Genetic and Demographic Connectivity in Brazilian Reef Environments

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Chapter 7
Genetic and Demographic Connectivity in Brazilian Reef Environments

Douglas F. M. Gherardi, Katia C. C. Capel, Cesar A. M. M. Cordeiro, Linda Eggertsen, Clarissa A. K. Endo, Luciana S. Lima, Tito C. M. Lotufo, and Carla Zilberberg

D. F. M. Gherardi (✉)
Laboratory of Ocean and Atmosphere Studies (LOA), Earth Observation and Geoinformatics Division, National Institute for Space Research (INPE),
São José dos Campos, São Paulo, Brazil
e-mail: douglas.gherardi@inpe.br

K. C. C. Capel
Institute of Biodiversity and Sustaintability (NUPEM), Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil

Departamento de Genética e Evolução, Universidade Federal de São Carlos,
São Carlos, Brazil

Centro de Biologia Marinha, Universidade de São Paulo, São Sebastião, Brazil

Cesar A. M. M. Cordeiro
Laboratory of Environmental Sciences, Universidade Estadual do Norte Fluminense,
Campos dos Goytacazes, RJ, Brazil

L. Eggertsen
Hawaiian Institute of Marine Biology, University of Hawaii at Manoa,
Hawaii, Kaneohe, USA

Reef Systems and Conservation Lab, Universidade Federal de Fluminense, Niteroi, Brazil

C. A. K. Endo
National Institute for Space Research (INPE), São José dos Campos, São Paulo, Brazil

Åkerblå AS, Bergen, Norway

L. S. Lima
National Institute for Space Research (INPE), São José dos Campos, São Paulo, Brazil

T. C. M. Lotufo
Instituto Oceanográfico, Universidade de São Paulo, São Paulo, Brazil

Instituto Coral Vivo, Arraial d’Ajuda, Brazil

C. Zilberberg
Institute of Biodiversity and Sustaintability (NUPEM), Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil

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Abstract Biological entities present multiple forms of connections between them in space and time, and at various scales. These links are established through the exchange of matter, energy, or information and produce different forms of connectivity. In this chapter we focus on three of these forms that were studied on Brazilian coral reefs. A first section deals with the exchange of information through genetic connectivity within an evolutionary timescale. We discuss the relevance of biogeographical barriers and marine currents to genetically structure populations of coral and fish species along the Brazilian coast. The second section concerns demographic connectivity within the biophysical context, on an ecological timescale. Current biophysical modeling tools were used to infer connectivity for fish and lobster species shedding light on the most relevant involved processes. In the third section, the focus is shifted to the ecological connectivity between coral reefs and adjacent habitats, involving mainly the movement of individuals. These migrations may be related to ontogenetic processes or foraging behavior. For Brazilian reef fish species, mangroves and estuaries are particularly important, and vertical and shore to shelf migrations are also discussed. Finally, we highlight that all these forms of connectivity must be considered within a sound conservation strategy. We hope this chapter not only summarizes the research on connectivity along Brazilian coral reefs, but also pinpoint questions that must be urgently addressed to produce a more complete picture of the functioning of these systems.

Keywords Demographic connectivity · Sea anemones · Biophysical · Microsatellites

7.1 Introduction

All living things and all ecosystems have multiple forms of connections that may involve the exchange of energy, matter or genetic information. In the marine realm, connectivity is a more complicated and less studied subject, in comparison with terrestrial ecosystems (Virtanen et al. 2020). Additionally, connectivity has multiple biological meanings, and all these concepts involve some sort of linkage between different elements across space and/or time. Connectivity patterns and processes interplay with many other aspects of an ecosystems' structure and function. However, the diversity of meanings and uses of "connectivity" carries a potential for confusion and misconceptions (Selkoe et al. 2016). Hence, we need to clearly define the core concepts used throughout this chapter.

Connectivity is at the core of the population definition and delimitation (Harwood 2009). In terms of population biology and conservation, it is essential to understand how dispersal affects population size in addition to its genetic or phenotypic variability and determine the *population connectivity*. Conversely, *Demographic connectivity* is the actual exchange of individuals between populations through dispersal, and as such is one of the most relevant types of connectivity. Demographic connectivity contributes to the demographic structure, and its determination is more complex than assessing a single process, involving the knowledge of many population parameters, such as death, birth, and migration (Lowe and Allendorf 2010).

Determining the demographic connectivity of a species is always challenging, as it demands information not easily obtainable. Hence, alternative approaches that shed light on population connectivity are more commonly used to describe patterns or test population connectivity hypotheses. The most direct and frequently used method worldwide in the marine realm involves the use of population genetics to infer patterns of gene flow between populations and may be defined as "the degree to which gene flow affects evolutionary processes within populations" (Lowe and Allendorf 2010), which can be estimated based on metrics, such as fixation indexes or from Bayesian structure analyses. As the name suggests, *genetic connectivity* is the main mechanism behind the genetic differentiation of populations of species living in different areas. Organism's dispersal is treated within this approach over evolutionary time scales (centuries to millennia) and is generally associated with the formation of broad biogeographic patterns that could, eventually, lead to populations developing unique genetic characteristics.

Demographic connectivity, on the other hand, focuses on processes within ecological timescales (days to decades), involving eggs and larval dispersal. However, juveniles and adults should also be considered in those processes, assuming that recruits will reproduce and, therefore, contribute to the gene pool at the newly settled location.

The exchange of individuals among marine populations is mainly governed by their interaction with the flow field and its different scales of motion. These are the fundamental drivers of larval dispersal, which is the reason why this process is better described in a biophysical context (Cowen and Sponaugle 2009). Connectivity integrates biological characteristics of organisms and physical mechanisms acting along their dispersal trajectory that need to be considered and are associated with reproduction. This may include reproductive aggregations, lifetime offspring production, growth, survival of lethal temperatures and larval behavior, such as active swimming, diel vertical movement (DVM) and pelagic larval duration (PLD).

Brooding corals, like *Favia gravida*, tend to recruit close to their parent colony (Gleason and Hofmann 2011), while the lecithotrophic larvae of the broadcast spawners *Mussismilia hispida* may have a longer PLD of up to 10 days (Pires et al. 2016). Spending more time in the plankton has the potential to increase the dispersion distance of eggs and larvae and, consequently, the chance to colonize new areas. All these processes are influenced by horizontal and vertical water velocities (advection and diffusion), temperature, salinity, and their variability at different spatial and temporal scales. Broadly speaking, water flow controls larval dispersal according to the balance between its mean and fluctuating components. The mean flow component is typically of large spatial scales, whereas the turbulent mesoscale (10–100 km) is related to the time of fluctuating flow. The former influences particles by advection and the latter by turbulent diffusive transport (Bauer et al. 1998).

The adaptive processes of marine organisms tend to respond to the mean ocean flow, but recruitment variability may reflect the stochastic component of the environment such as transient atmospheric systems, eddy formation and internal waves

(Sundby and Kristiansen 2015). This is generally the case for near-shore populations, which are submitted to stochastic variability with a characteristic timescale of 2–5 days, consequently, larval transport in coastal areas tend to be a spatially heterogeneous process (Siegel et al. 2008).

There is another form of connectivity involving the transfer or movement of individuals between different habitats. Processes like migration at the individual scale, and not only at the populational level, are of major interest for conservation. This type of connectivity highlights the importance of different habitats in the maintenance of the biodiversity and is especially useful for conservation planning, as policies often focus on a single habitat.

Reef fish metapopulation dynamics (see Box 7.1) are being studied using a diverse suite of dispersion models and continued refinements of genetic tools. Also important is the multidisciplinary integration of behavioral studies and tagging (natural and artificial) methods for pelagic larvae (Mora and Sale 2002; Sale and Kritzer 2003). At the end of the day, the dispersion of individuals tends to strike a balance between local extinction and the colonization of empty areas, which can be occupied or reoccupied over time.

