black circles represent the proportion of references in comparison to each other.

3.2 Is the knowledge being used in MPA creation?

Conservation was mentioned by 31% of the studies (n=28), referring to either species or taxonomic groups. Near 20% of the papers (n=19) mentioned conservation of areas or habitats, in which 7 used community ecology approaches, 11 used genetic tools, and 1 used GIS/remote sensing techniques (Suppl. Mat.; Table SM 1). Only six studies specifically mentioned or provided underlying information specific to MPA design: one using genetic data (Da Silva *et al.* 2015); two using community ecology approach (Villa-Nova *et al.* 2011, 2014); one using GIS/remote sensing (Magris *et al.* 2013) and three that adopted dispersal models (D'agostini *et al.* 2015, Ruddorf *et al.* 2009; Magris *et al.* 2016).

By analyzing the documentation of the 67 Brazilian MPA, only 27 present a management planning. From all MPA, 14 mention connectivity generically (1 mentions gene flow exclusively), 1 community connectivity, 8 ecosystem connectivity, 2 ecosystem and genetic connectivity, 2 genetic connectivity, and 1 population connectivity (Carr *et al.* 2017) in the Management Plannings or decrees of creation. However, from those, only 7 considered marine environment, such as in “biological connectivity with the nearby fishing grounds...”, “promote research integration of Fernando de Noronha and Atol emphasizing connectivity”, in Reserve of Rocas Atol documentation. The others mention connectivity considering terrestrial environment, for example “fragmented landscape, preventing connectivity between mangrove ecosystem and Atlantic forest, and the absence of wildlife corridors” in the Ecologic Station of Guanabara documentation (see Suppl. Mat. 2 for further information).

4. Discussion

Scientific studies in Brazil have focused on connectivity by means of primary research such as taxonomy, evolution (i.e., phylogeny) and community ecology – this is a somewhat narrow use of connectivity. Genetic methods allow assessing actual connectivity, mapping individuals moving among focal patches, or through landscape elements (Calabrese & Fagan 2004). Genetic studies of marine connectivity have begun in Brazil by the end of the last century (LEVY *et al.* 1998). Most of the genetic papers used data from mitochondrial DNA sequences (mtDNA; n=44, especially Cytochrome Oxidase I gene, COI, in 14 references), allozymes (n=13) and microsatellites (n=11) – other markers were less frequent (Suppl. Mat. 1). Sanger sequences are relatively cheap, but limited in the amount of information *per loci*, while microsatellites allow a higher number of information, but it is an expensive and laborious method (Avise 1994, Neigel 1995, Sunnucks 2000, Féral 2002, Hellberg *et al.* 2002, Schlötterer 2004, Gardner *et al.* 2010, Selkoe & Toonem 2006, St-Onge *et al.* 2013). Thus, in terms of information, results are, in the majority, from cheapest and less informative genetic markers.

The community ecology approach is related to the physical aspects of the landscape, such as size, shape, and location of the habitat patches, without taking into account any measure of dispersal ability (Calabrese & Fagan 2004). In these approaches, connectivity is inferred either by presence/absence of species in areas (Monteiro-Neto *et al.* 2008, Lacerda *et al.* 2014), abundance (Xavier *et al.* 2013), niche model (Fromentin *et al.* 2014) or trophic aspects (Claudino *et al.* 2015). GIS/remote sensing and dispersal modeling data represent studies of potential connectivity and combine physical attributes of the landscape with information about dispersal ability to predict how connected a given landscape or patch will be for a species, as defined by Calabrese & Fagan (2004). This perspective has been used in a GIS analysis of MPA distribution (Magris *et al.* 2013), in a spatial data on demographic analysis (Magris *et al.* 2017), in an advection/diffusion model of geostrophic currents generated by altimetry (Ruddorf *et al.* 2009), and in an eddy-resolving biophysical model (D’agostini *et al.* 2015). All studies covered the whole coast.

Although the term conservation has been frequently used, the majority of the papers adopted a generic concept of conservation, or superficial remarks, without guides to practical application to conservation issues like “the differences in the genetic structure among co-occurring species should be taken into consideration for the conservation of eventual evolutionary units along the Brazilian Province.” (Affonso & Galleti 2007) or “our results indicate that nitrogen-fixing bacterial guilds can be partially endemic to mangroves, and these communities are modulated by oil contamination, which has important implications for conservation strategies” (Dias *et al.* 2012). Other studies are more specific, although not decisive and still requiring a stronger link between scientific findings and applications on conservation, like “to better evaluate these impacts on the stocks of marine fishes from the São Paulo State and to build a solid knowledge base for conservation initiatives, an accurate identification system for these species is crucial” (Ribeiro *et al.* 2012).

In studies considering MPAs, the identification of critical habitats for conservation was raised by the community ecology approach. Examples are studies addressing the connectivity between threatened fish species and those targeted for fisheries in reef and non-reef habitats, including MPAs (Villa-Nova *et al.* 2011), or by modelling dispersal pathways for a suite of coral reef species in order to identify source, self-sustaining, and stepping-stone coral reef areas along the Brazilian coast, suggesting their prioritization for protection (Magris *et al.* 2016).

Connectivity has been investigated by several studies, but the uneven geographical distribution and spatial attributes (*e.g.*, size and spacing) of MPAs in Brazil (Magris *et al.* 2013) suggest a diminishing likelihood of populations being maintained over time. Although some studies produced dispersal data, which are important to understand the ecosystem dynamics, this information has not been converted into clear proxies for connectivity. These studies focused on technical innovation rather than on practical applications.

In fact, scientists are currently concerned with providing quality information on connectivity processes, derived from theoretical studies (Gaines *et al.* 2010a), models (Leslie *et al.* 2003, Berger *et al.* 2010), or based on empirical data (Hilaro *et al.* 2015, Baco *et al.* 2016). There are two important variables to be considered, (1) that patterns of connectivity have a strong interannual variability, and (2) that meso-scale ocean surface dynamics control the connectivity, with high kinetic energy reducing connectivity and larval recruitment (D'agostini *et al.* 2015). Connectivity analyses are also undertaken at several scales to achieve a variety of goals, such as fishery management (Gaines *et al.* 2010b), to identify the genetic structure of populations (Palumbi 2003), and to characterize the functioning of critical habitats when organisms move across the seascape, such as coral reefs, mangroves and other non-reef habitats (Mumby 2006, Villa-Nova *et al.* 2011). We identified a lack of applied studies supporting MPA design and management, with most of the information providing only basic understanding on connectivity patterns. This evidence reinforces the “research-implementation gap” (Knight *et al.* 2008), and could be reverted by focusing on integrative transdisciplinary research programs capable to produce synthetic and objective information of the actual functioning of marine ecosystems. For instance, research integrating traditional knowledge with regional and large-scale ocean models (Melià *et al.* 2016) could help to explain the observed high endemism found in coral and fish species. The study integrated larval advection pathways, genetic distances among populations, and observations on the conservation effectiveness of MPAs to manage the sustainability of small-scale fisheries.

The majority of the studies on connectivity related to conservation management focus on a few species when, ideally, multispecies models should be used to design MPAs. Although attempts of using multi-species connectivity have been made (López Duarte *et al.* 2012, Magris *et al.* 2016), methods suitable for populations of some species may be ineffective to others (White *et al.* 2014, Magris *et al.* 2018) because their biological features differ, such as recruitment and dispersal capabilities related to larval development (Jokiel 1990, Martel & Chia 1991, Miranda & Thiel 2008), and larval vertical migration (Bingham & Young 1991, Sponaugle *et al.* 2002, Fisher 2005, Szmant *et al.* 2006, Pineda *et al.* 2007, Carr *et al.* 2008, North *et al.* 2008, Butler Iv *et al.* 2011). There is also lack of knowledge on fecundity rates of target taxa like corals and reef fishes. The fate of the eggs released will also depend on spawning strategies, whether demersal or pelagic, for which ocean currents, water temperature and salinity vary significantly. These ocean features are seasonal, and cyclic variability of the ocean and the atmosphere causes different larval transport and survival conditions (Dias *et al.* 2014) that significantly affect both recruitment and self-recruitment (D'agostini *et al.* 2015).

It is demonstrated that connectivity processes deal with several spatial scales, from local / individual patterns to broad variables critical to regional connectivity, such as stepping-stone

patches. In fact, the decision of the scale to be used is critical and varies with the context, like the simplifying assumptions of the problem, hypotheses to be tested, model organisms, and even the expertise of the research team. For instance, fine-scale connectivity inferences demand high resolution data for ocean circulation simulations, including the effects of mesoscale activity, mixed-layer dynamics (Holt *et al.* 2014), and relevant ecological processes such as vertical migration and the influence of lunar cycle on the spawning time. Thus, the choice of the dispersive models, like biophysical (*e.g.*, Incze & Naime 2000; Griffin *et al.* 2001), advection-diffusion models using altimetry-derived geostrophic currents (*e.g.*, Polovina *et al.* 1999; Kobayashi 2006, Ruddorf *et al.* 2009 a,b), remote sensing data (*e.g.*, Chiswell *et al.* 2003), stochastic methods (*e.g.*, Siegel *et al.* 2003) or biophysical multispecies end-to-end models (*e.g.*, Rose *et al.* 2015), will depend on the scale of the process being investigated. Models basically simulate the interaction of current velocity and direction, surface and subsurface sea water temperature and salinity with biological variables, such as egg and larvae size and density, Planktonic Larvae Duration (Gaines *et al.* 2007), larval behavior (Young & Chia 1987) and vertical migration (Pineda *et al.* 2007).

The objectives to plan a MPA are also variable (Margules & Pressey 2000), then criteria should consider species' life-history, the relevance for the recovery of endangered, threatened and declining populations/species, the proportion of sensitive habitats, the biotopes or species functionally fragile or with slow recovery; and the fitness consequences and species, populations or communities with comparatively higher natural biological productivity (EBSA; Foley *et al.* 2010). Candidate areas for MPAs have to facilitate the connectivity of marine ecosystems by accounting geomorphological or oceanographic features (EBSA, COP 9) and water quality (Foley *et al.* 2010) for the exchange of larvae, nutrients, and food (U.S. Commission on Ocean Policy 2005). The inclusion of these objectives when planning MPAs is a daunting challenge and requires interdisciplinary and systemic studies to interpret them through the filter of available data on biodiversity features, providing the basis for effective conservation plans (Lockwood *et al.* 2002, Palumbi 2003, Treml *et al.* 2008, Botsford *et al.* 2009, Christie *et al.* 2010).

We presented a diagnostic on the nature of information about marine connectivity and its use for MPA planning and management. The majority of the studies focused on particular species and taxonomic groups (*e.g.*, fish), not necessarily providing information to be incorporated in conservation planning at multiple scales. Connectivity integrates several different approaches such as genetics, life history (reproduction, larval dispersal capacities, foraging, ecology), biophysical modeling, forming a comprehensive framework for conservation actions. However, there is not much integration across approaches. For instance, most of the genetic studies are not concerned with understanding the functioning of natural systems or what are the implications of their findings for conservation.

Much has been said on the importance of incorporating connectivity into management decisions (Almany *et al.* 2009, Green *et al.* 2014, Magris *et al.* 2014), but a few attention has been given to integrate these aspects into policy formulation. The Brazilian roadmap to achieve Aichi Targets is based on the Strategic National Plan of Protected Areas (*Plano Estratégico Nacional de Áreas Protegidas – PNAP*), created after the Rio 92 Convention on Biological Diversity (CBD). PNAP cites “connectivity” five times, one explicit to the marine environment: “...guarantee, by network of MPA the maintenance of connectivity among marine environments” (BRASIL 2006), but there are no guidelines to assess progress towards this goal. Consequently, the establishment of federal and state MPAs (from sustainable use to no-take areas) in the last years do not reflect that, and connectivity is largely neglected (Magris & Pressey 2018). “A MPA establishment should be based on the best available science ... [on] what we know now rather than delaying until more information is available” (Rome 2016), within an adaptive planning process (Grantham *et al.* 2009). However, MPAs have been historically created by political convenience and rarely enforced (Devillers *et al.* 2015, Magris & Pressey 2018), overlooking best practices in MPA management and far from constructing a national ecological functional MPA network based, for example, on connectivity.

It is also clear that connectivity is an under-investigated issue in Brazil, with fragmentary applications to design MPAs. Evidently, the lack of connectivity in the current MPA system neither imply that existing MPAs do not contribute to conservation nor connectivity supersede other ecological criteria used for MPA designation. Although some may say that connectivity is not important to Marine Reserve Planning (Costello and Conor 2019) we affirm that ecological and biological processes are related to connectivity processes. Thus, connectivity is, indeed, important. In this perspective, this study points out to challenges and opportunities for the implementation of marine and coastal MPA that will effectively contribute to the conservation efforts at local and broader scales. Moving forward, we call for future research efforts that focus on connectivity conservation at various scales, and policy actions enhancing integration of scientific information in the decision-making process, within an adaptive learning process.

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7. Supplementary material

Table SM 1. Papers found in the platforms Scielo and Web of Science, by the combination of terms of the following groups: 1: “(genetic diversity)”, “connectivity”, “genetic”, “geneflow”, “Phylogenetics” and “dispersal”; 2: “(marine protected areas)”; 3: “(brazilian coast)”, “brazil” and “marine”; 4: “fish”, “crustacea”, “coral”, “hydrozoa”, “scyphozoa”, “polychaeta”, “ascidian” and “larva” separated by tool of access connectivity, group of organisms studied (by species and phylum), if the study mentions conservation of species or groups, area, habitat or environment of study, and any kind of mention to Marine Protected Area (MPA). Numbers in bold are references that are plotted in Figure 2 and 3.