The real challenge lies in determining whether metapopulation structure exists among individuals and, if so, what form it takes. Not surprisingly, these are the least understood aspects of coral reef fish ecology. Behavioral reef fish studies indicate that larvae are not inanimate particles, but rather have quite developed behavioral and sensory capabilities (Leis 2007; Paris et al. 2007; Putman 2016). These capabilities include active swimming of larvae, which can influence both the competence to recruit back to the original population and/or to another population (Figueiredo et al. 2013).

For Brazilian coral reefs, connectivity is particularly relevant because of its discontinuous distribution along the shelf (see Chap. 3). Hence, we intend to focus on these three different forms of connectivity, and how they uncover patterns and processes relevant for Brazilian coral communities. We also want to show how these concepts may in fact be related to each other and contribute to a better assessment of coral reefs, highlighting that this knowledge is essential in planning effective conservation strategies.

Box 7.1: Metapopulation

Metapopulation represents the assemblage of discrete local populations in the same region that may become connected by different processes (e.g. migration, colonization, and extinction), forming a regional group of connected populations of a species (Levins 1970). It results from complex processes at local and regional scales. Local populations may increase or decrease as environmental conditions fluctuate or when submitted to a stochastic event. These may affect their growth and establishment as a spatial arrangement of habitat patches at a regional scale. In fact, population persistence to local or regional extinction may depend on spatial-temporal changes in connectivity. Therefore, levels of connectivity among local populations defines the vulnerability to local extinction (Hanski and Gilpin 1991).

The metapopulation structure is determined by the spatial arrangement of local populations', considering the species traits (Hanski 1998; van Nouhuys 2016). Distinct local populations must be identifiable, and organisms generally need to remain within those subpopulations, but there must be some mechanism for interpopulation dispersal. Additionally, in a metapopulation, the dynamics of local populations are determined by local demography and self-recruitment. It is difficult to evaluate the local population dynamics by itself, since the dynamics can be modified by replenishment from external sources (nearby populations) (Fig. 7.1).

The importance of the metapopulation concept to conservation is that it identifies a group of structured populations that can persist over time, isolated by inadequate areas to settle, in addition to the recognition of areas that are source or sink of migrants.

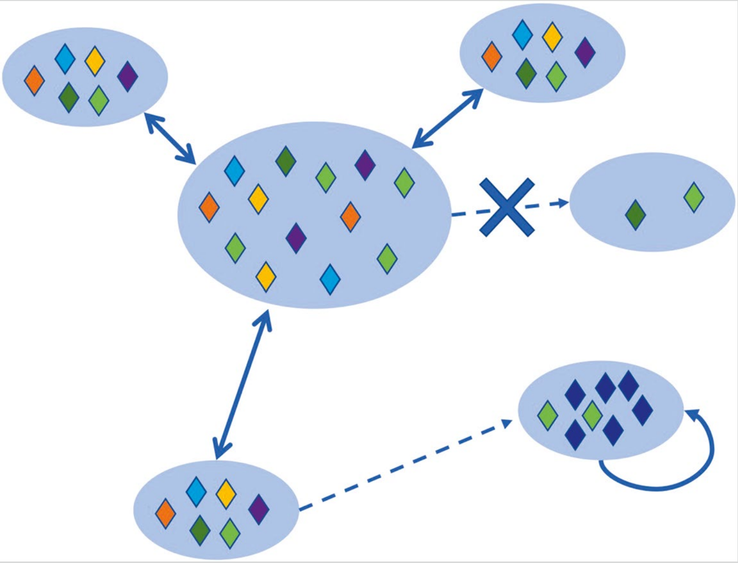

Fig. 7.1 Level of connection among populations in a system of habitat patches: connectivity may allow recovery after local extinction, while absence of connection results in increase of vulnerability and decrease of species diversity (island biogeography). Colored diamonds represent different species; arrows indicate typical mainland-island dispersal direction between populations (blue circles); dashed lines indicate weak connections directed to sink populations; cross indicate hard barrier

7.2 Gene Flow Between Reefs—Connectivity in the Evolutionary Timescale

In the last 50 years, the development of genetic tools has impacted many fields of the biological sciences, from basic unicellular functioning to ecosystem ecology. Following this development, an increasing number of studies aimed at unveiling aspects of organismic evolution using molecular tools, including marine organisms.

The first studies of population genetics using coral reef organisms in Brazil were conducted in the 1990s, using allozymes to evaluate the connectivity of sea anemones and sponges, rather than coral species, while working generally on a more regional scale (Russo et al. 1994; Klautau et al. 1999). With the turn of the century, and the availability of a plethora of molecular markers, the number of studies increased consistently, shifting the focus in the last decades to reef fish and scleractinian corals.

New studies have switched then from allozymes to the use of nuclear and mitochondrial loci (Santos et al. 2006; Neves et al. 2008; Nunes et al. 2011; de Souza et al. 2017), in addition to microsatellites (Peluso et al. 2018; Padua et al. 2018), providing more accuracy to unravel population genetic patterns (Bruford and Wayne 1993; Sunnucks 2000; Ellegren 2014). With the improvement of technologies and lower costs of high-throughput sequencing during the past two decades, genomic approaches have become a viable possibility to study ecological and evolutionary changes in non-model species (Ellegren 2014). Genomic studies enable a deeper understanding of genetic diversity and connectivity within and between populations, with the possibility to study large numbers of both neutral and non-neutral regions (Oleksiak and Rajora 2019). With such large numbers of polymorphic loci, it has become possible to identify small scale genetic structure, often not found with conventional markers (Crawford and Oleksiak 2016; Drury 2016), in addition to finding specific genes that might be under selection (Devlin-Durante and Baums 2017; Nielsen et al. 2020).

Such studies are critical to our understanding of the adaptation process and how species will respond to climate change. Reduced representation sequencing, which includes Genotyping-by-sequence (GBS) (Elshire et al. 2011) and restriction site-associated DNA sequencing (RAD-seq) (Baird et al. 2008; Andrews et al. 2016), are popular cost-effective methods that use restriction enzymes and size selection to sequence random portions of the genome. Both methodologies have been used to access genetic diversity and connectivity in coral reef organisms within the Pacific (Shinzato et al. 2016), Indian (Salas et al. 2019), Caribbean (Drury et al. 2016; Hammerman et al. 2018; Sturm et al. 2020), and Atlantic Oceans (Volk et al. 2021).

Within the Brazilian coast, the most comprehensive study focusing on scleractinian corals connectivity have used microsatellite markers, which are highly polymorphic markers, to evaluate genetic diversity and connectivity of the endemic species *Mussismilia hispida*, an important reef builder coral along the coast (Peluso et al. 2018). The study found five genetically differentiated populations along 3500 km of coastline, with gene flow being restricted mainly by ocean currents, and also raising evidence for the hypothesis that oceanic islands might have acted as refugia for corals during low sea-level periods in the Last Glacial Maximum (Leão et al. 2003; Pinheiro et al. 2017; Peluso et al. 2018). While similar patterns of gene flow breaks have been observed for other scleractinian species (e.g. *Favia gravida* and *Siderastrea radians*), this pattern is not a general rule. The scleractinians *Montastraea cavernosa* and *S. siderea*, and the hydrocoral *Millepora alcicornis* showed high genetic connectivity throughout their geographic range (Nunes et al. 2011; Souza et al. 2017), although these differences might actually be due to the mitochondrial and nuclear genetic markers with different levels of variability.

Discordances on connectivity patterns have also been observed for coral reef fishes, with species such as the yellowtail snapper *Ocyurus chrysurus* and the butterflyfish *Chaetodon striatus* displaying strong gene flow among a wide geographic range (da Silva et al. 2015; Liedke et al. 2020), while small cryptic fishes, such as the bridled goby *Coryphopterus glaucofraenum* and the rockpool blenny *Entomacrodus vomerinus* seem to be more affected by geographic and environmental barriers (Neves et al. 2016; Volk et al. 2021).

The most recurrent genetic pattern within the Brazilian coast is the differentiation between the Oceanic Islands (e.g., Fernando de Noronha and Rocas Atoll) and coastal regions, observed for both reef fishes and corals, and driven mainly by ocean currents and geographic distance (Nunes et al. 2011; Cunha et al. 2014; Neves et al. 2016; Peluso et al. 2018; Volk et al. 2021) (Fig. 7.2). Likewise, southern Brazil frequently harbors genetically distinct populations, which has been associated with the presence of a strong upwelling in the Cabo Frio region (22° S) that separates warm tropical reefs in the north from colder subtropical rocky reefs in the south, representing a region of ecological transition (Santos et al. 2006; Peluso et al. 2018; Volk et al. 2021). Additionally, ocean currents have been shown to prevent gene flow between the central and southern regions of Brazil (Volk et al. 2021). A third recurrent pattern is the isolation of the reef fish fauna from Saint Peter and Saint Paul Archipelago (0° N) a remote area in northern Brazil (Cunha et al. 2014; Peluso et al. 2018; Volk et al. 2021). Within the central region, different patterns of connectivity have been observed among corals and fishes (Neves et al. 2016; Peluso et al. 2018; Volk et al. 2021), which suggests the presence of semi-permeable barriers, such as the São Francisco River outflow. For instance, this outflow is the distribution break between the two species of hydrocorals (*M. brazilensis* and *M. nitida* (Souza et al. 2017)), while is not a barrier for larval dispersal of the coral *M. hispida* (Peluso et al. 2018).

Patterns of connectivity in Brazilian corals seem to be regulated by the following factors: geographical isolation, oceanic currents directing or restricting gene flow, the occurrence of upwelling likely limiting dispersal and settlement, freshwater discharges, fluctuations on the sea level, and the availability of substrate acting as a stepping-stone (Nunes et al. 2011; Neves et al. 2016; Peluso et al. 2018; Pinheiro et al. 2018). The main biogeographic barriers are shown in Fig. 7.2. However, a set of additional factors can influence dispersion and genetic connectivity of corals, fishes, and other invertebrates, including: differences in reproductive mode, despite not being a good predictor of dispersion (Guzmán et al. 2011; Peluso et al. 2018),

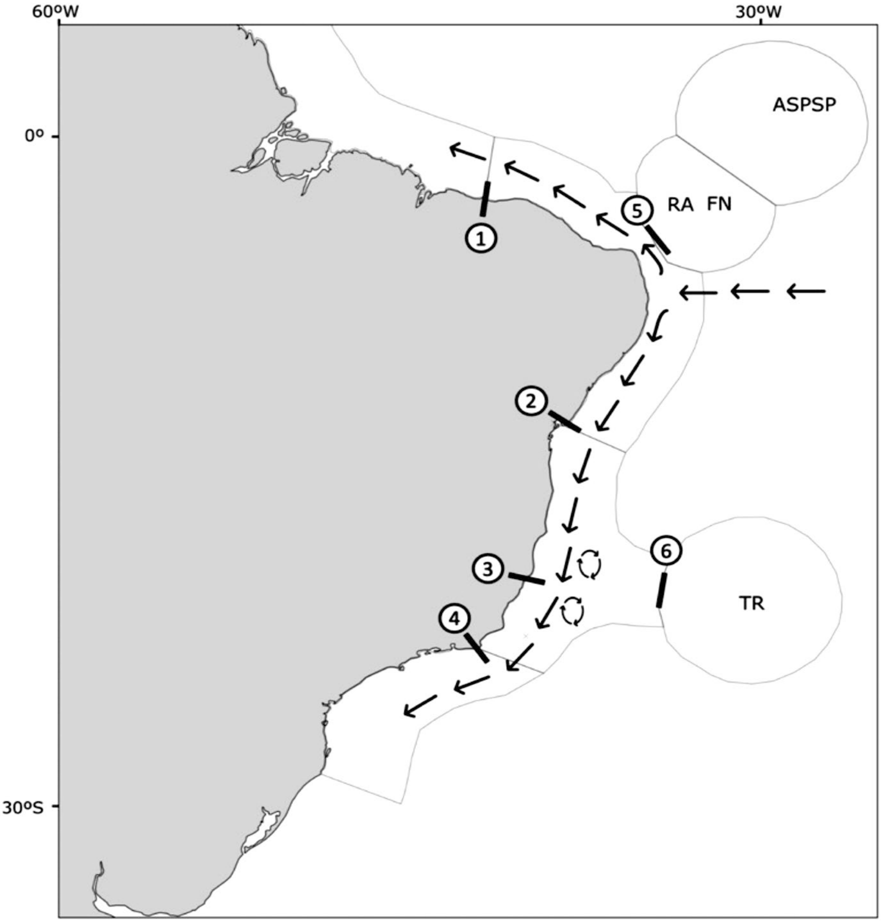

Fig. 7.2 Outline of the seven marine ecogeographic regions in Brazil according to Spalding et al. 2007 (see also Chap. 1 of this book). Arrows indicate the mean surface ocean current directions. Black bars indicate possible biogeographic barriers: (1) Amazon River; (2) São Francisco River; (3) Doce River; (4) strong upwelling; (5–6) long distances from available hard substrates

transport by rafting and artificial structures (Capel et al. 2019; Mantelatto et al. 2020), and adaptability to the new environment (Sexton et al. 2014).

Nevertheless, there is still scarce data on genetic connectivity of coral reef organisms along the Brazilian coast, and most studies have used only a few nuclear or mitochondrial loci. New approaches are now targeting a more comprehensive understanding of the ecological forces contributing to spatial patterns on population connectivity, combining genetic and environmental data in the recent field of seascape genomics (Selkoe et al. 2016). Future studies should focus on more sensitive markers, such as microsatellites or SNPs, and increase the number of target species to provide a fine scale analysis of the main patterns of connectivity within the Brazilian coast.

7.3 Biophysical Context of Demographic Connectivity in the Tropical South Atlantic

As previously mentioned, demographic connectivity involves the exchange of individuals between populations through the interaction of propagules (eggs and larvae) with the flow field. In most marine organisms, this process may involve a pelagic dispersal phase and ontogenetic migration of the juvenile phase to an adult habitat (Brown et al. 2016). As such, it tends to be highly variable both in space and time, making it very difficult to assess empirically. This is particularly true in the tropical South Atlantic where oceanic islands are connected with the north and northeast coast of Brazil (Peluso et al. 2018; Endo et al. 2019). Physical and biological models with different levels of complexity, from individual-based to end-to-end models, can be used not only to overcome practical limitations of empirical studies but also to test ecological hypotheses through *in silico* simulations (Box 7.2).

The use of models is justified by the fact that connectivity plays an important role in the maintenance and persistence of populations and their recovery from disturbance (Hughes et al. 2003; Green et al. 2015). In fact, model results suggest that persistence can be directly related to a certain threshold for the total amount of replacement through gain or loss of larvae over many generations, considering all possible paths (Botsford et al. 2009). There is also a more subtle, but not less important, consequence of connectivity that results from the influence of environmental conditions of the metapopulation on the mean phenotype of a subpopulation (Marshall and Morgan 2011). This implies that larvae moving from one site to another will likely have their post settlement fitness and survival reduced, compared to local recruits, especially along the nearshore-offshore gradient (Hamilton et al. 2008), as it is the case for the tropical South Atlantic (Endo et al. 2019).

Demographic connectivity in the tropical South Atlantic has been estimated using different methodological approaches, from single to multi-species, and from simple advective-diffusive to conservation planning models (e.g., Rudorff et al. 2009; Magris et al. 2016). A thorough review of the literature is beyond the scope of this chapter. Instead, we refer to the published research to synthesize what is known about biophysical modelling to estimate demographic connectivity in the region and point to some issues we consider deserve more attention in the future.

From a biophysical standpoint, the problem of demographic connectivity has been constrained by the survival of eggs and larvae, the complex nature of surface ocean circulation and the geographic distribution of reefs and other hard bottoms (e.g., rhodolith beds) habitats. In Brazil, these may form geographically isolated ecosystems in the oceanic islands, such as the São Pedro and São Paulo Archipelago (SPSP), Atol das Rocas (AR), Fernando de Noronha Archipelago (FN) and Trindade and Martim Vaz islands (TR). All of these are today important MPAs that ideally should form a network with other protected coastal reef habitats, including Parcel do Manuel Luis (ML), Recife dos Corais (RC), Costa dos Corais (CC), Abrolhos (AB), Arraial do Cabo and Cabo Frio (CF) (see Fig. 7.3). However, coastal MPAs are only some of the possible destinations of larvae from the oceanic islands, as they are part of, and behave as, an environmental continuum.