Reference #	Citation	Method	Organisms used	Groups	Environment	Goal: conservation of species or groups	Goal: conservation of areas	Mention MPA?
1	Claudino <i>et al.</i> (2015)	Community ecology	Not Applied	Fauna	Mangrove	No	No	No
2	Villa-Nova <i>et al.</i> 2014	Community ecology	Not Applied	Fauna	reef	No	Yes	Yes
3	Monteiro-Neto 2008	Community ecology	Not Applied	Fish	fishery	No	No	No
4	Pereira <i>et al.</i> 2010	Community ecology	Not Applied	Fish	seagrass bed	No	Yes	No
5	Macedo-Soares <i>et al.</i> 2010	Community ecology	Not Applied	Fish	coastal lagoon	No	Yes	No
6	Souza <i>et al.</i> 2013	Community ecology	Not Applied	Fish	reef	No	Yes	No
7	Villa-Nova <i>et al.</i> 2011	Community ecology	Not Applied	Fish	reef	No	Yes	Yes
8	Fromentin <i>et al.</i> 2014	Community ecology	Not Applied	Fish	fishery	No	No	No
9	Lacerda <i>et al.</i> 2014	Community ecology	Not applied	Fish and crustacean	estuary	No	Yes	No
10	Nóbrega <i>et al.</i> 2004	Genetic (Allozyme)	<i>Phallusia nigra</i> (Chordata)	Ascidian	benthos	No	No	No
11	Dias <i>et al.</i> 2006	Genetic (Allozyme)	<i>Symplegma rubra</i> (Chordata)	Ascidian	shore	No	No	No
12	Bouzon <i>et al.</i> 2014	Genetic (mtDNA)	<i>Didemnum granulatum</i> (Chordata)	Ascidian	benthos island	No	Yes	No
13	Dantas <i>et al.</i> 2012	Genetic (mtDNA)	<i>Larus dominicanus</i> (Chordata)	Fish	island	No	No	No
14	Stampar <i>et al.</i> 2012	Genetic (mtDNA)	<i>Isarachnanthus</i> spp. (Cnidaria)	Tube-anemones	not available	No	No	No
15	Neves <i>et al.</i> 2008	Genetic (Isozyme)	<i>Siderastrea stellata</i> <i>S. radians</i> (Cnidaria)	Scleractinians	reef	No	No	No
16	Nunes <i>et al.</i> 2009	Genetic (IGR)	<i>Montastraea cavernosa</i> (Cnidaria)	Scleractinians	reef	No	Yes	No
17	Nunes <i>et al.</i> 2011	Genetic (genomic DNA)	<i>Flavia fragum</i> , <i>F. graviora</i> , <i>Siderastrea siderea</i> , <i>S. radians</i> , <i>S. stellata</i> , <i>Porites astreoides</i> (Cnidaria)	Scleractinians	reef	No	Yes	No
18	Weber & Levy 2000	Genetic (allozyme)	<i>Callinectes danae</i> (Arthropoda)	Crustacean	estuary	No	No	No
19	Gonçalves <i>et al.</i> 2005	Genetic (AFLP)	<i>Litopenaeus vannamei</i> (Arthropoda)	Crustacean	farm	No	No	No

20	Lima <i>et al.</i> 2010	Genetic (microsatellite)	<i>Litopenaeus vannamei</i> (Arthropoda)	Crustacean	farm	No	No	No
21	Weber <i>et al.</i> 2012	Genetic (Allozyme)	<i>Callinectes sapidus</i> , <i>C. ornatus</i> , <i>C. danae</i> , <i>Arenaeus cribrarius</i> (Arthropoda)	Crustacean	estuary	No	No	No
22	Laurenzano <i>et al.</i> 2012	Genetic (mtDNA)	<i>Uca uruguayensis</i> (Arthropoda)	Crustacean	mangrove	No	No	No
23	Oliveira-Neto <i>et al.</i> 2014 a	Genetic (microsatellite)	<i>Ucides cordatus</i> (Arthropoda)	Crustacean	not clear	Yes	No	No
24	Lacerda <i>et al.</i> 2016	Genetic (microsatellite)	<i>Callinectes sapidus</i> (Arthropoda)	Crustacean	fishery	No	No	No
25	Maggioni <i>et al.</i> 2003	Genetic (microsatellite)	<i>Litopenaeus schmitti</i> (Arthropoda)	Crustacean	fishery	Yes	No	No
26	Diniz <i>et al.</i> 2005	Genetic (AFLP)	<i>Panulirus argus</i> (Arthropoda)	Crustacean	not clear	No	No	No
27	Freitas <i>et al.</i> 2007	Genetic (RAPD)	<i>Litopenaeus vannamei</i> (Arthropoda)	Crustacean	farm	Yes	No	No
28	Oliveira-Neto <i>et al.</i> 2007	Genetic (RAPD and RFLP)	<i>Ucides cordatus</i> (Arthropoda)	Crustacean	mangrove	No	No	No
29	Oliveira-Neto <i>et al.</i> 2008	Genetic (mtDNA)	<i>Cardisoma guanhumi</i> (Arthropoda)	Crustacean	estuary	Yes	No	No
30	Ituarte <i>et al.</i> 2012	Genetic (mtDNA)	<i>Neohelice granulata</i> (Arthropoda)	Crustacean	beach	No	No	No
31	Gusmão <i>et al.</i> 2013	Genetic (Allozyme and RFPL of mtDNA)	<i>Xiphopenaeus</i> sp. (Arthropoda)	Crustacean	fishery	Yes	No	No
32	Wieman <i>et al.</i> 2014	Genetic (mtDNA)	<i>Uca maracoani</i> (Arthropoda)	Crustacean	not clear	No	Yes	No
33	Rodríguez-Rey <i>et al.</i> 2014	Genetic (mtDNA)	<i>Scyllarides brasiliensis</i> (Arthropoda)	Crustacean	benthos island	No	Yes	No
34	Carvalho-Batista <i>et al.</i> 2014	Genetic (mtDNA)	<i>Artemesia longinaris</i> (Arthropoda)	Crustacean	coast	No	No	No
35	Rodríguez-Rey <i>et al.</i> 2016	Genetic (mtDNA and rDNA)	<i>Johnngarthia lagostoma</i> (Arthropoda)	Crustacean	benthos island	No	No	No
36	Lessios <i>et al.</i> 2001	Genetic (mtDNA)	<i>Diadema</i> sp. (Echinodermata)	Sea-urchin	not available	No	No	No
37	Rodrigues <i>et al.</i> 2008	Genetic (mtDNA)	<i>Cynoscion acoupa</i> (Chordata)	Fish	estuary	No	No	No
38	Mendonça <i>et al.</i> 2009	Genetic (mtDNA)	<i>Rhizoprionodon lalandii</i> (Chordata)	Fish	fishery	Yes	No	No
39	Rodriguez-Filho <i>et al.</i> 2009	Genetic (mtDNA)	Chordata	Fish	not available	Yes	No	No
40	Xavier <i>et al.</i> 2012	Community Ecology	Chordata	Fish	mangrove-reef	No	Yes	No
41	Ribeiro <i>et al.</i> 2012	Genetic (mtDNA)	Not applied	Fish	fishery	No	Yes	No
42	Mai <i>et al.</i> 2014	Genetic (microsatellite)	<i>Mugil liza</i> (Chordata)	Fish	fishery	No	Yes	No
43	Torres <i>et al.</i> 2015	Genetic (ISSR,mtDNA)	<i>Hemiramphus brasiliensis</i> , <i>H. balao</i> (Chordata)	Fish	fishery	Yes	No	No
44	Levy <i>et al.</i> 1998	Genetic (Allozyme)	<i>Micropogonias furnieri</i> (Chordata)	Fish	fishery	Yes	No	No
45	Affonso 2004	Genetic (RAPD and microsattellites)	<i>Holocanthus ciliaris</i> , <i>H. tricolor</i> , <i>Pomacanthus parus</i> , <i>P. arcuatus</i> ,	Fish	reef	No	No	No

			<i>Centropyge aurantonotus, Chaetodon striatus</i> (Chordata)					
46	Rocha 2004	Genetic (mtDNA)	<i>Halichoeres maculipinna, H. cyanocephalus, H. garnoti</i> (Chordata)	Fish	fishery	No	No	No
47	Molina & Galleti 2004	Genetic (cytogenetics)	<i>Abudefduf saxatilis, Microspathodon chrysurus, Amphiprion frenatus</i> (Chordata)	Fish	not available	No	No	No
48	Costagliola <i>et al.</i> 2004	Genetic (mtDNA)	<i>Thalassoma noronhanum</i> (Chordata)	Fish	benthos island	No	No	No
49	Lima <i>et al.</i> 2005	Genetic (Allozyme and mtDNA)	<i>Bathygobius soporator</i> (Chordata)	Fish	benthos island	No	No	No
50	Santos <i>et al.</i> 2006	Genetic (mtDNA)	<i>Macrodon ancylodon</i> (Chordata)	Fish	coastal water	No	No	No
51	Galetti <i>et al.</i> 2006	Genetic (cytogenetics)	Chordata	Fish	reef	No	No	No
52	Afonso & Galleti 2007	Genetic (RAPD)	<i>Holacanthus ciliaris, Pomacanthus paru, Chaetodon striatus</i> (Chordata)	Fish	reef	Yes	No	No
53	Silva- Oliveira <i>et al.</i> 2008	Genetic (mtDNA)	<i>Epinephelus itajara</i> (Chordata)	Fish	fishery	Yes	Yes	No
54	Prodócimo <i>et al.</i> 2008	Genetic (mtDNA)	<i>Centropomus parallelus</i> (Chordata)	Fish	not available	Yes	No	No
55	Vasconcellos <i>et al.</i> 2008	Genetic (Allozyme, mtDNA)	<i>Ocyurus chrysurus</i> (Chordata)	Fish	fishery	No	No	No
56	Tatarenkov <i>et al.</i> 2011	Genetic (microsatellite)	<i>Kryptolebias ocellatus</i> (Chordata)	Fish	not available	No	No	No
57	Gomes <i>et al.</i> 2012	Genetic (mtDNA)	<i>Lutjanus purpureus</i> (Chordata)	Fish	fishery	Yes	No	No
58	Karl <i>et al.</i> 2012	Genetic (mtDNA microsatellite)	<i>Ginglymostoma cirratum</i> (Chordata)	Fish	island	Yes	Yes	No
59	Mendonça <i>et al.</i> 2013	Genetic (mtDNA)	<i>Rhizoprionodon lalandii</i> (Chordata)	Fish	coastal sea	Yes	No	No
60	Benevides <i>et al.</i> 2014	Genetic (ISSR)	<i>Epinephelus itajara</i> (Chordata)	Fish	estuary and coast	Yes	No	No
61	Oliveira <i>et al.</i> 2014	Genetic (mtDNA and rDNA)	<i>Centropomus undecimalis</i> (Chordata)	Fish	fishery	No	No	No
62	Watanabe <i>et al.</i> 2014	Genetic (Haplotype (?))	<i>Anableps anableps</i> (Chordata)	Fish	estuary	No	No	No
63	Rodrigues <i>et al.</i> 2014	Genetic (mtDNA)	<i>Macrodon atricauda</i> (Chordata)	Fish	coast	No	No	No
64	Souza <i>et al.</i> 2015 a	Genetic (mtDNA)	<i>Cephalopholis fulva</i> (Chordata)	Fish	coast	Yes	No	No
65	Souza <i>et al.</i> 2015 b	Genetic (mtDNA)	<i>Mytella charruana</i> (Chordata)	Fish	not available	No	No	No
66	Damasceno <i>et al.</i> 2015	Genetic (mtDNA)	<i>Epinephelus itajara</i> (Chordata)	Fish	not available	Yes	Yes	No
67	Gomes <i>et al.</i> 1998	Genetic (RAPD)	<i>Hirundichthys affinis</i> (Chordata)	Fish	not available	Yes	No	No
68	Artico <i>et al.</i> 2010	Genetic (mtDNA)	<i>Otaria flavescens</i> (Chordata)	Mammal	dead animal	Yes	No	No
69	Cunha <i>et al.</i> 2005	Genetic (mtDNA)	<i>Sotalia fluviatilis, S. guianensis</i> (Chordata)	Mammal	coastal	Yes	No	No
70	Caballero <i>et al.</i> 2010 a	Genetic (mtDNA)	<i>Sotalia fluviatilis S. guianensis</i>	Mammal	not available	Yes	No	No

(Chordata)								
71	Caballero <i>et al.</i> 2010 b	Genetic (genomic DNA)	<i>Sotalia fluviatilis</i> , <i>S. guianensis</i> (Chordata)	Mammal	dead animal	Yes	No	No
72	Moreira <i>et al.</i> 2011	Genetic (microsatellite)	<i>Octopus vulgaris</i> (Mollusca)	Mollusc	fishery	Yes	No	No
73	Galvão <i>et al.</i> 2012	Genetic (mtDNA, rRNA)	<i>Cassostrea</i> sp. (Mollusca)	Mollusc	estuary	Yes	Yes	No
74	Andrade <i>et al.</i> 2003	Genetic (Isozyme)	<i>Nodilittorina lineolata</i> , <i>Littoraraia flava</i> , <i>L. angulifera</i> (Mollusca)	Mollusc	mangrove and rocky shore	No	No	No
75	Arruda <i>et al.</i> 2009	Genetic (mtDNA)	<i>Anomalocardia brasiliensis</i> (Mollusca)	Mollusc	not available	No	No	No
76	Sales <i>et al.</i> 2013	Genetic (mtDNA and rDNA)	<i>Octopus vulgaris</i> , <i>O. insularis</i>	Mollusc	fishery	No	No	No
77	de Souza <i>et al.</i> 2013	Community Ecology	Chordata	Fish	fishery	No	Yes	No
78	José & Solferini 2007	Genetic (Allozyme)	<i>Collisella subrugosa</i> (Mollusca)	Mollusc	fishery	No	No	No
79	Andrade <i>et al.</i> 2011	Genetic (genomic DNA)	<i>Ototyphlonemertes</i> sp. (Nemertea)	Nemertea	rocky shore	No	No	No
80	Dias <i>et al.</i> 2012	Genetic (genomic DNA)	Not applied	Not applied	benthos	No	No	No
81	Padua <i>et al.</i> 2013	Genetic (microsatellite)	<i>Clathrina aurea</i> (Porifera)	Sponge	mangrove	No	No	No
82	Lazoski <i>et al.</i> 2000	Genetic (Allozyme)	<i>Chondrosia reniformis</i> (Porifera)	Sponge	not available	No	No	No
83	Zilberberg <i>et al.</i> 2006	Genetic (Allozyme)	<i>Chondrilla nucula</i> (Porifera)	Sponge	coastal sea	No	No	No
84	Shamblin <i>et al.</i> 2015	Genetic (microsatellite)	<i>Chelonia mydas</i> (Chordata)	Green turtle	coast	Yes	No	No
85	Teschima <i>et al.</i> 2016	Genetics (mtDNA)	<i>Grapsus grapsus</i> (Crustacean)	Crustacean	islands	No	No	Yes
86	da Silva <i>et al.</i> 2015	Genetics (mtDNA and genomic)	<i>Ocyurus chrysurus</i> (Chordata)	Fish	fishery	Yes	No	No
87	Magris <i>et al.</i> 2013	GIS/remote sensing	Not applied	MPAs	MPAs	No	No	Yes
88	Magris <i>et al.</i> 2017	spatial data on demographically analysis	Reef species	Not applied	Reef	Yes	Yes	Yes
89	D'Agostini <i>et al.</i> 2015	Dispersal model	<i>Mycteroperca</i> sp. (Chordata)	Fish	coast	No	No	Yes
90	Ruddorf <i>et al.</i> 2009	Dispersal model	Not applied	Larvae	coast sea	No	No	No

Table SM 2. Federal Marine Protected Areas of all kind of protection and uses from the Brazilian government database. I: name of the MPA; II: Does it have a Management Planning?; III: Does the Management Planning or the Decree mention Connectivity?; IV: Is connectivity mentioned for marine environment? V: Classification of connectivity type according to Carr et al. (2017).