The ecological concept behind this idea has been summarized for large marine ecosystems (Sherman 1991), defined as large (>200,000 km^2) geographical regions sharing common submarine topography, productivity and trophically linked populations that are submitted to the same hydrographic regime. The idea of targeting large recruitment areas (LRAs) outside MPAs for conservation, as proposed by Endo et al. (2019) for Brazil, is supported by evidences suggesting that MPAs network designs should include other relevant recruitment areas and migration corridors (Green et al. 2015).

Results from biophysical simulations of dispersal using the grazing reef fish *Sparisoma* as a model species (Endo et al. 2019) indicate that austral summertime mortality rates are significantly higher than winter, but interannual variabilities are not significant. In this study. Mortality by lethal temperature varied for different sites, with hypothermia being more prevalent especially where upwelling of cooler waters occurs, such as in CF and SPSP. The southern branch of the South Equatorial Current (sSEC) is in its northernmost position (~10°S) during the austral spring/summer coincident with the southernmost position of the Intertropical Convergence Zone (ITCZ) and a positive wind stress curl (Rodrigues et al. 2007). This configuration induces the sSEC bifurcation to be positioned at lower latitudes and increases the southward water transport of BC carrying larvae from CC to AB (Fig. 7.3). During the winter this connection seems to be lost, as the sSEC bifurcation moves southwards and the BC transport around CC is reduced.

The low demographic connectivity among MPAs in the tropical South Atlantic, estimated by biophysical modelling, raises concern about the network fragility (Fig. 7.4). Particularly, the low level of local retention (CC and TR, only) suggests

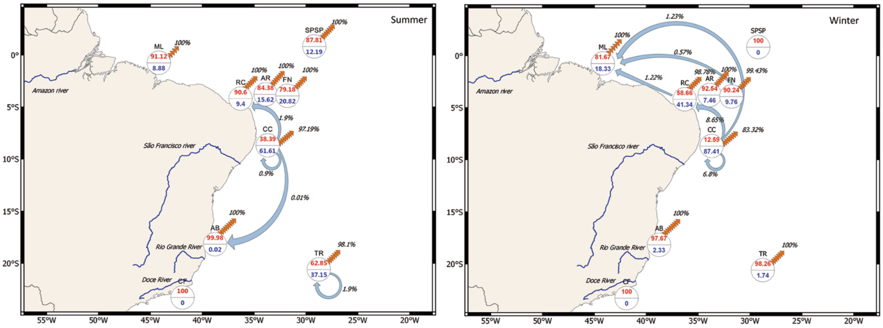

Fig. 7.3 Summary maps of larval mortality (red) and survival (green) per site for summer and winter. The orange arrows indicate the percentage of larvae that is exported from each area and does not recruit in any MPA. Blue arrows indicate the origin and destination sites of those larvae that actually recruit. Figures near blue arrows are total percentages of recruitment and local retention. *ML* Parcel do Manuel Luis, *RC* Recife dos Corais, *CC* Costa dos Corais, *SPSP* São Pedro and São Paulo Archipelago (SPSP), *AR* Atol das Rocas, *FN* Fernando de Noronha Archipelago, *TR* Trindade and Martim Vaz islands, *AB* Abrolhos, *CF* Cabo Frio

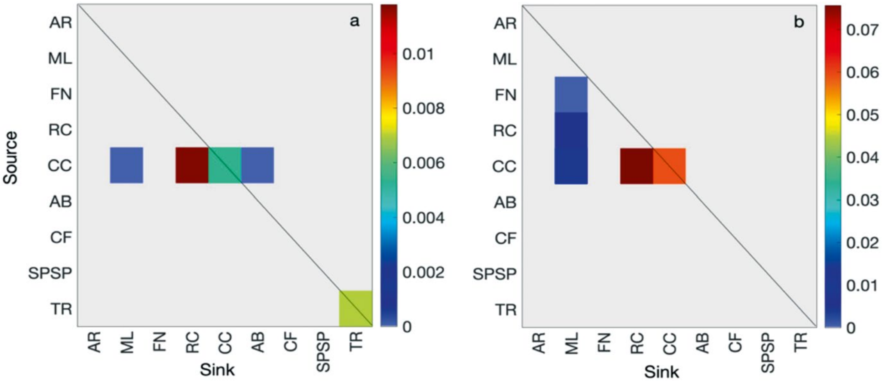

Fig. 7.4 Transition probability matrix for the summer (**a**) and winter (**b**) considering the five coastal areas and the four oceanic islands. The five coastal MPAs: Parcel do Manuel Luis (ML), Recife dos Corais (RC), Costa dos Corais (CC), Abrolhos (AB) and Arraial do Cabo and Cabo Frio (CF); and the four oceanic islands: São Pedro and São Paulo Archipelago (SPSP), Atol das Rocas (AR), Fernando de Noronha Archipelago (FN) and Trindade and Martim Vaz islands (TR). Note the different color scales for summer and winter (from Endo et al. 2019)

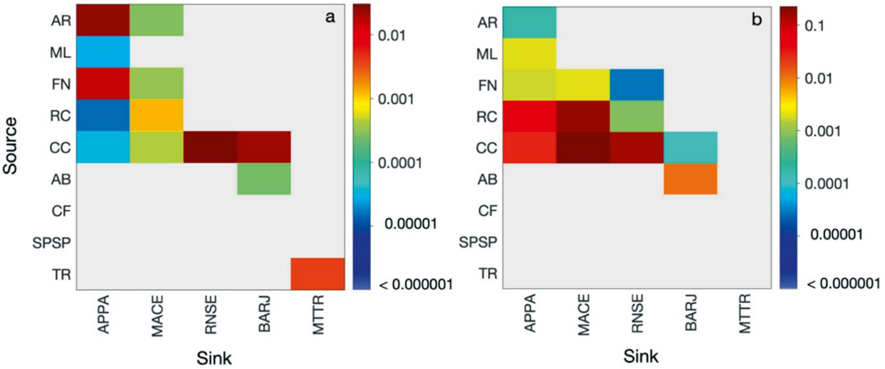

Fig. 7.5 Transition probability matrix for the summer (**a**) and winter (**b**) computed from simulations including non-protected coastal environments called Large Recruitment Areas (LRAs). Spawning (source) sites are the same as in Fig. 7.3. The LRAs are APPA, Amapá to Pará; MACE, Maranhão to Ceará; RNSE, Rio Grande do Norte to Sergipe; BARJ, Bahia to Rio de Janeiro and MTTR, Vitória-Trindade chain. Note the different color scales for summer and winter (from Endo et al. 2019)

that this important self-seeding process can be a limiting factor for long-term resilience of some MPAs. Despite this scenario of fragility, overall connectivity in the tropical South Atlantic increases if simulations consider Large Recruitment Areas (LRAs), that include non-protected coastal environments (Fig. 7.5). Under such conditions, it becomes evident that both CC and RC form an important hub connecting northern and southern MPAs. Also, CC and AB (further south) appear as important sources of recruitment for both subtropical and temperate environments.

The interplay of reproduction, transport, survival and settlement of reef fish larvae constitutes a highly complex process that can be quantitatively approached to generate meaningful ecological scenarios. Limitations regarding the realism of these biophysical simulations, such as adult fecundity, predation, larval motility and substrate cues, need to be considered when interpreting results. However, if numerical experiments are designed based on well-constructed hypotheses, they can be simple enough for a balanced assessment of important conservation issues.

In fact, model results showed that for *Sparisoma* populations living in the tropical South Atlantic the estimated demographic connectivity among MPAs is extremely low and probably contributes to their isolation. The simulated LRAs gives further indication that the implementation of Large Marine Protected Areas (Lewis et al. 2017) could help improve connectivity between offshore and coastal environments and strengthen the north-south connection along the tropical Brazilian coast. It is important to understand whether these patterns of connectivity hold true for simulations with other organisms, to determine if this is a general process.

Box 7.2: Biophysical Modelling

Biophysical modelling has been traditionally used as a complementary and exploratory tool for fisheries monitoring. These models can also provide information on dispersal, growth and survival through the interaction of physical and biological conditions, especially for present known distributions of organisms and oceanographic conditions (North et al. 2009). Future levels of connectivity can be also simulated for ocean warming scenarios using biophysical models that incorporate information originated from dynamic ocean model downscaling (Lima et al. 2021).

Biophysical modelling can be viewed as a combination of three different elements: a hydrodynamic model that simulates the ocean physics and the environment within which the biological interactions will occur; a particle tracking model that models the path and movement of the particles and a coupled individual based model (IBM) that incorporates as many biological traits, behavior and processes of the targeted species as possible.

The hydrodynamic model consists of a set of discrete equations that resolve variables as 3D velocities, turbulence, salinity, temperature, density among other variables in different pre-set spatio-temporal scales. The particle tracking model estimates the trajectories of the released particles, which requires that the hydrodynamical model is previously validated with observational measurements.

The IBM or the biological model may include a multitude of biological factors, from larval pelagic duration to growth rates and predation. The IBM is also set to consider processes over a certain spatio-temporal variation. From the biological perspective it can include processes evolving the reproduction process, such as spawning activity and egg production. It is also possible to include egg buoyancy and mortality. As the egg hatches and starts its development as a larva it is possible to include growth, dispersal, pelagic larval duration, feeding, horizontal and vertical swimming behavior, mortality, predation and many others.

Despite all complexity that can be included in biophysical models, the larvae can also be considered as passive particles that are only transported by the ocean currents (Treml et al. 2008). By only including the coupling between the hydrodynamical and the particle tracking model, it is still possible to emulate a few biological characteristics, such as spawning time, initial density and pelagic larval duration. However, the particles do not have any behavior and are transported passively by the main flow from one point to another. For example, the connectivity of spiny lobster in the Tropical Atlantic was studied using a simple advective-diffusive model using Lagrangian dispersion (Rudorff et al. 2009). By using an IBM more biological characteristics are considered, increasing the biological realism of the model and providing more details of the factors mediating mortality in the early life stages (Peck and Hufnagl 2012).

From spawning to larval dispersal and settlement in distant ecosystems there are a lot of smaller processes involved. Although the use of models helps to shed some light into these complex and unknown processes, the uncertainties associated with the different modeling approaches must be considered when using the results for management settings.

7.4 Reefs and Their Neighbors—Connectivity at the Scale of Individuals

7.4.1 Ecological Connectivity

The tropical coastal seascape comprises a mosaic of habitats such as mangroves, seagrass meadows, macroalgal beds, mudflats, rocky and biogenic reefs. Many species migrate between those habitats for various reasons. It is common especially among fish and crustaceans to utilize multiple habitats during their life, on varying temporal and spatial scales. This section will focus mainly on fish species because of their intrinsic higher mobility and because they are among the most studied group in Brazilian seascapes.

Migrations include foraging, tidal and ontogenetic migrations, where fish utilize separate habitats as juveniles and adults (Nagelkerken 2009). These movements happen on different temporal and spatial scales, such as short-term foraging migrations during a few hours, up to ontogenetic migrations, which may take years to complete (Pina-Amargós and González-Sansón 2009). Several species that spend their adult life stages on reefs utilize mangroves and seagrass meadows as foraging or nursery grounds (Nagelkerken et al. 2000). These movements result in transfer of energy, nutrients and carbon between habitats and is commonly referred to as *ecological connectivity* (Nagelkerken 2009). Multi-habitat seascapes allow species to take advantage of resources in several habitats and usually support higher fish abundance and diversity compared to less diverse seascapes (Olds et al. 2012). This has implications for management of coastal areas, since alterations or degradations of one habitat also affect adjacent habitats through these mobile links (Goodridge Gaines et al. 2020). Additionally, more than 40% of the reef fish species that use multiple habitats (e.g., mangroves, seagrass meadows, estuaries) are considered threatened in Brazil (Vila-Nova et al. 2011). Several species from both commercially and ecologically important families utilize non-reef habitats during their life. In Brazilian waters, species from the families Lutjanidae, Epinephelidae, Carangidae and Haemulidae are recorded to move between estuaries and mangroves to nearby reefs (Xavier et al. 2012; Chaves et al. 2013).

7.4.2 Main Coastal Habitats

Most research on connectivity has focused on ontogenetic migrations. In the Caribbean, mangroves and seagrasses serve as nursery and foraging habitats for a variety of species including different trophic groups and several keystone species, such as parrotfish (Ogden and Quinn 1984). In the Pacific, seagrass meadows seem to be primarily used as nurseries, while mangroves contain a less diverse juvenile fish assemblage (Igulu et al. 2014). Mangroves in Brazil are in general subjected to low salinity and their roots are usually colonized by oysters and brown algae (*Bostrichia* spp., Cordeiro-Marino et al. 1992) which provides little structural complexity when compared to sponges, for instance, and are not very palatable for herbivorous fish (Pereira et al. 2017).

Brazilian tropical reefs are patchily distributed along the tropical coast and formed by cemented terraces, fringing reefs, patch reefs and pinnacle reefs (Chap. 1). Bank and fringing reefs are the dominant features among Brazilian reefs and most of them have a tidal regime that affects the access to the leeward side of reefs (Chap. 1). Globally, the reef flat is a common feature of fringing reefs, where soft sediment and macroalgae beds flourish in waters sheltered by the reef formations. These calm habitats are used by several reef species as feeding grounds, functioning as large tidepools that may shelter many juvenile individuals, or even larger predators during high tide (Chaves et al. 2013; Harborne 2013).

Seagrass meadows are commonly cited in literature as important nursery and foraging areas for fish and crustaceans in the Pacific and the Caribbean (Boström et al. 2006; Huijbers et al. 2013) but they may play a less important role for fish along the Brazilian seascapes (Eggertsen et al. 2017). The seagrasses occurring in Brazil are small species (of the genera *Halodule*, *Halophila* and *Ruppia*) that provide limited structural complexity (Copertino et al. 2016). Large seagrass meadows are uncommon in Brazil and also underrepresented in coastal protected areas which makes them vulnerable to human pressure.

7.4.3 Types of Migrations in Brazilian Seascapes

7.4.3.1 Within-Habitat Movements

Movements within habitats, either ontogenetic or daily foraging migrations, have only been inferred for Brazilian reef systems based on indirect evidence, supported by field observations of behavior (feeding, mating, and/or agonistic). Few studies have used methods such as tagging techniques to directly quantify these migrations. Most of these techniques are expensive and time consuming (Box 7.3; Whoriskey and Hindell 2016) and, therefore, have rarely been applied in studies along Brazilian reef environments. However, passive acoustic telemetry has recently been conducted to study the movements of parrotfishes of the *Sparisoma* genus on reefs in Tamandaré (Pernambuco) (Giancalone et al. 2016) and Scarid parrotfishes and groupers (*Mycteroperca bonaci*) on reefs in Abrolhos (Bahia) (Hackradt et al. in prep.).