I. Name of the MPA	II	III	IV	V
REVIS do Arquipélago de Alcatrazes	No	No	Not Applied	Not Applied
APA Costa das Algas	No	No	Not Applied	Not Applied
APA da Baleia Franca	No	No	Not Applied	Not Applied
APA da Barra do Rio Mamanguape	Yes	Yes	No	Ecosystem
APA de Anhatomirim	Yes	Yes	Yes	population
APA de Cairuçu	Yes	No	Not Applied	Not Applied
APA de Cananéia-Iguape-Peruíbe	Yes	Yes	yes	Genetic
APA de Fernando de Noronha - Rocas - São Pedro e São Paulo	Yes	No	gene flow only	Genetic
APA de Guapimirim	Yes	No	Not Applied	Not Applied
APA da Costa dos Corais	Yes	No	Not Applied	Not Applied
APA de Guaraqueçaba	Yes	No	Not Applied	Not Applied
APA de Piaçabuçu	Yes	Yes	No	ecosystem
APA Delta do Parnaíba	Yes	No	Not Applied	Not Applied
APA do Arquipélago de São Pedro e São Paulo	No	No	Not Applied	Not Applied
APA do Arquipélago de Trindade e Martim Vaz	No	No	Not Applied	Not Applied
Arie Ilha do Ameixal	No	No	Not Applied	Not Applied
Arie Ilhas da Queimada Pequena e Queimada Grande	No	No	Not Applied	Not Applied
ARIE Manguezais da Foz do Rio Mamanguape	Yes	Yes	No	Ecosystem and genetic
Esec da Guanabara	Yes	Yes	Yes	Ecosystem
Esec de Carijós	Yes	Yes	No	Ecosystem
Estação Ecológica Garequeçaba	No	No	Not Applied	Not Applied
ESEC de Marajá- Jipioca	No	No	Not Applied	Not Applied
Esec de Tamoios	Yes	No	Not Applied	Not Applied
Esec de Tupiniquins	Yes	Yes	Yes	ecosystem
Esec do Taim	No	No	Not Applied	Not Applied
Esec Tupinambás	No	No	Not Applied	Not Applied
Mona das Ilhas de Trindade e Martim Vaz	No	No	Not Applied	Not Applied
Mona do Arquipélago de São Pedro e São Paulo	No	No	Not Applied	Not Applied
Monumento Natural das Ilhas Cagarras	Yes	No	Not Applied	Not Applied
Parna da Lagoa do Peixe	Yes	No	Not Applied	Not Applied
Parna da Restinga de Jurubatiba	Yes	No	Not Applied	Not Applied
Parna de Jericoacoara	Yes	Yes	No	Ecosystem and genetic
Parna do Cabo Orange	Yes	Yes	No	Ecosystem

Parna do Superagui	No	No	Not Applied	Not Applied
Parna dos Lençois Maranhenses	Yes	No	Not Applied	Not Applied
Parque Nacional Marinho das Ilhas dos Currais	No	No	Not Applied	Not Applied
Parna Marinho de Fernando de Noronha	Yes	No	Not Applied	Not Applied
Parna Marinho dos Abrolhos	Yes	No	Not Applied	Not Applied
Rebio Atol das Rocas	Yes	Yes	Yes	Community
Rebio de Comboios	Yes	Yes	No	Ecosystem
Rebio de Santa Isabel	No	No	Not Applied	Not Applied
Rebio Marinha do Arvoredo	Yes	Yes	Yes	Genetic
Resex de São João da Ponta	No	No	Not Applied	Not Applied
Resex Mãe Grande de Curuçá	No	No	Not Applied	Not Applied
Resex Acaú-Goiana	No	No	Not Applied	Not Applied
Resex Arapiranga-Tromai	No	No	Not Applied	Not Applied
Resex da Baía do Tubarão	No	No	Not Applied	Not Applied
Resex Marinha Baía de Iguape	No	No	Not Applied	Not Applied
Resex Batoque	No	No	Not Applied	Not Applied
Resex Cassurubá	No	No	Not Applied	Not Applied
Resex Chocoaré- Mato Grosso	No	No	Not Applied	Not Applied
Resex de Canavieiras	No	No	Not Applied	Not Applied
Resex de Cururupu	No	No	Not Applied	Not Applied
Resex Marinha Delta do Parnaíba	No	No	Not Applied	Not Applied
Resex Itapetininga	No	No	Not Applied	Not Applied
Resex Gurupi-Piriá	No	No	Not Applied	Not Applied
Resex Marinha Lagoa do Jequiá	No	No	Not Applied	Not Applied
Resex Maracanã	No	No	Not Applied	Not Applied
Resex Marinha Corumbau	No	No	Not Applied	Not Applied
Resex Marinha de Caeté-Taperaçu	Yes	Yes	Yes	Ecosystem
Resex Marinha de Soure	No	No	Not Applied	Not Applied
Resex Marinha de Tracuateua	No	No	Not Applied	Not Applied
Resex Marinha do Arraial do Cabo	No	No	Not Applied	Not Applied
Resex Pirajubaé	No	No	Not Applied	Not Applied
Resex Prainha do Canto Verde	No	No	Not Applied	Not Applied
Revis de Santa Cruz	No	No	Not Applied	Not Applied
Revis Ilha dos Lobos	No	No	Not Applied	Not Applied

Chapter 2: Metanalysis of gene flow along the Brazilian coast

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ABSTRACT

Connectivity is one of the major variables to be considered in conserving marine resources under human pressures. Gene flow is one proxy used to connectivity. Brazilian EEZ is a huge area of the Southwest Atlantic including diversified and hotspots of biodiversity. Thus, the goal of this study is to assess gene flow and networks of connectivity in the Brazilian EEZ. Our main goal was to verify the higher distance where connectivity still occurs. We based our inference on a survey of published studies with data on gene flow/connectivity for 17 coastal Brazilian states and islands, and compared the data with established Brazilian MPAs. The 24 resulted studies were scored for connectivity strength from 0 to 3, depending on the original value of the indexes. We used UCINET network analysis software to analyze the connectivity networks at the regional level. The relative contribution of areas to maintain genetic connectivity was inferred by using Eigenvector centrality. We performed a Pearson's correlation test in R to compare the relationship between the number of studies and the scores of connectivity. A logistic regression analysis tested the hypothesis of the strength of the connection vs distance between each pair of areas. A Chi square test verified differences in the frequencies of each strength for every 200 km. Results showed that connectivity is significantly higher between lower distances. The highest distance with significant connectivity is 3,800 km. Higher distances have only 1% of chance to have connectivity strength 3, and are predominantly strength 1. There was a low-level of connectivity among areas in Southeastern and Southern Brazil and high levels of connectivity among areas in the Northeastern and Northern Brazil. Indeed, some areas like the Amazonian coast of Pará and several areas at the Northeastern

coast are key areas for structuring populations. Islands had mostly low and intermediate levels of connectivity with coastal areas, but knowledge on the connectivity of oceanic islands is nearly nonexistent. We conclude there is a need of establishing new MPAs to act as stepping-stones in a network, as well as the necessary increase in marine connectivity studies, including connectivity assessments among MPAs.

Keywords: metanalysis, connectivity, gene flow, conservation

1. Introduction

There is a scientific claim for conserving marine life and habitats due to anthropogenic impacts such as overfishing, global climate changes, pollution and habitat loss (Lotze *et al.* 2006, Halpern *et al.* 2008, 2012). An important tool for that is the creation and management of Marine Protected Areas (MPA). Models to design MPA networks include discussions about size, distance and distribution of the reserves (Leslie *et al.* 2003, Jones *et al.* 2007, Gaines *et al.* 2010, Grober-Dunsmore *et al.* 2010, Paris-Limouzy 2011, Green *et al.* 2013, Burt *et al.* 2014, Magris *et al.* 2015). Remoteness may be generally associated with lower exchanging rates of individuals among different areas, inducing speciation (Witacker *et al.* 2008) and increasing endemism (Brigs 2007). There are two concurrent models to design MPA networks, (1) the model of stepping-stones in which individuals' exchanges occur among adjacent areas; and (2) the model of islands in which migration occurs equally among all patches of preserved habitats in a network (Palumbi 2003). In order to choose the best design for conservation goals, it is decisive to understand the connectivity among the of the MPA network (Jones *et al.* 2007, Foley *et al.* 2010, Gaines *et al.* 2010, Grober-Dunsmore *et al.* 2010, Magris *et al.* 2014).

Connectivity can be quantified through different approaches, such as structural, actual and potential (Calabrese & Fagan 2004, Sanches *et al.* 2019), in different biological scales, such as population, genetic, community, and ecosystem connectivity (Carr *et al.* 2017). Considering genetic connectivity, gene flow represents the genetic exchange among populations (Palumbi 2003). Gene flow is involved in evolutionary processes by modulating genetic variability, resilience against environmental disturbances, and fitness (Palumbi 2003, Saens-Agudelo 2009), tending to genetically homogenize populations (Mayr 1963). Low or inexistent gene flow promotes isolation, which may cause extinction after acute declines, or speciation (Hellberg 2009). In terms of conservation, isolated places are more vulnerable because they present more difficult recovery after being impacted. When populations live close to each other, gene flow tend to be higher among them (Kinlan & Gaines 2003, Palumbi 2003), specially between adjacent populations (Slatkin 1993) and, in such cases, the stepping-stone model of MPA would not be the best choice.

MPA spatial distribution based on dispersal distances vary according to the oceanographic dynamics of each area and the dispersal potential of each species. Dispersal potential is influenced by biological factors such as fecundity, location and time of spawning (Sponaugle *et al.* 2002), Planktotrophic Larvae Duration (PLD, Levin *et al.* 1987), and vertical swimming (Sponaugle *et al.* 2002, Pineda *et al.* 2007). For instance, models for connectivity of coral reef species across the Indo-Pacific Ocean estimate that >95% of larval settlement occurs within 155 km of the source population (Treml *et al.* 2012). Complementarily, the distance between MPAs in order to promote connectivity was estimated in 10-20km in average for 32 different species (Shanks 2003). A similar result was observed for elemental fingerprinting of the chemical signals imparted to larval shells or otoliths of 7 species at different locations, with the greatest distance dispersed for the gastropod *Mytilus galloprovincialis* 37 km in average (López-Duarte *et al.* 2012).

Different approaches based on gene flow rise dispersal distances to hundreds of kilometers, because it considers the phenomenon over generations. Fixation index (FST) for 90 marine species resulted in longest dispersals ranging 25-270 km for macroalgae, ~700km for fish and 20-500 km for long-dispersing barnacles, bivalves, and sea anemones (Kinlan & Gaines 2003); index M^* indicated that localities with higher levels of gene flow were isolated by less than 1,600 km for the coral *Balanophyllia elegans* (Hellberg 1994). Data compilation from genetic studies for deep-sea connectivity estimated dispersal distances based on isolation-by-distance slopes ranging from 0.24 km to 2,028 km, differing in relation to taxonomic and life-history factors (Baco *et al.* 2016).

Considering that biological features interacts with environmental conditions, a wide variety of distances between MPAs would contemplate a wide variety of species by a given network (Palumbi 2004). In other words, different species would be contemplated in different distances and designs, and variable distances would be better than fixed distances among small MPAs (Kaplan & Botsford 2005). Hence, gene flow analysis can help to determine population structure, evolution, dynamics and community responses to disturbances, enhancing conservation planning frameworks (Palumbi 2003, Saens-Agudelo 2009). However, we have noticed that Brazilian MPAs documents frequently ignore gene flow in the design of the MPA.

The goal of this study is to assess gene flow and networks of connectivity in the Brazilian EEZ, in order to verify extremes of distance in which connectivity still occurs for the Brazilian coast.

2. Methods

Data base

We surveyed the platforms Scielo and Web of Science to compile studies on connectivity related to conservation of marine systems and Brazilian MPAs. We have used the following

combinations: 1: “(genetic diversity)”, “connectivity”, “genetic”, “gene flow”, “phylogenetic” and “dispersal”; 2: “(Brazilian coast)”, “Brazil” and “marine”; 3: “larvae”, “marine invertebrates” and “marine vertebrates”. We also checked for cross references that did not appear in the survey of the platforms. For each reference, we extracted data of statistical indexes of genetic distance and genetic differences for 24 studies providing genetic information, compressing regional-scale to characterize connectivity integrated over many generations (Suppl. Mat. 1), regarding that local scale is inadequate to describe broad processes involving connectivity (Kinlan & Gaines 2003). We did not contemplate phylogenetic studies because we considered only studies that in any moment were thought or designed to answer connectivity questions.

Statistical descriptors

We scored the connectivity strength (CS) to make measures quantitatively comparable across all studies. The parameters were: 0 – no connectivity or no information; 1 – [0.7-1] (= high divergence or genetic distance; low connectivity); 2 – [0.3-0.69] (= intermediary divergence or genetic distance; intermediary connectivity); 3 – [0-0.29] (= low divergence or genetic distance; high connectivity).

Analysis

We used UCINET network analysis software (Borgatti *et al.* 2002) to draw and analyze the connectivity networks. For this analysis, we linked each study with the respective coastal Brazilian state (Amapá - AP, Pará - PA, Maranhão - MA, Piauí - PI, Ceará - CE, Rio Grande do Norte - RN, Paraíba - PB, Pernambuco - PE, Alagoas - AL, Sergipe - SE, Bahia - BA, Espírito Santo - ES, Rio de Janeiro - RJ, São Paulo - SP, Paraná - PR, Santa Catarina - SC and Rio Grande do Sul - RS) and or islands (Saint Peter and Saint Paul - SPSP, Rocas atoll - AR, Fernando de Noronha - FN, Abrolhos - AB, Trindade - TR) based on the description of the study sites (henceforth termed “areas”). The CS between each pair of areas was represented by the statistically significant scores provided above. When we had more than one score representing the CS between two areas, we adopted the higher value as an indicator of the actual connectivity between the two areas, maximizing the connectivity of the relationship. We also totaled the number of studies indicating connectivity for each pair of areas to contrast with the maximum CS. We used Eigenvector centrality to estimate the relative contribution of areas to maintain genetic connectivity (Borgatti *et al.* 2002) for both analyses. This centrality metric measures the relative importance of each area based on their position within a network; thus it is useful to identify the key areas contributing to maintain the overall genetic connectivity of marine populations. Finally, we performed a Pearson’s correlation test in R to compare the relationship between the number of studies and the CS.

We tested the hypothesis that connectivity is inversely related to the distance between sites by using a logistic regression analysis considering CS vs. distance between each pair of areas. We

considered the midpoint of the coastline of each state as the reference to distances among areas. Distances to the islands were distances from the midpoint of each state to the closest point of the island coastline (Supp. Mat. 2). We performed a Chi square test to check differences in the frequencies of CS 1, 2, 3 at every 200 km. For this analysis, we did not consider the states, but the CSs occurring at every 200 km (the lowest distance between areas was 152 km, for Paraíba and Pernambuco States). Both analyses were performed without the CS 0, because the lack of information could cause a bias.

3. Results

The survey resulted in data for 32 species, *viz.* 4 mollusks, 3 corals, 4 crustaceans, 18 fishes, with 3 studies including more than one species (Suppl. Mat. 1). Connectivity is significantly higher between lower distances, with a CS = 3 predominating for closer sites while distant ones have CS = 1, when connectivity is present ($X^{2c} = 436.19$; $DF = 68$; $p < 0.05$; Figure 1).

Figure 1: CS frequency: frequency of connectivity strength (CS) in relation to 200 km distance intervals. CS = 0, no data (Green); CS = 1, FST 0.7-1 (high divergence or genetic distance; low connectivity) (Yellow); CS = 2, FST 0.3-0.69 (intermediary divergence or genetic distance; intermediary connectivity) (Red); CS = 3, FST 0-0.29 (low divergence or genetic distance; high connectivity) (Blue).

The highest distance with higher connectivity is ~3,800km (Figure 1), but regions behave differently. Logistic regression test shows that chance of CS = 3 between farther sites (more than 1000km apart) is 0.99 times lower than CS = 1 ('OR', Table 1).

Table 1: Statistical analysis of logistic regression of connectivity strength (CS) in relation to 200 km distance intervals.

CS = 1, FST 0.7-1 (high divergence or genetic distance; low connectivity); CS = 2, FST 0.3-0.69 (intermediary divergence or genetic distance; intermediary connectivity); CS = 3, FST 0-0.29 (low divergence or genetic distance; high connectivity).

	General Logistic Regression Model							OR		Analysis of Deviance Table (Chi)				
	Estimate	Std. Error	z value	Pr(> z)	Confidence Interval		Result	Confidence Interval 95%		Df	Deviance	Resid. Df	Resid. Dev	
					95% (Wald's)	2.5%		97.5%	2.5%					97.5%
Intercept	1.7024	0.2781	6.121	9.31e-10	1.1573	2.2476	5.4875	3.1814	9.4654	Null model		217	301.31	
distance	-0.0008	0.0001	-6.358	2.05e-10	-0.0010	0.0005	0.9991	0.9989	0.9994	1	62.977	216	238.34	2.091e-15

Mapping the ecological networks of areas (states and islands) based on genetic data revealed areas with key roles in structuring and sharing populations in the network, *viz.* the coast of Pará State and several areas of the Northeastern coast (CE, RN, PB, PE). Islands had mainly low and intermediate levels of connectivity with coastal areas, *e.g.*, AR and FN are only connected to other islands and RN (Figure 2). AB, a hotspot of biodiversity in Brazil, is not connected to any other site (significantly or not significantly, Figures 2, 3). There was low-level of connectivity among southeastern and southern Brazil states (ES, RJ, SP, PR, SC, RS) and high-level for the northeastern and northern states (AP, PA, MA, PI, CE, RN, PB, PE, AL, SE, BA) (Figure 2).

Considering non-significant results for connectivity indexes, FN and AR have low importance in the eigenvector centrality ($ec = 0.068$) contrasting with CE, PB, PE, BA high importance in the network connectivity (Figure 2B). States with a large number of studies were ES ($ec = 0.412$), PE, ($ec = 0.381$), PB ($ec = 0.356$), BA ($ec = 0.351$) and RN ($ec = 0.339$) (Figure 2). Similarly, oceanic islands presented the lowest number of studies, with SPSP ($ec = 0.001$), TR ($ec = 0.002$), FN ($ec = 0.015$), AR ($ec = 0.031$) and AB ($ec = 0.036$) (Figure 4) – knowledge on the connectivity for these islands is nearly nonexistent, even though these are well known hotspots of biodiversity with high endemism (Moura 2000), demonstrating they were little studied. Concluding, there is subtle positive correlation between CS and the number of papers for each area (Figure 5).

Figure 2 : Eigenvector centrality of statistical indexes of genetic distance and differences for references reporting genetic data in the Brazilian EEZ for significant results for each relation in Brazilian EEZ. Legend: CS = 0, no connectivity or no information, CS = 1: FST 0.7-1 (high divergence or genetic distance; low connectivity), CS = 2: FST 0.3-0.69 (intermediary divergence or genetic distance; intermediary connectivity); CS = 3, FST 0-0.29 (low divergence or genetic distance; high connectivity). Areas: Amapá - AP, Pará - PA, Maranhão - MA, Piauí - PI, Ceará - CE, Rio Grande do Norte - RN, Paraíba - PB, Pernambuco - PE, Alagoas - AL, Sergipe - SE, Bahia - BA, Espírito Santo - ES, Rio de Janeiro - RJ, São Paulo - SP, Paraná - PR, Santa Catarina - SC, Rio Grande do Sul - RS and the islands Saint Peter and Saint Paul - SPSP, Rocas atoll - AR, Fernando de Noronha - FN, Abrolhos - AB, Trindade - TR). Colours: five classes equally divided from purple to red (min to max).

Figure 3 : Eigenvector centrality of statistical indexes of genetic distance and differences for references reporting genetic data in the Brazilian EEZ for not significant results for each relation in Brazilian EEZ. Legend: CS = 0, no connectivity or no information; CS = 1: FST 0.7-1 (high divergence or genetic distance; low connectivity); CS = 2: FST 0.3-0.69 (intermediary divergence or genetic distance; intermediary connectivity); CS = 3: FST 0-0.29 (low divergence or genetic distance; high connectivity). Areas: Amapá - AP, Pará - PA, Maranhão - MA, Piauí - PI, Ceará - CE, Rio Grande do Norte - RN, Paraíba - PB, Pernambuco - PE, Alagoas - AL, Sergipe - SE, Bahia - BA, Espírito Santo - ES, Rio de Janeiro - RJ, São Paulo - SP, Paraná - PR, Santa Catarina - SC, Rio Grande do Sul - RS and the islands Saint Peter and Saint Paul - SPSP, Rocas atoll - AR, Fernando de Noronha - FN, Abrolhos - AB, Trindade - TR). Colours: five classes equally divided from purple to red (min to max).

Figure 4 : Eigenvector centrality of statistical indexes of genetic distance and differences for references reporting genetic data in the Brazilian EEZ for the number of references for each relation in Brazilian EEZ. Legend: CS = 0, no connectivity or no information, CS = 1: FST 0.7-1 (high divergence or genetic distance; low connectivity); CS = 2: FST 0.3-0.69 (intermediary divergence or genetic distance; intermediary connectivity); CS = 3, FST 0-0.29 (low divergence or genetic distance; high connectivity). Areas: Amapá - AP, Pará - PA, Maranhão - MA, Piauí - PI, Ceará - CE, Rio Grande do Norte - RN, Paraíba - PB, Pernambuco - PE, Alagoas - AL, Sergipe - SE, Bahia - BA, Espírito Santo - ES, Rio de Janeiro - RJ, São Paulo - SP, Paraná - PR, Santa Catarina - SC, Rio Grande do Sul - RS and the Islands Saint-Peter and Saint Paul - SPSP, Rocas atoll - AR, Fernando de Noronha - FN, Abrolhos - AB, Trindade - TR). Colours: five classes equally divided from purple to red (min to max).

Figure 5 Correlation between the number of studies and CS. Pearson's correlation test result $R^2 = 0.6848$, $t = 4.2029$.
 $df = 20$, $p\text{-value} = 0.0004377$.

4. Discussion

The understanding of the relationship between distance and gene flow is a necessary step to clarify individual and community patterns, especially effective when more than one genetic marker and one species is considered. High gene flow occurs in sites closer than 200 km, but relative high rates of gene flow may still occur up 1,600 km (Hellberg 1994). In fact, connectivity was demonstrated for populations distant up to 7,000 km from each other (Palumbi 2003). Genetic differences among distant populations are related to larvae exchange and thus the action of ocean currents enhances dispersal (Barber *et al.* 2000, Teixeira *et al.* 2013, Hilario *et al.* 2015), besides biological (Palumbi 2003) and ecological features (Affonso & Galleti 2007). For Brazil, connectivity also increases between closer areas (Figure 1) even considering disconnected (insular) sites (*e.g.*, RN and AR/FN). However, gene flow in Brazilian EEZ is not constrained by or coincident with ecoregions boundaries (*cf.* Spalding *et al.* 2007), like represented in connections between PA and RN/PE/AL/BA and between ES, RJ and CE/PB/PE, separated by very high distances. Also, concerning dispersive potential, species in our analysis have a wide diversity of life histories, including those with planktotrophic larvae (*e.g.*, *Centropomus parallelus*, *Micropogonias furnieri*, *Macrodon ancylodon*, *Lutjanus purpureus*), and some pelagic adults (*e.g.*, *L. purpureus*,

Macrodon atricauda), increasing chances for dispersal (Wood et al. 2014, Fisher 2005) (Suppl. Mat.).

Patterns of connectivity are variable concerning the Brazilian regions and model species. Low connectivity occurs among areas in southeastern and southern Brazil (cf. Carvalho-Batista *et al.* 2014 for *Artemesia longinaris*; Gusmão *et al.* 2015 for *Xiphopenaeus* sp. 1 and sp. 2). Coastal sites at northern and northeastern Brazil (for example AP and PI) are important isolated areas. For instance, significant genetic differences were found among populations of the reef fish *Epinephelus itajara* from northeastern (with three structured populations) and northern Brazil (Damasceno *et al.* 2015), what must be related to slow growth rates, longevity and the behavior of the species (Bullock *et al.* 1992), such as location fidelity (Koenig *et al.* 2007), which increases fishing rates and population's decline (Damasceno *et al.* 2015), *i.e.*, genetic variability decreases in limited populations (Hartl & Clark 2010). Moreover, habitat peculiarities and destruction could have negative results in genetic variability (Damasceno *et al.* 2015). However, other northeastern areas (*e.g.*, RN, PE, BA) seem also to be important sources of material (D'Agostini *et al.* 2015), in which low population structure and intraspecific genetic distance is found for species with planktotrophic larvae, like *Nodilittorina lineolata* and *Littorina flava* (Andrade *et al.* 2003).

The position of key connectivity areas, such as ES, corroborated previous patterns, like no differences considering *Xiphopenaeus* sp. 2 between ES and RJ/SP/SC. However, differently from our hubs, where RN is well connected to ES and RJ, *Xiphopenaeus* sp. 1 seems to be isolated in RN (Gusmão *et al.* 2015).

Oceanic islands display a dual behavior regarding the potential to act as hubs or isolated areas. Ecologically, for instance, proximity makes the richness of seaweeds, gastropods and reef fish for TR and FN higher than the remote SPSP (Hachich *et al.* 2016). In that perspective, several complex variables concerning dispersal dynamics have to be considered to build a reasonable scenario for connectivity in the southwestern Atlantic. Environmental changes, such as the impact of climate change on Sea Surface Temperature (SST), surface winds, ocean chemistry and circulation may affect the dynamics of population gene flow and adaptation. For instance, climate change may impact the gene flow of *Mycteroperca* sp. from a reef complex in northeastern Brazil currently dominated by a predominant north-south flow (D'Agostini *et al.* 2015). World trends of ocean warming for the western boundary currents (Wu *et al.* 2012) may intensify surface flow and poleward shift of the mid-latitude extension of the Brazil Current. In fact, El Niño simulations has shown that the release of spiny lobster larvae from the remote Ascension Island may reach further east and southwest, connecting the population from Ascension to those located in northeastern Brazil and Fernando de Noronha Archipelago (Rudorf *et al.* 2009a, b).

MPA system for the Brazilian EEZ cannot be considered well-connected in relation to size and distance of the protected areas (Magris *et al.* 2013). There are large gaps between no-take MPAs in northeastern and northern Brazil, such as ~2,000 km between AB and CE, decreasing to 200 km in the southeastern, such as ES and RJ (Vila-Nova *et al.* 2014). It is timely to highlight that a very vulnerable area is AB, the largest and richest coral reef system in the South Atlantic, with at least 6 endemic species (Francini-Filho *et al.* 2013), and the largest continuous rodolith bed in the world (Amado-Filho *et al.* 2012), presently threatened by oil and gas exploration in its vicinities (Mazzei *et al.* 2016). AB no-take areas promote greater reef fish biomass and positive effects on benthic communities such as coral cover and macroalgae diversity (Bruce *et al.* 2012). Still, AB is considered a sink area, connected and receiving individuals from other MPAs (D'Agostini *et al.* 2015), although our results suggest it to be rather isolated. Therefore, AB (and other oceanic islands) shall have a design of MPA network assuring gene flow based, for instance, on a stepping-stone model, what is hardly consistent with oil and gas exploration concessions on its surroundings.

Differences in the connectivity network and the location of areas with high gene flow within that emphasize the need of specific studies designed to fulfill the knowledge gaps, ensuring efficient managing plans. Anyhow, our results reinforce the need to create new MPAs taking into account the distance among areas. However, our analysis considering distances of Brazilian states and islands seems equivocated and the same analysis should be conducted considering latitudes. This because these distances are not equitable and analysis are in bias and patterns of biodiversity due to latitudinal variation is well known (Gaston 2000, Willig *et al.* 2003, Kerswell 2006). Considering Brazilian EEZ linear configuration, an island model would not necessarily be the best choice, and stepping-stones would work better in a network of MPAs. Brazilian data is clearly deficient to have a better picture of our conservation efficiency, regarding studies from basic taxonomy and natural history to evaluations of connectivity among populations and MPAs.