Ontogenetic migrations are the most cited movements inferred by size distribution of species. Cordeiro (2009) observed an increase in the average size of fishes from reef flats towards the fore reef zone in shallow coastal reefs of Paraíba state, especially for Acanthurids, *Chaetodon striatus* (Chaetodontidae), *Anisotremus virginicus* (Haemulidae), *Abudefduf saxatilis* (Pomacentridae) and *Haemulon parra* (Haemulidae) (Fig. 7.6). The same pattern was observed by Querino (2011) on other reefs in Paraíba where the mean size of Acanthurids, *Abudefduf saxatilis*, *Halichoeres poeyi* (Labride) and *L. jocu* (Lutjanidae) was larger on reefs than in macroalgal beds closer to the shore. Intertidal pools are also cited as temporary habitats for juveniles of several reef fish species who migrate to other areas of the reefs after growing to larger sizes (Dumaresq 2019), reinforcing the existence of ontogenetic changes in spatial distribution of reef fishes. However, all authors agree that it is not possible to discard the effects of different predation rates, fishing pressure and other anthropogenic stressors that usually are higher close to shore and may influence the observed

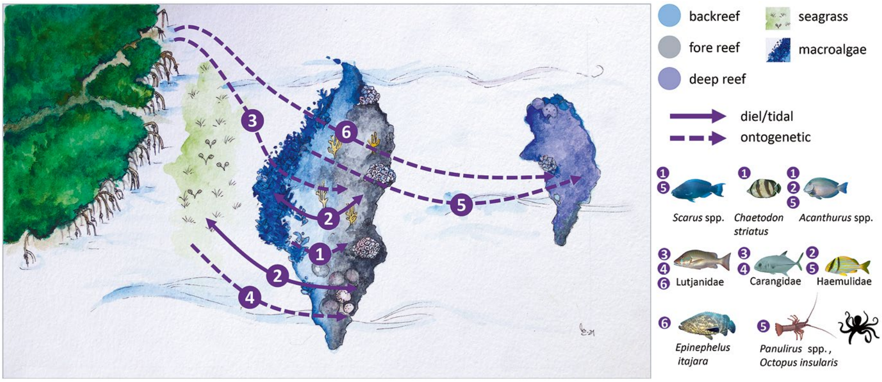

Fig. 7.6 Ecological connectivity between mangroves, seagrass meadows and reefs through migrations of some reef species

size distributions. Still, as the same pattern has been consistently observed on multiple reefs in various locations and studies, it is likely that juveniles from a number of species settle in more sheltered areas such as macroalgae and/or rhodolith beds, in the reef flat zone, later moving to deeper areas when they outgrow the benefits of their nursery (Costa et al. 2020).

7.4.3.2 Between-Habitat Movements: Fishes and Other Animals

Most of the tropical reefs along the Brazilian coast are influenced by coastal rivers with seasonal regimes (Chap. 1). Because of varying freshwater influxes, most estuaries are dominated by tides, with the higher salinities during high tide facilitating migration of transient marine species also to upper zones of estuaries. Such movements vary in time, either as ontogenetic migrations or daily foraging movements (Fig. 7.6). The first is better reported based on inferences of uneven spatial distribution of different size categories. The second, daily foraging migrations, has been observed and reported by fishermen but is poorly described in literature. Similar to what is reported for the Caribbean and the Pacific, grunts (Haemulidae), barracudas (Sphyraenidae) and snappers (Lutjanidae), as well as the goliath grouper (*Epinephelus itajara*) have been observed in estuary mouths close to reefs in Brazil (Ferreira et al. 2014), usually as juveniles. Contrastingly, in Brazil, juvenile parrotfish have been little recorded in non-reef habitats.

At the same time, there are differences in habitat use for the same species between biogeographic provinces. The yellow-tailed snapper (*Ocyurus chrysurus*), which in the Caribbean almost exclusively utilize *Thalassia* seagrass meadows as a nursery habitat, has not been recorded in shallow seagrass (*Halodule*) meadows in Brazil (Eggertsen et al. 2017). Differences in seascape configuration and habitat complexity may have shaped these patterns. There is still limited evidence for obligatory dependency of Brazilian reef fish species on seagrass meadows as a nursery habitat.

Inferences about ontogenetic migration of Carangidae, Sphyraenids and Lutjanidae are also mainly based on size distributions. One exception is presented by Soeth et al. (2020), confirming ontogenetic movements of *Chaetodipterus faber* juveniles from mangroves to reefs using otolith fingerprints. In general, *Lujtanus jocu*, *Lutjanus synagris* and *Lutjanus alexandrei* are the most cited reef fish species observed occupying estuaries as juveniles (Pereira et al. 2010; Reis-Filho et al. 2019). Species from the Carangidae family (*Caranx latus*, *Carangoides bartholomaei*, *Oligoplites* sp.), Scombridae (*Scomberomorus brasiliensis*), Haemulidae and Gerreidae have also been recorded to occupy estuaries and/or seagrass meadows as juveniles. However, some of these species have pelagic habitats as adults, and in many cases forage over unconsolidated substrates, which place them as "reef-associated" species but not as residents (Reis-Filho et al. 2019; Soeth et al. 2020). To date, there has been no other published evidence of ontogenetic reef fish migration using tracking or tagging methods.

Ontogenetic migrations to deeper reefs have been indicated by authors who recorded larger individuals of certain species exclusively at greater depths. Larger specimens of five Lutjanidae species (*L. analis*, *L. chrysurus*, *L. jocu*, *L. synagris* and *L. vivanus*) have consistently been detected in deeper reefs in the states of Ceará, Rio Grande do Norte, Pernambuco, Alagoas and Bahia (Frédou and Ferreira 2005), adding to the evidence of ontogenetic migrations occurring in this family.

Octopuses (*Octopus insularis*, Batista and Leite 2016) and lobsters (*Panulirus* genus, Cruz et al. 2020) have also been observed to attain larger sizes on deeper reefs while their juvenile stages are associated with shallow areas within reef seascapes. In general, large-bodied species possess higher mobility, increasing their odds to reach deep reefs further from the coast. However, it is almost impossible to distinguish the importance of anthropogenic pressure on these patterns, selecting for smaller specimens on shallower reefs and thus influencing size distributions (Harborne 2013).

Although evidence of ontogenetic movements exists, the mechanism underpinning these migrations are not completely explained. Fitness maximization, through pre-settlement preferences (Brown et al. 2016), predation pressure, growth maximization and reproductive behavior (Haywood and Kenyon 2009) are among the most accepted processes involved in ontogenetic changes in habitats.

Crustaceans such as lobsters, crabs and shrimps perform ontogenetic, reproduction and diel migrations either from reef to estuaries, or from estuaries to reefs in Caribbean and Pacific ecosystems (Krumme 2009). Megafauna such as manatees (*Trichechus manatus*, Paludo and Langguth 2002), sea turtles, sharks and rays also use multiple habitats including estuaries and reefs, due to reproduction, ontogenetic and foraging migrations. None of these species are obligatory associated with reefs, but their home range encompass a large seascape including reefs.

In general, we know little about ecological effects of ecological connectivity in Brazil, as well as implications for management. This is a vast field yet to explore in Brazilian tropical reefs.

Box 7.3: Tracking Movement

Most tagging techniques consist of attaching an identifiable mark to individuals of a target species and then recapture or observations the tagged individuals to analyze their movements in space and time. The most popular techniques involve acoustic tags that emit signals detectable either passively, by stationary hydrophones, or actively, by a human operated hydrophone (Hussey et al. 2015), or with a hydrophone mounted on an underwater autonomous vehicle (White et al. 2016). Global Positioning System (GPS) tags use a similar principle, but utilize orbital satellites as receivers that transmit the captured information to a land-based center. The choice of tagging method will depend on the main objectives of the study (e.g., diel activity, home range, long distance movements) and the available budget.

Acoustic tagging has been widely applied to reef fishes (Pittman et al. 2014), but also to sea turtles (Chevis et al. 2017), marine mammals (Lydersen et al. 2002) and invertebrates (e.g., jellyfish—Mooney et al. 2015). Additional information can also be obtained from sensors included in some tags that register and transmit environmental information (e.g., depth, salinity, temperature, dissolved oxygen), the animal's 3D acceleration or physiological state (e.g., heart rate, temperature) (Cooke et al. 2004; Nassar et al. 2018). The movement information is then analyzed to extrapolate the path or area used by the studied animals based on the frequency of detections and their coordinates (Calenge et al. 2009). Information such as site fidelity, energy expenditure, feeding activity and reproduction among others can also be obtained from the combination of detections and complementary data from associated sensors and visual observations, when present.