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7. Suppl. Material

Table 1: Papers surveyed in Scielo and Web of Science, by searching the combination of terms 1: “(genetic diversity)”, “connectivity”, “genetic”, “geneflow”, “Phylogenetics” and “dispersal”; 2: “(marine protected areas)”; 3: “(Brazilian coast)”, “brazil” and “marine”; 4: “fish”, “crustacea”, “coral”, “hydrozoa”, “scyphozoa”, “polychaeta”, “ascidian” and “larva” separated by tool of access connectivity, group of organisms studied (by species and phylum), if the study mentions conservation of species or groups, area, habitat or environment of study, and any kind of mention to “MPA”. References, Methodology, Organism used, Groups, Type of Larvae/juvenile (planktonic or not) and Behavior of the adult (Benthic or pelagic, migrates or not). Numbers in bold are references that are plotted in Figure 2 and 3.

#	References	Methodology	Model organisms	Groups	Larvae/ juvenile	Adult behaviour
1	Ituarte <i>et al.</i> 2012	Genetic (mtDNA)	<i>Neohelice granulata</i> (Arthropoda)	Crustacean	planktonic	benthic, not migratory
2	Rodríguez-Rey <i>et al.</i> 2014	Genetic (mtDNA)	<i>Scyllarides brasiliensis</i> (Arthropoda)	Crustacean	planktonic	benthic, not migratory
3	Rodríguez-Rey <i>et al.</i> 2016	Genetic (mtDNA and rDNA)	<i>Johnngarthia lagostoma</i> (Arthropoda)	Crustacean	planktonic	benthic, migratory
4	Teschima <i>et al.</i> 2016	Genetics (mtDNA)	<i>Grapsus grapsus</i> (Crustacean)	Crustacean	planktonic	benthic, not migratory
5	Levy <i>et al.</i> 1998	Genetic (allozyme)	<i>Micropogonias furnieri</i> (Chordata)	Fish	planktonic	pelagic
6	Lima <i>et al.</i> 2005	Genetic (allozyme and mtDNA)	<i>Bathygobius soporator</i> (Chordata)	Fish	direct	settled benthic, not migratory
7	Santos <i>et al.</i> 2006	Genetic (mtDNA)	<i>Macrodon ancylodon</i> (Chordata)	Fish	planktonic	pelagic
8	Prodocimo <i>et al.</i> 2008	Genetic (mtDNA)	<i>Centropomus parallelus</i> (Chordata)	Fish	planktonic	pelagic
9	Vasconcellos <i>et al.</i> 2008	Genetic (Allozyme, mtDNA)	<i>Ocyurus chrysurus</i> (Chordata)	Fish	planktonic	reef-associated
10	Gomes <i>et al.</i> 2012	Genetic (mtDNA)	<i>Lutjanus purpureus</i> (Chordata)	Fish	planktonic	pelagic
11	Karl <i>et al.</i> 2012	Genetic (mtDNA microsatellite)	<i>Ginglymostoma cirratum</i> (Chordata)	Fish	no larva	reef-associated species
12	Mendonça <i>et al.</i> 2013	Genetic (mtDNA)	<i>Rhizoprionodon lalandii</i> (Chordata)	Fish	no larva	demersal and pelagic
13	Benevides <i>et al.</i> 2014	Genetic (ISSR)	<i>Epinephelus itajara</i> (Chordata)	Fish	planktonic	benthic, no migration
14	Oliveira <i>et al.</i> 2014	Genetic (mtDNA and rDNA)	<i>Centropomus undecimalis</i> (Chordata)	Fish	planktonic	free swimming
15	Watanabe <i>et al.</i> 2014	Genetic (haplotype)	<i>Anableps anableps</i> (Chordata)	Fish	direct	Estuarine
16	Rodrigues <i>et al.</i> 2014	Genetic (mtDNA)	<i>Macrodon atricauda</i> (Chordata)	Fish	planktonic	free swimming
17	Damasceno <i>et al.</i> 2015	Genetic (mtDNA)	<i>Epinephelus itajara</i> (Chordata)	Fish	planktonic	benthic, no migration
18	da Silva <i>et al.</i> 2015	Genetics (mtDNA and genomic)	<i>Ocyurus chrysurus</i> (Chordata)	Fish	planktonic	reef-associated species
19	Andrade <i>et al.</i> 2011	Genetic (mtDNA)	<i>Ototyphlonemertes</i> sp (Chordata)	Nemertea	planktonic	benthic, no migration
20	Afonso & Galletti 2007	Genetic (RAPD)	<i>Holacanthus ciliaris</i> , <i>Pomacanthus paru</i> , <i>Chaetodon</i> <i>striatus</i> (Chordata)	Fish	planktonic	reef-associated species
21	Andrade <i>et al.</i> 2003	Genetic (Isozyme)	<i>Nodulittorina lineolata</i> , <i>Littoraraia flava</i> , <i>Littoraraia</i> <i>angulifera</i> (Mollusca)	Mollusk	planktonic	rocky shores and mangroves associated species

2	Arruda <i>et al.</i> 2009	Genetic (mtDNA)	<i>Anomalocardia brasiliiana</i> (Mollusca)	Mollusk	planktonic	settled
2	Neves <i>et al.</i> 2008	Genetic (Isozyme)	<i>Siderastrea stellata Siderastrea</i> <i>radians</i> (Cnidaria)	Scleractinians	planktonic	sessile
2	Nunes <i>et al.</i> 2009	Genetic (IGR)	<i>Montastraea cavernosa</i> (Cnidaria)	Scleractinians	planktonic	sessile
4						

Table 2: Distances between localities in Brazilian EEZ (Amapá - AP, Pará - PA, Maranhão - MA, Piauí - PI, Ceará - CE, Rio Grande do Norte - RN, Paraíba - PB, Pernambuco - PE, Alagoas - AL, Sergipe - SE, Bahia - BA, Espírito Santo - ES, Rio de Janeiro - RJ, São Paulo - SP, Paraná - PR, Santa Catarina - SC and Rio Grande do Sul -RS and islands: Saint Peter and Saint Paul - SPSP, Rocas atoll -AR, Fernando de Noronha - FN , Abrolhos - AB, Trindade - TR).

Point 1 Point 2 Strait distance (Km)

RS	RS	0
RS	SC	577
RS	PR	891.5
RS	SP	1251.5
RS	RJ	1880.5
RS	ES	2394.5
RS	BA	3056.5
RS	SE	3604
RS	AL	3800
RS	PE	4008
RS	PB	4160
RS	RN	4423.5
RS	CE	4915
RS	PI	5234.5
RS	MA	5587.5
RS	PA	6188.5
RS	AP	6768.5
RS	TR	2494.07
RS	AB	1975.88
RS	FN	3657.02
RS	SPSP	4284.68
RS	AR	3617.04
SC	RS	577
SC	SC	0
SC	PR	314.5
SC	SP	674.5
SC	RJ	1303.5
SC	ES	1817.5
SC	BA	2479.5
SC	SE	3027
SC	AL	3223
SC	PE	3431
SC	PB	3583
SC	RN	3846.5

SC	CE	4338
SC	PI	4657.5
SC	MA	5010.5
SC	PA	5611.5
SC	AP	6191.5
SC	TR	2115.21
SC	AB	1434.5
SC	FN	3181.94
SC	SPSP	3815.27
SC	AR	3124.3
PR	RS	891.5
PR	SC	314.5
PR	PR	0
PR	SP	671
PR	RJ	989
PR	ES	1503
PR	BA	1854
PR	SE	2712.5
PR	AL	2908.5
PR	PE	3116.5
PR	PB	3268.5
PR	RN	3532
PR	CE	4023.5
PR	PI	4343
PR	MA	4696
PR	PA	5297
PR	AP	5877
PR	TR	2098.16
PR	AB	1262.27
PR	FN	3080.94
PR	SPSP	3704.73
PR	AR	3008.8
SP	RS	1251.5
SP	SC	674.5
SP	PR	671
SP	SP	0
SP	RJ	629
SP	ES	1143
SP	BA	1805
SP	SE	2352.5
SP	AL	2548.5
SP	PE	2756.5
SP	PB	2908.5
SP	RN	3172
SP	CE	3663.5
SP	PI	3983
SP	MA	4336
SP	PA	4937

SP	AP	5517
SP	TR	1788.83
SP	AB	1120.35
SP	FN	2801.94
SP	SPSP	3458.06
SP	AR	2745.93
RJ	RS	1880.5
RJ	SC	1303.5
RJ	PR	989
RJ	SP	629
RJ	RJ	0
RJ	ES	514
RJ	BA	1176
RJ	SE	1723.5
RJ	AL	1919.5
RJ	PE	2127.5
RJ	PB	2279.5
RJ	RN	2543
RJ	CE	3034.5
RJ	PI	3354
RJ	MA	3707
RJ	PA	4308
RJ	AP	4888
RJ	TR	1337.1
RJ	AB	633.91
RJ	FN	2367.54
RJ	SPSP	3000
RJ	AR	2299.12
ES	RS	2394.5
ES	SC	1817.5
ES	PR	1503
ES	SP	1143
ES	RJ	514
ES	ES	0
ES	BA	662
ES	SE	1209.5
ES	AL	1405.5
ES	PE	1613.5
ES	PB	1765.5
ES	RN	2029
ES	CE	2520.5
ES	PI	2840
ES	MA	3193
ES	PA	3794
ES	AP	4374
ES	TR	1105.4
ES	AB	232.91
ES	FN	1967.41

ES	SPSP	2602.66
ES	AR	1924.11
BA	RS	3056.5
BA	SC	2479.5
BA	PR	1854
BA	SP	1805
BA	RJ	1176
BA	ES	662
BA	BA	0
BA	SE	547.5
BA	AL	743.5
BA	PE	951.5
BA	PB	1103.5
BA	RN	1367
BA	CE	1858.5
BA	PI	2178
BA	MA	2531
BA	PA	3132
BA	AP	3712
BA	TR	1308.57
BA	AB	405.62
BA	FN	1336.42
BA	SPSP	1941.03
BA	AR	1279.05
SE	RS	3604
SE	SC	3027
SE	PR	2712.5
SE	SP	2352.5
SE	RJ	1723.5
SE	ES	1209.5
SE	BA	547.5
SE	SE	0
SE	AL	196
SE	PE	404
SE	PB	556
SE	RN	819.5
SE	CE	1311
SE	PI	1630.5
SE	MA	1983.5
SE	PA	2584.5
SE	AP	3164.5
SE	TR	1329.66
SE	AB	805.15
SE	FN	936.1
SE	SPSP	1576.96
SE	AR	873.07
AL	RS	3800
AL	SC	3223

AL	PR	2908.5
AL	SP	2548.5
AL	RJ	1919.5
AL	ES	1405.5
AL	BA	743.5
AL	SE	196
AL	AL	0
AL	PE	208
AL	PB	360
AL	RN	623.5
AL	CE	1115
AL	PI	1434.5
AL	MA	1787.5
AL	PA	2388.5
AL	AP	2968.5
AL	TR	1354.23
AL	AB	943.12
AL	FN	758.52
AL	SPSP	1373.78
AL	AR	690.11
PE	RS	4008
PE	SC	3431
PE	PR	3116.5
PE	SP	2756.5
PE	RJ	2127.5
PE	ES	1613.5
PE	BA	951.5
PE	SE	404
PE	AL	208
PE	PE	0
PE	PB	152
PE	RN	415.5
PE	CE	907
PE	PI	1226.5
PE	MA	1579.5
PE	PA	2180.5
PE	AP	2760.5
PE	TR	1485.88
PE	AB	1146.96
PE	FN	560.81
PE	SPSP	1188.06
PE	AR	497.41
PB	RS	4160
PB	SC	3583
PB	PR	3268.5
PB	SP	2908.5
PB	RJ	2279.5
PB	ES	1765.5

PB	BA	1103.5
PB	SE	556
PB	AL	360
PB	PE	152
PB	PB	0
PB	RN	263.5
PB	CE	755
PB	PI	1074.5
PB	MA	1427.5
PB	PA	2028.5
PB	AP	2608.5
PB	TR	1596.08
PB	AB	1290.84
PB	FN	440.64
PB	SPSP	1073.75
PB	AR	356.75
RN	RS	4423.5
RN	SC	3846.5
RN	PR	3532
RN	SP	3172
RN	RJ	2543
RN	ES	2029
RN	BA	1367
RN	SE	819.5
RN	AL	623.5
RN	PE	415.5
RN	PB	263.5
RN	RN	0
RN	CE	491.5
RN	PI	811
RN	MA	1164
RN	PA	1765
RN	AP	2345
RN	TR	1879.25
RN	AB	1552.62
RN	FN	378
RN	SPSP	975.86
RN	AR	266.6
CE	RS	4915
CE	SC	4338
CE	PR	4023.5
CE	SP	3663.5
CE	RJ	3034.5
CE	ES	2520.5
CE	BA	1858.5
CE	SE	1311
CE	AL	1115
CE	PE	907

CE	PB	755
CE	RN	491.5
CE	CE	0
CE	PI	319.5
CE	MA	672.5
CE	PA	1273.5
CE	AP	1853.5
CE	TR	2263.11
CE	AB	1984
CE	FN	709.66
CE	SPSP	1161.8
CE	AR	594.67
PI	RS	5234.5
PI	SC	4657.5
PI	PR	4343
PI	SP	3983
PI	RJ	3354
PI	ES	2840
PI	BA	2178
PI	SE	1630.5
PI	AL	1434.5
PI	PE	1226.5
PI	PB	1074.5
PI	RN	811
PI	CE	319.5
PI	PI	0
PI	MA	353
PI	PA	954
PI	AP	1534
PI	TR	2257.16
PI	AB	2259.43
PI	FN	1027.64
PI	SPSP	1427.25
PI	AR	867.76
MA	RS	5587.5
MA	SC	5010.5
MA	PR	4696
MA	SP	4336
MA	RJ	3707
MA	ES	3193
MA	BA	2531
MA	SE	1983.5
MA	AL	1787.5
MA	PE	1579.5
MA	PB	1427.5
MA	RN	1164
MA	CE	672.5
MA	PI	353

MA	MA	0
MA	PA	601
MA	AP	1181
MA	TR	2826.51
MA	AB	2535.97
MA	FN	1293
MA	SPSP	1685.03
MA	AR	1177.41
PA	RS	6188.5
PA	SC	5611.5
PA	PR	5297
PA	SP	4937
PA	RJ	4308
PA	ES	3794
PA	BA	3132
PA	SE	2584.5
PA	AL	2388.5
PA	PE	2180.5
PA	PB	2028.5
PA	RN	1765
PA	CE	1273.5
PA	PI	954
PA	MA	601
PA	PA	0
PA	AP	580
PA	TR	3347.95
PA	AB	3037.87
PA	FN	1792.77
PA	SPSP	2111.48
PA	AR	1648.29
AP	RS	6768.5
AP	SC	6191.5
AP	PR	5877
AP	SP	5517
AP	RJ	4888
AP	ES	4374
AP	BA	3712
AP	SE	3164.5
AP	AL	2968.5
AP	PE	2760.5
AP	PB	2608.5
AP	RN	2345
AP	CE	1853.5
AP	PI	1534
AP	MA	1181
AP	PA	580
AP	AP	0
AP	TR	3765.22

AP	AB	3417.42
AP	FN	2133.92
AP	SPSP	2380.85
AP	AR	2007.43
TR	RS	2494.07
TR	SC	2115.21
TR	PR	2098.16
TR	SP	1788.83
TR	RJ	1337.1
TR	ES	1105.4
TR	BA	1308.57
TR	SE	1329.66
TR	AL	1354.23
TR	PE	1485.88
TR	PB	1596.08
TR	RN	1879.25
TR	CE	2263.11
TR	PI	2257.16
TR	MA	2826.51
TR	PA	3347.95
TR	AP	3765.22
TR	TR	0
TR	AB	1047.1
TR	FN	1900.99
TR	SPSP	2373.14
TR	AR	1894.22
AB	RS	1975.88
AB	SC	1434.5
AB	PR	1262.27
AB	SP	1120.35
AB	RJ	633.91
AB	ES	232.91
AB	BA	405.62
AB	SE	805.15
AB	AL	943.12
AB	PE	1146.96
AB	PB	1290.84
AB	RN	1552.62
AB	CE	1984
AB	PI	2259.43
AB	MA	2535.97
AB	PA	3037.87
AB	AP	3417.42
AB	TR	1047.1
AB	AB	0
AB	FN	1697.72
AB	SPSP	2329.17
AB	AR	1650.19

FN	RS	3657.02
FN	SC	3181.94
FN	PR	3080.94
FN	SP	2801.94
FN	RJ	2367.54
FN	ES	1967.41
FN	BA	1336.42
FN	SE	936.1
FN	AL	758.52
FN	PE	560.81
FN	PB	440.64
FN	RN	378
FN	CE	709.66
FN	PI	1027.64
FN	MA	1293
FN	PA	1792.77
FN	AP	2133.92
FN	TR	1900.99
FN	AB	1697.72
FN	FN	0
FN	SPSP	631.72
FN	AR	156.58
SPSP	RS	4284.68
SPSP	SC	3815.27
SPSP	PR	3704.73
SPSP	SP	3458.06
SPSP	RJ	3000
SPSP	ES	2602.66
SPSP	BA	1941.03
SPSP	SE	1576.96
SPSP	AL	1373.78
SPSP	PE	1188.06
SPSP	PB	1073.75
SPSP	RN	975.86
SPSP	CE	1161.8
SPSP	PI	1427.25
SPSP	MA	1685.03
SPSP	PA	2111.48
SPSP	AP	2380.85
SPSP	TR	2373.14
SPSP	AB	2329.17
SPSP	FN	631.72
SPSP	SPSP	0
SPSP	AR	727.05
AR	RS	3617.04
AR	SC	3124.3
AR	PR	3008.8
AR	SP	2745.93

AR	RJ	2299.12
AR	ES	1924.11
AR	BA	1279.05
AR	SE	873.07
AR	AL	690.11
AR	PE	497.41
AR	PB	356.75
AR	RN	266.6
AR	CE	594.67
AR	PI	867.76
AR	MA	1177.41
AR	PA	1648.29
AR	AP	2007.43
AR	TR	1894.22
AR	AB	1650.19
AR	FN	156.58
AR	SPSP	727.05
AR	AR	0

Chapter 3: Go with the flow: connectivity among Brazilian mangroves under a genetic perspective

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ABSTRACT

Networks of Marine Protected Areas are a key strategy to conserve marine biodiversity against anthropogenic pressures, due to the maintenance of connectivity among areas. Connectivity guarantees gene flow and resilience. It is affected by oceanographic processes, especially in mangroves, where spatial discontinuity configures an island aspect and tide variation influences the persistence and recruitment of juveniles. Considering mangrove vulnerability due to its suppression that can affect gene flow, the understanding of mangrove connectivity is essential to its conservation and management. SNPs markers are one of available tools to estimate gene flow. They access more information than regular genes, providing a higher statistical power. Moreover, gene flow can be different, according to idiosyncrasies in the life history, especially in larval dispersal. Therefore, our goal was to quantify gene flow among Brazilian mangroves, considering SNPs markers and two species of mangroves' crustaceans: one with direct larval development (*Monokallipseudes schubarti*) and one with indirect (*Clibanarius vittatus*). We have sampled from Salinópolis (Pará State) to Laguna (Santa Catarina State – southern limit of mangroves in the western Atlantic Ocean). As expected, *C. vittatus* presented higher connectivity than *M. schubarti* and consequently population structure is higher for *M. schubarti*, elevating the vulnerability of *M. schubarti* in scenarios of mangrove suppression. There is no significant correlation between gene flow and population distance for both species. All mangroves have proved to be important to other mangroves, but no stepping-stones have been identified among mangrove sites. Our results show that connectivity exist among preserved and non-preserved mangroves. However, mangrove suppression

can, in the future, compromise gene flow and a study focusing on mangroves as stepping-stones has to be undertaken. There is still time to recover impacted mangroves, as long as policies change their focus to mangroves' importance concerning also gene flow.

Keywords: connectivity, mangroves, gene flow, SNP, *Clibanarius vittatus*, *Monokalliapseudes schubarti*, larval development

1. Introduction

Establishment of Marine Protected Areas (MPA) is a key strategy to conserve marine biodiversity against environmental pressures (Bensusan 2014) such as climate change, overfishing and pollution (Lotze *et al.* 2006, Halpern *et al.* 2008, 2012, 2015), and loss of marine resources (McCauley *et al.* 2015). The effectiveness of the conservation, however, is not exclusively based on individual MPAs, rather on the network of MPAs that ultimately increase their connectivity (CDB 2011). Therefore, conservation efficiency drops in isolated MPAs (Manel *et al.* 2019) and raises for MPAs better connected, resulting in higher ecosystem and populational resilience (Lockwood *et al.* 2002, Palumbi 2003, Saens-Agudelo 2009).

Quantification of connectivity among areas may be estimated by analyses of populational gene flow. It is expected that intense gene exchange leads to genetically more homogeneous populations, and lower exchange lead to isolate and differentiated populations (Hellberg 2009). There are different approaches to quantify the genetic similarity within and among populations, considering uniform frequencies of alleles and genetic variation related to evolutionary time (Hedgcock 1986), interpreted in terms of polymorphism (Ridley 2006, Hartl & Clark 2010). Genetic information can be accessed through a variety of molecular markers, each one providing particular information, such as the Amplified Fragment Length Polymorphisms (AFLPs) (Vos *et al.* 1995, Wilding *et al.* 2001, Ostrow 2004, Hoffman *et al.* 2013), like Single Nucleotide Polymorphism (SNPs).

SNPs are an effective and recent approach to population genetics applied to conservation (Morin *et al.* 2004). SNPs are formed by restriction enzymes and characterized by single nucleotide differences at the same position in a given fragment. Although SNPs use the same strategy of RFLPs, SNPs result in a much higher density of information (Vignal *et al.* 2002) because of their high genome coverage (Gardner *et al.* 2010). SNPs are bi-allelic, therefore not suitable for parenthood studies. Bias may occur during the sequencing process or by mutation (Vignal *et al.* 2002), but this can be overcome by bioinformatics analyses. SNPs have higher genotyping efficiency, data quality, genome-wide coverage, and analytical simplicity (Morin *et al.* 2004). SNPs are also more effective to assess population structure in comparison with traditional genetic markers

(Glover *et al.*, 2010) because they have codominant inheritance and provide thousands of loci for the analyses (Seeb *et al.* 2011, Provan *et al.* 2013), increasing statistical power.

Gene flow is influenced by oceanographical (*e.g.*, ocean currents) and biological processes (*e.g.*, variety of natural history and life cycle, such as pelagic species, transportation of seeds, propagules and larvae of benthic and demersal species; Barber *et al.* 2000). Indeed, the biological diversity of dispersive processes is another key component to define priority areas for conservation and management (Lockwood *et al.* 2002, Palumbi 2003, Trembl *et al.* 2008, Botsford *et al.* 2009, Christie *et al.* 2010). Theoretically, a long period in the plankton (= pelagic duration, PD) during life cycles with indirect development and planktotrophic larvae (Levin *et al.* 1987, McEdward 2000) would increase the advection distance, enhancing gene flow and connectivity (Grantham *et al.* 2003). The opposite would be expected for species with direct development, although there still have passive advection of adults or eggs migrating by rafting (Jokiel 1990), surface floating or drifting (Martel & Chia 1991), or even actively by swimming. Gene flow can decrease by local circulation and increasing larval retention, a usually common phenomenon in mangroves (Cowen *et al.* 2006, Figueiredo *et al.* 2013).

This relationship between larval development and dispersal distance has been documented for some species of fish, echinoderms, mollusks, and crustaceans (Scheltema 1971, 1975, 1978, Beckwitt 1985, Hedgecock 1986, 2007, Young *et al.* 1997, Palumbi 2003, Sotka *et al.* 2004, Cowen *et al.* 2006, Botsford *et al.* 2009, Hellberg 2009, Planes *et al.* 2009, Saenz-Agudelo *et al.* 2009, Christie *et al.* 2010, Ma *et al.* 2011). Adaptive features (Wray & Raff 1991) would influence differences in gene flow (Hedgecock 1986).

Gene flow has been also evaluated for different habitats such as coral reefs (Affonso 2004, Galetti *et al.* 2006, Afonso & Galletti 2007, Neves *et al.* 2008, Nunes *et al.* 2009, 2011, Botsford 2009, Postaire *et al.* 2017), sand beaches (Ituarte *et al.* 2012), and islands (Costagliola *et al.* 2004, Lima *et al.* 2005, Dantas *et al.* 2012, Bouzon *et al.* 2014, Rodríguez-Rey *et al.* 2014, 2016, Steinberg *et al.* 2016, Teschima *et al.* 2016). However, very few is known about mangrove connectivity, even though the major importance of this habitat concerning marine conservation (CDB 2011).

Mangroves are ecosystems at relatively low latitudes (= generally between the tropics) located between marine and terrestrial environments, related to an estuarine dynamics interacting with the tidal regime (Schaeffer-Novelli 1991, Alongi 2015). Mangroves are key areas for ecosystem services, serving as nurseries and breeding sites for crustaceans, birds, reptiles, mammals, and many other semi terrestrial and estuarine organisms (Alongi 2002, 2015; Krauss *et al.* 2008; Vaslet *et al.* 2010, Lee *et al.* 2014); protecting the coastal zone from the impact of the waves (Lee *et al.* 2014), tsunamis and cyclones (Alongi 2015); cycling organic matter (Lalli &

Parsons 2006, Duke *et al.* 2007, Amaral *et al.* 2010); providing food, wood, and medicine for traditional communities (Alongi 2015); providing the fisheries stock (Lalli & Parsons 2006, Duke *et al.* 2007, Amaral *et al.* 2010) and storing over 95% of the carbon in the soil, not in the trees, differently from terrestrial forests (Donato *et al.* 2011) and, therefore, playing an important role in controlling effects of global climate change (Lee *et al.* 2014).

Mangroves and their ecosystem services are threatened by wood exploitation for construction (Saenger *et al.* 1983), habitat loss due to urbanization processes and human settlement, mariculture, shrimp farm, and agriculture (Saenger *et al.* 1983, Richards & Friess 2015), vulnerable to oil spill (Santos *et al.* 2007) and global climate change phenomena, such as coastal erosion, reduction of silt deposition, disturbances by cyclones and hurricanes (Richards & Friess 2015). These anthropogenic pressures were intensified in the XX century, and have generated an estimated loss of 35-86% of the world's mangrove area, a pace that shall make mangroves disappear by 2107 (Duke *et al.* 2007). Besides, considering its spatial discontinuity, mangroves can be considered islands, fitting to an Island Biogeography perspective (McArthur & Wilson 1967). Thus, degradation of mangroves along the coast can certainly compromise gene flow among them.

Extensive areas in Brazil are under intensive degradation (Spalding *et al.* 2007, Magris 2010). Brazilian mangroves are distributed between 04°30'N and 28°30'S (between the states of Amapá and Santa Catarina), assigned as areas of permanent preservation in the Brazilian forest code (APP, Federal Law 12.651/2012). Human activities in mangroves, either for private, public and / or social interests, depend on legal permits, and all vegetation suppressed must be reforested. Mangroves connect Atlantic Rainforest and marine areas, forming a continuous resilient ecosystem.

Estuarine biota (including mangroves) interacts with more than one habitat, what is reflected in the differences among the life stages or feeding habits (Sheaves 2009). Some sites work as stepping-stones to distant areas either in the context of MPA networks or non-preserved areas (Roberts 1997, in McArthur & Wilson 1967). This happens for mangroves and coral reefs communities (Sheaves 2005, Mumby 2006, Mumby & Hastings 2008, Unsworth *et al.* 2008, Xavier *et al.* 2012).

We used two benthic species with different life cycles to infer connectivity among Brazilian mangroves. Benthic organisms are good models to study connectivity, and may include from sessile adults and free-living adults, including all possibilities such as vagile adults, sessile larvae, free-living larvae, etc. The hermit crab *Clibanarius vittatus* (Bosc 1802) (Crustacea, Anomura), with planktotrophic larvae (Fotheringham & Bagnall 1976), is distributed from Florida (USA) to Santa Catarina State (Brazil) (Melo 1999, Negri *et al.* 2012). Population dynamics (Turra & Leite 2000, Sandford 2003, Sant'Anna *et al.* 2008, Mantelatto *et al.* 2010), embryology and reproduction (Turra & Leite 2001, 2007, Hess & Bauer 2002), toxicology (Sant'Anna *et al.* 2012,

2014), behavioral ecology (Caine 1975, Lowery & Nelson 1988, Rittschof *et al.* 1995, Turra & Leite 2002), and spatial distribution (Turra *et al.* 2000, Sampaio *et al.* 2009, Kelly & Turner 2011) was studied for fragmented areas of the Brazilian coast.