7.5 Connectivity in the Conservation Context: The Missing Parts in the Puzzle

At this point, it should be clear that all types of connectivity discussed in this chapter are relevant to coral reef conservation. However, the conservation strategy continuously evolves, resulting in a temporal mosaic of initiatives conceived under different sets of paradigms in a timeline. For instance, the first reef areas included in MPAs were created in 1979 for Rocas Atoll biological reserve. By then, the singularity of the target areas was the most important reason to propose the creation of a conservation unit. As a more complete picture of the biology of most marine species emerged with the use of a wide array of technological advancements, stemming from satellite imagery to high throughput DNA sequencing, paradigms have shifted to include connectivity as one of the key processes to be considered (D'Aloia et al. 2017; Virtanen et al. 2020).

Even though connectivity is considered an important aspect for marine spatial planning in conservation, it still focuses on a few target species, lacking a true integrative or multi-specific approach (Magris et al. 2016, 2018). Additionally, conservation demands from multilateral agreements have also influenced not only the location of new MPAs, but also their size and level of legal protection (Giglio et al. 2018). Hence, despite the technical and academic discussions and proposed guidelines, the outcomes of conservation actions is the result of complex negotiations, frequently asymmetrical in terms of influence.

Within the scope of Brazilian Coral Reefs, there is a consistent body of knowledge that has accumulated during the past decade. There is a scientific consensus about the importance of connectivity processes for the design of marine protected areas (MPA) networks, especially when the replenishment of local populations become dependent on nearby habitats (Planes et al. 2009). It has been advocated that MPAs should ensure the persistence of metapopulations by conserving the mechanisms that drive adult replacement and the survival rate at very low levels of recruitment in local subpopulations (Sale et al. 2010; Burgess et al. 2014; Mcleod et al. 2019; Roberts et al. 2021). This usually involves taking decisions about the size, spacing and location of individual MPAs to maximize connectivity and conservation benefits (Green et al. 2015). Factors, such as larval dispersal and self-recruitment (as the proportion of locally produced offspring that remain in the same population), species home range, ontogenetic habitat shifts, and resource availability should influence the choice of MPA's size.

The effective protection of habitats and management of fishery reserves, based on MPAs networks, can be particularly sensitive to their spatial distribution and sizes. For reef fish larvae that settle close to their parents and or have high rates of self-recruitment, their connectivity via the exchange of individuals may be limited to short distances, demanding a closely spaced network. Obviously, optimum MPA spacing depends on the availability of suitable habitats for recruitment, especially for species that undergo ontogenetic habitat shifts or spawning migrations. The general principle, however, that guides the definition of MPAs to sustain fisheries yields states that harvested fish species should be able to persist inside MPAs and sustain yield outside through spillover of larvae and adults (Burgess et al. 2014). Despite the mounting scientific evidence highlighting the role of larval dispersal to connectivity and, consequently, to MPA effectiveness, it remains a challenge to measure it in the field and it is a major source of uncertainty (for a review, see Burgess et al. 2014).

Within the Brazilian context, Ferreira et al. (2022) showed that connectivity was indeed a key factor for MPAs effectiveness, regardless of their fully or partially protected status. It seems now obvious or even intuitive to think of connectivity as an integral part of conservation spatial planning, however, even in recent years, this was not at the core of the Brazilian strategy. For instance, the Environment Ministry has implemented and regularly updated the designation of areas prioritized for conservation actions. The methods followed explicitly the systematic conservation planning strategy, proposed by Margules and Pressey (2000). Connectivity was considered as a process that may be targeted for conservation however, it was not a core property of the areas to be prioritized. Hence, the maps of areas and proposed actions rarely, if at all, take connectivity into account (Environment Ministry Ordinance 463, December 18th 2018).

Resulting from these combined processes, the country has a mosaic of MPAs and conservation actions that, combined with the lack of resources, has produced poor results. The creation of two large MPAs around sensitive oceanic islands that exclude their most critical habitats clearly illustrates this problem (Giglio et al. 2018). Brazilian coral reefs are biodiversity treasures that are deeply connected to virtually all marine and coastal biomes. Therefore, connectivity must be further studied and fully incorporated into conservation strategies and methods.

7.6 Final Remarks: The Way Forward

Connectivity is a cornerstone for coral reef biology and conservation (Magris et al. 2016) because local population persistence can be strongly dependent on external subsidies via larval supply (network persistence). From the basic biological knowledge to conservation and resources management, ignoring these processes certainly produce an incomplete picture, many times resulting in ineffective decisions.

Considering what is known for Brazilian reef organisms, there are still many blanks to fill. Accurate data and reliable biophysical models, genetic population structure and assessments of migration and individual movements of key species are essential to advance the knowledge on Brazilian coral reefs. Beyond the need for basic information about the evolutionary history and biology of reef organisms, the maintenance of essential ecosystems services depends on this knowledge. So, we can identify some relevant questions that need to be addressed to turn the conservation of reef ecosystems in the South Atlantic Basin more effective:

(1) Do current biophysical models explain adequately the genetic structure of keystone species in reef ecosystems?
(2) How connectivity regulates/modulates the populational structure of keystone species?
(3) Is the functional structure of reef ecosystems regulated or modulated by connectivity processes?
(4) How connectivity processes are affected by climate changes and what are the projected consequences for the resilience and conservation of reef ecosystems?
(5) Will climate change impacts on connectivity compromise the effectiveness of current MPAs?

It is beyond the scope of this chapter to tackle on all aspects of conservation strategies, but one must now and again claim for more effective plans, considering not only connectivity issues but all the aspects indicated by the large body of work continuously produced.

References

Andrews KR, Good JM, Miller MR et al (2016) Harnessing the power of RADseq for ecological and evolutionary genomics. Nat Rev Genet 17:81–92. https://doi.org/10.1038/nrg.2015.28

Baird NA, Etter PD, Atwood TS et al (2008) Rapid SNP discovery and genetic mapping using sequenced RAD markers. PLoS One 3:e3376. https://doi.org/10.1371/journal.pone.0003376

Batista AT, Leite TS (2016) Octopus insularis (Cephalopoda: Octopodidae) on the tropical coast of Brazil: where it lives and what it eats. Braz J Oceanogr 64:353–364. https://doi.org/10.1590/s1679-87592016123406404

Bauer S, Swenson MS, Griffa A et al (1998) Eddy-mean flow decomposition and eddy-diffusivity estimates in the tropical Pacific Ocean: 1. Methodology 103:30855–30871. https://doi.org/10.1029/1998JC900009

Boström C, Jackson EL, Simenstad CA (2006) Seagrass landscapes and their effects on associated fauna: a review. Estuar Coast Shelf Sci 68:383–403. https://doi.org/10.1016/j.ecss.2006.01.026

Botsford LW, White JW, Coffroth M-A et al (2009) Connectivity and resilience of coral reef metapopulations in marine protected areas: matching empirical efforts to predictive needs. Coral Reefs 28:327–337. https://doi.org/10.1007/s00338-009-0466-z

Brown CJ, Harborne AR, Paris CB, Mumby PJ (2016) Uniting paradigms of connectivity in marine ecology. Ecology 97:2447–2457. https://doi.org/10.1002/ecy.1463

Bruford MW, Wayne RK (1993) Microsatellites and their application to population genetic studies. Curr Opin Genet Dev 3:939–943. https://doi.org/10.1016/0959-437X(93)90017-J

Burgess SC, Nickols KJ, Griesemer CD et al (2014) Beyond connectivity: how empirical methods can quantify population persistence to improve marine protected-area design. Ecol Appl 24:257–270. https://doi.org/10.1890/13-0710.1

Calenge C, Dray S, Royer-Carenzi M (2009) The concept of animals' trajectories from a data analysis perspective. Eco Inform 4:34–41. https://doi.org/10.1016/J.ECOINF.2008.10.002

Capel KCC, Creed J, Kitahara MV et al (2019) Multiple introductions and secondary dispersion of Tubastraea spp. in the Southwestern Atlantic. Sci Rep 9:13978. https://doi.org/10.1038/s41598-019-50442-3

Chaves LTC, Pereira PHC, Feitosa JLL (2013) Coral reef fish association with macroalgal beds on a tropical reef system in North-Eastern Brazil. Mar Freshw Res 64:1101. https://doi.org/10.1071/MF13054