The second species model we studied is *Monokalliapseudes schubarti* (Mañé-Garzón, 1949) (previously *Kalliapseudes schubarti*) (Crustacea, Tanaidacea), a mangrove species with direct development occurring in sandy-loam estuaries and tidal flats (Freitas-Junior *et al.*, 2013). The species is tubicolous, acting as a community builder and food source for numerous species of other crustaceans, fish, and poultry (Leite 1995, Pennafirme & Soares-Gomes 2005). It is distributed from Cabo Frio (Rio de Janeiro State) to Uruguay (Rosa-Filho & Benvenuti 1998), being a dominant species in several mangroves in southern Brazil (Leite 1995, Nucci *et al.* 2001, Amaral *et al.* 2003). Studies on *M. schubarti* are restricted to faunal composition (Pagliosa & Barbosa 2006, Rodriguez-Gallego *et al.* 2006, Amaral *et al.* 2010, Cardoso *et al.* 2011), taxonomy (Leite & Leite 1997, Larsen *et al.* 2009, Araújo-Silva & Larsen 2010), ecotoxicological tests to environmental licensing (Pennafirme & Soares-Gomes 2005, 2009, Rodriguez-Gallego *et al.* 2006), population biology (Fonseca & D'Incao 2003, Leite *et al.* 2003, Pennafirme & Soares-Gomes 2005, 2006), and spatial-temporal distribution (Leite 1995, Leite *et al.* 2003, Rosa & Bemvenit 2006, Freitas-Junior *et al.* 2013).

The goal of this study is to investigate connectivity among Brazilian mangroves based on a comparative analysis of two species with different life histories: the indirect larval development of *Clibanarius vittatus* contrasted with the direct development of *Monokalliapseudes schubarti*. We hypothesize differences in the genetic populational structure of *C. vittatus* and *M. schubarti*, with higher structured populations for *M. schubarti* due to its direct development. Finally, we intend to assess the extent of mangroves acting as stepping-stones, discussing its protection under Brazilian laws.

2. Methods

Genetic connectivity

Site selection was primarily defined for locations where both *C. vittatus* and *M. schubarti* co-occurred, but complemented by locations where only *C. vittatus* occurred because of its broader distribution (Figure 1). Specimens of *C. vittatus* were sampled by hand, identified and stored in 70% ethanol. Postmortem, organisms were taken off the shells, dissected, and gills and pleopods muscles were put into ethanol PA. Specimens of *M. schubarti* were collected with gardening shovel, storage in identified tubes, separated from mud, identified and kept in salt water for 24 hours to defecate and therefore avoid interference of alien DNA in the extractions. After that period, organisms were fixed in ethanol PA. *C. vittatus* DNA was extracted by the PureLink® Genomic

DNA Kits (Invitrogen – Life Technologies), according to the protocol applied for mammal tissue extraction, and *M. schubarti* DNA was extracted with ammonium acetate protocol and overnight digestion. DNA was quantified using Qubit. SNPs of both species were identified by the 2b-RAD protocol (Wang *et al.* 2012). Libraries were dual-indexed during library preparation, all libraries were pooled for single-end sequencing with the NextSeq® 500/550 High Output Kit v2 (75 cycles). Target fragments of ~170 base pairs were purified with AMPure (Agencourt) by adding 0.9x vol from the library (~90 ul), mixing with the pipette, incubating for 2 minutes on the stand and putting in the magnetic field for 2 minutes. Supernatant was transferred to a new tube, where it was added 200 ul of ethanol 80%. Supernatant was removed and the content dried on the countertop off the magnetic board for 5 minutes with 20 ul of H₂O MiliQ. Libraries were sequenced using Illumina NextSeq sequencer. Output data was treated using the version 2.1 of the pipeline (Wang *et. al.* 2012). Quality metrics, prior and after quality filtering, were generated using the fastQC software. Reads were truncated at base 36 (TruncateFastq.pl), and reads with more than 18 bases with quality below 20 were removed from analysis (QualFilterFastq.pl). Adaptors were removed by using bbdut software. De novo assembly process was conducted separately for each species, samples with the biggest sequenced library, for each geographical site, were selected as starting point for this assembly (BuildRef.pl). Alignment was conducted using the SHRiMP aligner with the command line (gmap --qv-offset 33 -Q --strata -o 3 -N 8), multi-mappers or weak hit reads (alignments spanning less than 32bp or 30 matching bases) removed from the analysis (SamFilter.pl). SNPs with at least 20x coverage were genotyped and considered heterozygous if MAF $\geq$ 25% (NFGenotyper.pl), and all samples of each species were combined into a genotype table (CombineGenotypes.pl). The last filtering steps removed SNPs non-polymorphic, than 2 different genotypes (PolyFilter.pl), samples with low coverage, less than 1,500 SNPs for *C. vittatus* and 200 for *M. schubarti* (LowcovSampleFilter.pl), SNPs shared in too few samples, 30 samples for both species (MDFilter.pl), removal of repetitive sites identified by an excessive number of SNPs, more than 3 SNPs per site (RepTagFilter.pl), finally a representative SNP was selected for each site (OneSNPPerTag.pl). R programming language was used to track the quality metrics of each sample and generate the plots that allowed the analysis of a range of thresholds for each individual filtering step to generate the genotype tables. To understand population structures, we calculated heterozygosity (HT) and F_{IT} of each location for both species considering the parametrization of Lemes & Otto (2017) for SNP markers (in R). To quantify genetic connectivity we used the genet.dist (package hierfstat, R) to generate the pairwise F_{ST} among all populations. Significance levels were evaluated considering variances between the results and the value of the whole population. We conduct hierarchical cluster analysis with multiscale bootstrap with number of bootstrap 1,000 to verify the grouping of localities, according to pairwise F_{ST} . Mantel test was

performed with genetic distances and linear geographical coastline distances (Supplemental Information 1, “Coastline_Distance”) in order to understand whether there is relationship between these factors.

Figure 1: Localities where A: *Clibanarius vittatus* and B: *Monokalliapseudes schubarti* were sampled (1: Laguna, SC; 2: Florianópolis, SC; 3: Paranaguá, PR; 4: Cananeia, SP; 5: São Sebastião, SP; 6: Paraty, RJ; 7: Mangaratiba, RJ; 8: Vitória, ES; 9: Natal, RN; 10: Galinhos, RN; 11: Fortaleza, CE; 12: Salinópolis, PA).

3. Results

Clibanarius vittatus – Total Heterozygosity for all populations (0.0420) was lower than all subpopulations (except for Pr 0.0416), and FIT for all localities ~ 1 (Table 1). There is no correlation between distance and connectivity (Mantel statistic $r = 0.09149$, $p = 0.35964$; Figure 2). There were basically two groups divided at a shared zone between the coast of the states of São Paulo and Rio de Janeiro, one group formed by São Sebastião northwards (Vt, Na, Ga, Ft); and the second with Pt, Mg and the southern mangroves (Fl, Pr, Cn) (Figure 3A). Pairwise F_{ST} analysis shows that Ss, Mg, Vt, Na, Ga, Ft may be considered isolated mangroves, even though there is significant gene flow among these localities, and Ft is the most isolated (Table 2). Pr is the most connected mangrove (Table 2); Fl is highly connected to Pr ($F_{ST}=0.077$), Cn ($F_{ST}=0.130$), SI ($F_{ST}=0.189$, also connected to Pt, $F_{ST}=0.154$) (Table 2).

Monokalliapseudes schubarti – Total Heterozygosity for all populations (0.1495) was lower than Fl (0.19) and Cn (0.15), and FIT for all localities ~ 1 (Table 1). Although not significant, Fl is the most connected mangrove and Pt is the most isolated, with all pairwise $F_{ST} < 0.301$ (Table 3). Cluster analysis resulted in a significant structure considering populations of both species in two major groups, [Fl, Cn X Pt, Lg, Ss] (Figure 3B). There is also no correlation between distance and connectivity among the mangroves (Mantel statistic $r: 0.1709$, $p = 0.3$, Figure 2).

Figure2: Relationship between Pairwise FST vs. distances between mangroves (in Km) for (A) *Clibanarius vittatus* and (B) *Monokalliapseudes schubarti*. Mantel test result is significant considering bootstrap repeated 1,000 times A: $r=0.09149$, $p=0.35964$; B: $B=0.1709$, $p=0.3$.

Table 1: Localities and basic descriptors for *Clibanarius vittatus* and *Monokalliapseudes schubarti*. N = number of individuals; HT = heterozygosity; and FIT per locality.

Localities					<i>C. vittatus</i>		<i>M. schubarti</i>			
	Mangroves	Latitude	Longitude	N	HT	Fit	N	HT	Fit	
1	Laguna (SC)	Lg	28.50	48.76			13	0.0563	0.9989	
2	Florianópolis (SC)	Fl	27.58	48.50	22	0.0488	0.9997	21	0.1955	0.9963
3	Paranaguá (PR)	Pr	25.50	48.50	17	0.0416	0.9997			
4	Cananeia (SP)	Cn	25.00	47.92	21	0.0461	0.9997	22	0.1575	0.9970
5	São Sebastião (SP)	Ss	23.81	45.40	24	0.0557	0.9997	11	0.0852	0.9984
6	Paraty (RJ)	Pt	23.21	44.71	27	0.0458	0.9997	10	0.0144	0.9997
7	Mangaratiba (RJ)	Mg	22.90	43.87	22	0.0519	0.9997	18	0.0554	0.9989
8	Vitória (ES)	Vt	20.30	40.29	21	0.0583	0.9996			
9	Natal (RN)	Na	5.75	35.20	24	0.0582	0.9996			
10	Galinhos (RN)	Ga	5.10	36.26	13	0.0554	0.9997			
11	Fortaleza (CE)	Ft	3.69	38.59	27	0.0605	0.9996			
12	Salinópolis (PA)	Sl	0.59	47.32	26	0.0510	0.9997			
TOTAL					244	0.0419		95	0.1495	

Table 2. Pairwise genetic differentiation (F_{ST}) among Brazilian mangrove populations of *Clibanarius vittatus*. Bold means significant results according to the Chi Square test.

	Fl	Pr	Cn	Ss	Pt	Mg	Vt	Na	Ga	Ft
Pr	0.07768417									
Cn	0.1306079	0.04531701								
Ss	0.2459844	0.1606935	0.2136172							
Pt	0.1274278	0.04213693	0.09506065	0.2104371						
Mg	0.2007987	0.1155078	0.1684316	0.283808	0.1652515					
Vt	0.2759105	0.1906196	0.2435433	0.3589198	0.2403632	0.3137342				
Na	0.2750175	0.1897266	0.2426503	0.3580268	0.2394702	0.3128412	0.3879529			
Ga	0.2422644	0.1569735	0.2098972	0.3252737	0.2067171	0.280088	0.3551998	0.3543068		
Ft	0.3026746	0.2173837	0.2703074	0.3856839	0.2671274	0.3404983	0.41561	0.414717	0.3819639	
Sl	0.189693	0.1044021	0.1573258	0.2727023	0.1541457	0.2275166	0.3026284	0.3017354	0.2689823	0.3293925

Table 3. Pairwise genetic differentiation (F_{ST}) among Brazilian mangrove populations of *Monokalliapseudes schubarti*. Bold means significant results according to the Chi Square test.

	Lg	Fl	Cn	Ss	Pt
Fl	0.1626601				
Cn	0.2891022	0.1737533			
Ss	0.5294669	0.0666114	0.1930535		
Pt	0.7647004	0.3018449	0.4282871	0.6686517	
Mg	0.6284445	0.165589	0.2920312	0.5323958	0.7676294

F_{ST} among localities are different for both species, indicating that populations are differently structured. Comparing values of pairwise F_{ST} among mangroves with co-occurrence of both species (Fl, Cn, Ss, Pt, Mg), populations of *M. schubarti* are less connected (have higher values of pairwise F_{ST}) than *C. vittatus* (Mantel statistic $r=0.08099$, $p=0.0009$ Figure 4), although these results are not significant ($p=0.41667$).

Figure 3: Cluster dendrogram (Ward. D method) with Euclidean distances of pairwise FST: A. *Clibanarius vitattus* with two groups (Ss, Vt, Na, Ga, Ft X Fl, Pr, Cn, Pt, Mg). B. *Monokalliapseudes schubarti* with two groups (Fl, Cn X Lg, Ss, Pt). Red values are AU (Approximately Unbiased) p -values, and green values are BP (Bootstrap Probability) values. Clusters with AU larger than 95% are highlighted by red circles.

Figure 4: Relationship between pairwise FST of *Clibanarius vittatus* and *Monokalliapseudes schubarti* for mangroves where they co-occur (Fl, Cn, Ss, Pt, Mg). Mantel test result is $r = 0.08099$, $p = 0.0009$, significant considering bootstrap of repeated 1,000 times.

4. Discussion

This is the first study on Brazilian mangrove connectivity approaching different larval development and dispersal capabilities, as well as using SNP markers. Previous studies were based on mangrove crabs with planktotrophic larvae, such as *Ucides cordatus* (Oliveira-Neto *et al.* 2007; Britto *et al.* 2018) and *Uca uruguayensis* (Laurenzano *et al.* 2012). Gene flow estimated for *U. cordatus* among all localities (Britto *et al.* 2018, highest FST = 0.02, for Cananeia/Fortaleza) was higher than those *C. vittatus* (FST = 0.270 for the same localities). This difference may be explained by intrinsic variations of the larval biology of the species (Oliveira-Neto *et al.* 2007) and by the number and type of markers used for estimation (one gene/marker for Oliveira-Neto *et al.* 2007 and Laurenzano *et al.* 2012; 9 microsatellites for Britto *et al.* 2018; 3,854 SNPs herein).

Previous approaches (Oliveira-Neto *et al.* 2007; Laurenzano *et al.* 2012; Britto *et al.* 2018) did not find correlation between geographic distance and genetic variability for species with high dispersive planktotrophic larvae. In our results, surprisingly, Salinópolis is more connected to localities in southern/southeastern Brazil (Florianópolis, FST = 0.1889; Paranaguá, FST = 0.104; Cananeia, FST = 0.157; and Paraty) than to closer localities in northeastern Brazil (Natal, FST = 0.301; Galinhos, FST = 0.268; and Fortaleza, FST = 0.329). Oceanographic processes may be interfering in this high connectivity. Considering larval duration of ~57 days (Young & Hazlett 1978), and the distance between Salinópolis and Florianópolis over 4,700 km along a straight

coastline, dispersal process probably occurred mangrove by mangrove, in a stepping-stone model, with events dependent of marine currents.

Larvae and adults of *C. vittatus* have different abilities to respond to salinity and temperature. The larvae present high mortality due to salinity and temperature variation (Young & Hazlett 1978, Young 1979), affects their development (Kircher 1967), osmoregulation (Young 1979), growth (Lowery & Nelson 1988), and recruitment on estuaries (Kelly & Turner 2011). On the other hand, adults of *C. vittatus* can migrate among estuaries (Hazlett 1981), selecting habitats with fine mud (such as mangroves), seagrass beds (Lowery & Nelson 1988), and rocky shores (Kelly & Turner 2011) to live. Still, *C. vittatus* is cosmopolitan (Mello 1999), with adults tolerant to variation in temperature, salinity, and water level (Fotheringham 1975), what shows a high plasticity to environmental conditions, after settlement, which could increase dispersal potential and rates.

Clibanarius vittatus presented higher differentiation among populations than within populations, resulting in two structured clusters: I: Ss/Ga/Ft/Vt/Na and II: Fl/Mg/Pr/Cn/Pt (Figure 3A). This pattern corroborates the definitions of provinces for decapod distributions, corresponding to the Brazilian Province and II as the Argentinian Province, (Boschi 2000). The separation of these two regions could be justified by a mechanism of larval filter in the cold-water upwelling area in Cabo Frio (Silveira *et al.* 2000). However, this does not explain the connection between Ss and Northeast and North mangroves. Pt and Mg mangroves are inside protected bays and the geographic position of Ss is more open to the sea (even though a small part of SS coast is protected by the presence of Ilhabela municipality across the channel). It would be possible that during the last glaciation period, when sea level fluctuated 130 m (Lambeck *et al.* 2002). In Southwestern Atlantic, the oscillation was of circa 60m, which influenced connections among populations separated by barriers (Ludt & Rocha 2015). This could increase Ss exposure to the action of marine currents, *viz.* the Brazilian Current flowing southwards (Tait 1998), stronger at the summer in the southern hemisphere (Rezende *et al.* 2011), eventually connecting populations from Na, Vt, Ss, and the North Brazil Current (NBC) flowing northwards (Tait 1998), always intense (Rezende *et al.* 2011), connecting populations from Na, Ga, Ft, Sa. Still, from the South Pole, there is the Falkland Current (Tait 1998), which can be intensified during the winter of the southern hemisphere (D'Agostini *et al.* 2015).

Contrarily, the low connectivity of *M. schubarti* is consistent with other estuarine species with direct development resulting in high genetic variability and low gene flow, such as for the tanaidaceans *Mesokalliapseudes macsweenyi* (Drumm & Kreiser 2012) and *Zeuxo holdichi* (Larsen *et al.* 2014). Individuals of *M. schubarti* live inside U-shaped tubes of fine mud, up to 15 cm deep (Bemvenuti 1987, Capitoli *et al.* 1978). Females of the species carry juveniles inside the marsupium,

decreasing its dispersal potential (Mané-Garzón, 1949). Besides, mangroves are environments that are susceptible to unique tidal regimes, what affects larval retention differently for each mangrove. In fact, mangrove habitat discontinuity promotes a barrier to gene flow and isolates-by-distance populations of *Avicenia marina*, whose propagule dispersal is limited by the gaps of stepping-stones presences (Binks *et al.* 2018).

However, some species with limited dispersal capabilities may have long-distance dispersal mediated by rafting on floating substrata such as algae (*e.g.*, *Sargassum* sp.) or mangrove propagules, like in *Zeuxo exsargasso*, with no genetic divergence throughout its distribution (Bamber 2012, Larsen *et al.* 2014). In such cases, the action of marine currents is evident, forming convergence zones of multiple rafts increasing gene flow (Thiel & Haye 2006).

Monokalliapseudes schubarti populations have a more restricted distribution range than *C. vittatus*, but they also presented higher differentiation among populations than within populations, clustered in two major groups, Fl, Cn (mangroves in islands) X Pt, Lg, Ss (Figure 3B). This pattern and the genetic similarity of Laguna with São Sebastião and Paraty could be due to intense coastal navigation, both for touristic and of artisanal fisheries. On the other hand, the post-glacial marine transgression, elevated sea-level, submerging Paranaguá, Cananéia and Florianópolis (Angulo & Lessa 1997), which could have increased gene flow among these three areas, isolating Fl and Cn.

The species *M. schubarti* coherently exhibit patterns with the fact that mangroves are habitats dependent of directly local circulation. Genetic similarity between the islands' populations could be related to occasional coastal upwelling, which can be intensified by the estuarine outflow contribution, changing water density (Santos 2009). Coastal upwelling is observed during the summer in South Equator from Santa Marta (Laguna) to Santa Catarina Island (Florianópolis) (Pereira *et al.* 2008) and from Cananeia to Cabo Frio (Mesquita *et al.* 1978). During the winter, N-E coastal circulation is forced by successive strong and frequent wind pulses southwards with estuarine outflow, affecting the direction and intensity of coastal waters, changing horizontal stratification, and promoting upwelling (Santos 2009). Therefore, differences in estuarine outflow and saltwater and estuarine water balance can affect coastal circulation and, therefore, dispersal and connectivity rates.

The relationship between estuarine and coastal circulations is complex. Recruitment of *C. vittatus* is related to reproductive activity, which, by itself, is dependent of shell availability (Sant'Anna *et al.* 2008). On the other hand, the species *M. schubarti* presents a continuous reproductive activity as a strategy to the small number of eggs produced (Lewis 1998, Leite *et al.* 2008). However, changes in the circulation related to seasonality could influence dispersal and recruitment more significantly than other features, such as the number of larvae released.

Our data shows that connectivity among the Brazilian mangroves is significantly different for organisms with direct (*M. schubarti*) and indirect (*C. vittatus*) development. Indeed, some general studies already described divergences concerning gene flow and isolation, showing that there is no regular pattern (see Suppl. Mat. 1 for references and species).

Finally, our results proved that all mangroves are important in the connectivity net, especially considering the creation of restricted areas of conservation. One of them, São Sebastião, however, seems to work as a stepping-stone, considering its relationships with other mangroves, and its geographic position and, therefore, it is crucial to be considered in conservation networks.

5. Conclusion

Brazilian mangroves are at risk. It is evident the importance of using more than one biological model to infer connectivity among marine areas, especially considering mangroves, because of their particular dynamics. We sampled in areas with variable environmental quality and conditions, registering impacted mangroves such as Florianópolis with rubbles; Paranaguá with oil outcome from harbor activities; São Sebastião (Araçá Bay) under anthropogenic pressure of growing urbanization (including its harbor); Paraty and Mangaratiba with sewage outlet over the mangrove area; and Vitoria and Natal with mangroves reduced to a few trees also with sewage outlet. On the other hand, Laguna, Galinhos, Fortaleza, and Salinópolis are almost pristine sites, and exhibiting an amazing variety of formations and structures. All this data reinforces the need to protect well preserved mangroves and guarantee reforestation and protection for those already degraded. Reforestation projects in southern Brazilian mangroves showed that fauna and flora compositions are able to be recovered over years (Rovai *et al.* 2012, Oortman 2014, Sanches *et al. in prep.*). However, mangrove functionality depends on the removal of stressors (Oortman 2014), which includes guarantee connectivity among mangroves.

As we see in our results, there is connectivity among mangroves preserved and not preserved. This is of paramount importance to recover impacted mangroves, as long as policies change their focus to the importance of the mangroves network. One issue that has to be further investigated is how many mangrove areas are working as stepping stones for the network, like São Sebastião, for instance, and therefore are of ultimate importance to be preserved.

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8. Supplementary Material 1: List of papers that worked with differences in gene flow due to larval development

Reference	Species	Phylum	Min PLD	type of larvae	Pattern of gene flow PhiST
Kelly & Palumbi 2010	<i>Phragmatopoma californica</i>	Annelida	18	pelagic	0.01978
	<i>Balanus glandula</i>	Arthropoda	14	pelagic	NA
	<i>Cancer antennarius</i>	Arthropoda	60	pelagic	NA
	<i>Cancer productus</i>	Arthropoda	100	pelagic	NA
	<i>Emerita analoga</i>	Arthropoda	70	pelagic	neg 0.0151
	<i>Hemigrapsus nudus</i>	Arthropoda	30	pelagic	0.438
	<i>Idotea cf. stenops</i>	Arthropoda	0	non-pelagic	0.861
	<i>Idotea kirchanskii</i>	Arthropoda	0	non-pelagic	0.145
	<i>Idotea montereyensis</i>	Arthropoda	0	non-pelagic	0.087
	<i>Lophopanopeus bellus</i>	Arthropoda	30	pelagic	0.00727
	<i>Pachygrapsus crassipes</i>	Arthropoda	30	pelagic	NA
	<i>Pagurus granosimanus</i>	Arthropoda	70	pelagic	0.103
	<i>Pagurus hirsutiusculus</i>	Arthropoda	67	pelagic	0.357
	<i>Pagurus samuelis</i>	Arthropoda	51	pelagic	0.104
	<i>Pagurus venturensis</i>	Arthropoda	50	pelagic	0.252
	<i>Pandalus platyceros</i>	Arthropoda	150	pelagic	neg 0.0062
	<i>Petrolisthes cinctipes</i>	Arthropoda	30	pelagic	0.01456
	<i>Pollicipes polymerus</i>	Arthropoda	42	pelagic	0.034
	<i>Pugettia gracilis</i>	Arthropoda	120	pelagic	0.00252
	<i>Semibalanus cariosus</i>	Arthropoda	90	pelagic	neg 0.0006
	<i>Tetraclita squamosa</i>	Arthropoda	20	pelagic	0.011
	<i>Tigriopus californicus</i>	Arthropoda	28	pelagic	0.98
	<i>Anthopleura elegantissima</i>	Cnidaria	30	pelagic	0
	<i>Cucumaria pseudocurata</i>	Echinodermata	0	non-pelagic	0.5
	<i>Parastichopus parvimensis</i>	Echinodermata	50	pelagic	0.0001
	<i>Pisaster giganteus</i>	Echinodermata	60	pelagic	neg 0.0261
	<i>Pisaster ochraceus</i>	Echinodermata	76	pelagic	NA
	<i>Pycnopodia helianthoides</i>	Echinodermata	70	pelagic	0.137
	<i>Strongylocentrotus franciscanus</i>	Echinodermata	70	pelagic	0.009
	<i>Acanthina spirata</i>	Mollusca	0	non-pelagic	0.5
	<i>Alderia modesta</i>	Mollusca	35	pelagic	0.00838
	<i>Alderia willowi</i>	Mollusca	2	both	0.01197
	<i>Aplysia californica</i>	Mollusca	30	pelagic	0.0084
	<i>Calliostoma ligatum</i>	Mollusca	7	pelagic	neg 0.009
	<i>Cyanoplax dentiens</i>	Mollusca	6	pelagic	0.039
	<i>Fissurella volcano</i>	Mollusca	4	pelagic	0.01089
	<i>Haliotis rufescens</i>	Mollusca	4	pelagic	0.007
	<i>Katharina tunicata</i>	Mollusca	7	pelagic	0.02932
	<i>Lottia austrodigitalis</i>	Mollusca	5	pelagic	neg 0.038
	<i>Lottia digitalis</i>	Mollusca	5	pelagic	0.611
	<i>Lottia new sp. cf pelta</i>	Mollusca	5	pelagic	neg 0.033
	<i>Lottia paradigitalis</i>	Mollusca	5	pelagic	0.00055
	<i>Lottia pelta</i>	Mollusca	5	pelagic	0.561
	<i>Macoma nasuta</i>	Mollusca	35	pelagic	0.01147
	<i>Mytilus californianus</i>	Mollusca	9	pelagic	neg 0.001
	<i>Nucella emarginata</i>	Mollusca	0	non-pelagic	0.5
	<i>Nucella ostrina</i>	Mollusca	0	non-pelagic	0.2
	<i>Olivella biplicata</i>	Mollusca	1	non-pelagic	0.00621
	<i>Lirabuccinum (Searlesia) dira</i>	Mollusca	0	non-pelagic	1
	<i>Tegula (Chlorostoma) funebris</i>	Mollusca	5	pelagic	0.01674

FINAL CONSIDERATIONS

I conclude my thesis with the understanding that connectivity is an under-investigated issue in Brazil, with fragmentary applications to design MPAs. Evidently, the lack of connectivity in the current MPA system neither imply that existing MPAs do not contribute to conservation nor connectivity supersede other ecological criteria used for MPA designation.

However, among available data, there are differences in the connectivity network and the location of areas with high gene flow within that emphasize the need of specific studies designed to fulfill the knowledge gaps, ensuring efficient managing plans. Considering Brazilian EEZ linear configuration, an island model would not necessarily be the best choice, and stepping-stones would work better in a network of MPAs. Brazilian data is clearly deficient to have a better picture of our conservation efficiency, regarding studies from basic taxonomy and natural history to evaluations of connectivity among populations and MPAs.

Still, considering Brazilian mangroves, it is evident the importance of using more than one biological model to infer connectivity among marine areas, especially considering mangroves, because of their particular dynamics. We sampled in areas with variable environmental quality and conditions, registering impacted mangroves and pristine sites, and exhibiting an amazing variety of formations and structures. There is connectivity among mangroves preserved and not preserved. This is of paramount importance to recover impacted mangroves, as long as policies change their focus to the importance of the mangroves network. One issue that has to be further investigated is how many mangrove areas are working as stepping stones for the network, like São Sebastião, for instance, and therefore are of ultimate importance to be preserved.

All this data reinforces the need to protect well preserved mangroves and guarantee reforestation and protection for those already degraded, which includes guarantee connectivity among mangroves. Finally, our results reinforce the need to create new MPAs taking into account the distance among areas, and points out to challenges and opportunities for the implementation of marine and coastal MPA that will effectively contribute to the conservation efforts at local and broader scales.

Moving forward, I call for future research efforts that focus on connectivity conservation at various scales, and policy actions enhancing integration of scientific information in the decision-making process, within an adaptive learning process. In fact, in times of apps that call cabs, pay checks and share complex information, researchers should be involved in platforms of sharing research plannings and data, considering all parts of knowledge in order to generate more effective effort towards conservation policies.