Chevis M, Godley B, Lewis J et al (2017) Movement patterns of juvenile hawksbill turtles Eretmochelys imbricata at a Caribbean coral atoll: long-term tracking using passive acoustic telemetry. Endanger Species Res 32:309–319. https://doi.org/10.3354/esr00812

Cooke SJ, Hinch SG, Wikelski M et al (2004) Biotelemetry: a mechanistic approach to ecology. Trends Ecol Evol 19:334–343. https://doi.org/10.1016/J.TREE.2004.04.003

Copertino MS, Creed JC, Lanari MO et al (2016) Seagrass and submerged aquatic vegetation (VAS) habitats off the coast of Brazil: state of knowledge, conservation and main threats. Braz J Oceanogr 64:53–80. https://doi.org/10.1590/S1679-875920161036064sp2

Cordeiro CAMM (2009) Estrutura da comunidade de peixes recifais do litoral sul da Paraíba

Cordeiro-Marino M, Braga MRA, Eston VR et al (1992) Mangrove macroalgal communities of Latin America: the state of art and perspectives. In: Seelinger U (ed) Coastal plant communities of Latin America. Elsevier, pp 51–64

Costa ACP, Garcia TM, Paiva BP et al (2020) Seagrass and rhodolith beds are important seascapes for the development of fish eggs and larvae in tropical coastal areas. Mar Environ Res 161:105064. https://doi.org/10.1016/j.marenvres.2020.105064

Cowen RK, Sponaugle S (2009) Larval dispersal and marine population connectivity. Annu Rev Mar Sci 1:443–466. https://doi.org/10.1146/annurev.marine.010908.163757

Crawford DL, Oleksiak MF (2016) Ecological population genomics in the marine environment. Brief Funct Genomics 15:342–351. https://doi.org/10.1093/bfgp/elw008

Cruz R, Santana JVM, Barreto CG et al (2020) Towards the rebuilding of spiny lobster stocks in Brazil: a review. Crustaceana 93:957–983. https://doi.org/10.1163/15685403-bja10073

Cunha IMC da, Souza AS de, Dias EA, et al (2014) Genetic multipartitions based on D-loop sequences and chromosomal patterns in Brown Chromis, *Chromis multilineata* (Pomacentridae), in the Western Atlantic. Biomed Res Int 2014:1–11. https://doi.org/10.1155/2014/254698

D'Aloia CC, Daigle RM, Côté IM et al (2017) A multiple-species framework for integrating movement processes across life stages into the design of marine protected areas. Biol Conserv 216:93–100. https://doi.org/10.1016/j.biocon.2017.10.012

da Silva R, Veneza I, Sampaio I et al (2015) High levels of genetic connectivity among populations of yellowtail snapper, Ocyurus chrysurus (Lutjanidae—Perciformes), in the Western South Atlantic revealed through multilocus analysis. PLoS One 10:e0122173. https://doi.org/10.1371/journal.pone.0122173

de Souza JN, Nunes FLD, Zilberberg C et al (2017) Contrasting patterns of connectivity among endemic and widespread fire coral species (Millepora spp.) in the tropical Southwestern Atlantic. Coral Reefs 36:701–716. https://doi.org/10.1007/s00338-017-1562-0

Devlin-Durante MK, Baums IB (2017) Genome-wide survey of single-nucleotide polymorphisms reveals fine-scale population structure and signs of selection in the threatened Caribbean Elkhorn coral, *Acropora palmata*. PeerJ 5:e4077. https://doi.org/10.7717/peerj.4077

Drury C, Dale KE, Panlilio JM et al (2016) Genomic variation among populations of threatened coral: Acropora cervicornis. BMC Genomics 17:286. https://doi.org/10.1186/s12864-016-2583-8

Dumaresq GM (2019) Assembleias de peixes recifais em poças de maré tropicais: elementos estruturadores e mudanças em sua composição (1999 e 2018)

Eggertsen L, Ferreira CEL, Fontoura L et al (2017) Seaweed beds support more juvenile reef fish than seagrass beds in a South-Western Atlantic tropical seascape. Estuar Coast Shelf Sci 196:97–108. https://doi.org/10.1016/j.ecss.2017.06.041

Ellegren H (2014) Genome sequencing and population genomics in non-model organisms. Trends Ecol Evol 29:51–63. https://doi.org/10.1016/J.TREE.2013.09.008

Elshire RJ, Glaubitz JC, Sun Q et al (2011) A robust, simple genotyping-by-sequencing (GBS) approach for high diversity species. PLoS One 6:e19379. https://doi.org/10.1371/journal.pone.0019379

Endo CAK, Gherardi DFM, Pezzi LP, Lima LN (2019) Low connectivity compromises the conservation of reef fishes by marine protected areas in the tropical South Atlantic. Sci Rep 9. https://doi.org/10.1038/s41598-019-45042-0

Ferreira HM, Reuss-Strenzel GM, Alves JA, Schiavetti A (2014) Local ecological knowledge of the artisanal fishers on Epinephelus itajara (Lichtenstein, 1822) (Teleostei: Epinephelidae) on Ilhéus coast—Bahia State, Brazil. J Ethnobiol Ethnomed 10:51. https://doi.org/10.1186/1746-4269-10-51

Ferreira HM, Magris RA, Floeter SR, Ferreira CEL (2022) Drivers of ecological effectiveness of marine protected areas: a meta-analytic approach from the Southwestern Atlantic Ocean (Brazil). J Environ Manag 301:113889. https://doi.org/10.1016/j.jenvman.2021.113889

Figueiredo J, Baird AH, Connolly SR (2013) Synthesizing larval competence dynamics and reef-scale retention reveals a high potential for self-recruitment in corals. Ecology 94:650–659. https://doi.org/10.1890/12-0767.1

Frédou T, Ferreira BP (2005) Bathymetric trends of northeastern Brazilian snappers (Pisces, Lutjanidae): implications for the reef fishery dynamic. Braz Arch Biol Technol 48:787–800. https://doi.org/10.1590/S1516-89132005000600015

Giancalone VM, Simon T, Ferreira BP, et al (2016) A pilot study on movement patterns of Brazilian reef fish using acoustic telemetry

Giglio VJ, Pinheiro HT, Bender MG et al (2018) Large and remote marine protected areas in the South Atlantic Ocean are flawed and raise concerns: comments on Soares and Lucas (2018). Mar Policy 96:13–17. https://doi.org/10.1016/j.marpol.2018.07.017

Gleason DF, Hofmann DK (2011) Coral larvae: from gametes to recruits. J Exp Mar Biol Ecol 408:42–57. https://doi.org/10.1016/J.JEMBE.2011.07.025

Goodridge Gaines LA, Olds AD, Henderson CJ et al (2020) Linking ecosystem condition and landscape context in the conservation of ecosystem multifunctionality. Biol Conserv 243:108479. https://doi.org/10.1016/j.biocon.2020.108479

Green AL, Maypa AP, Almany GR et al (2015) Larval dispersal and movement patterns of coral reef fishes, and implications for marine reserve network design. Biol Rev 90:1215–1247. https://doi.org/10.1111/brv.12155

Guzmán BE, Nuñes JJ, Vejar A et al (2011) Genetic diversity and population structure of two South American marine gastropods, Crepipatella dilatata and C. fecunda (Gastropoda : Calyptraeidae): distinct patterns based on developmental mode. Ita J Zoo 78:444–454

Hamilton SL, Regetz J, Warner RR (2008) Postsettlement survival linked to larval life in a marine fish. Proc Natl Acad Sci 105:1561–1566. https://doi.org/10.1073/pnas.0707676105

Hammerman NM, Rivera-Vicens RE, Galaska MP et al (2018) Population connectivity of the plating coral Agaricia lamarcki from Southwest Puerto Rico. Coral Reefs 37:183–191. https://doi.org/10.1007/s00338-017-1646-x

Hanski I (1998) Metapopulation dynamics. Nature 396:41–49. https://doi.org/10.1038/23876

Hanski I, Gilpin M (1991) Metapopulation dynamics: brief history and conceptual domain. Biol J Linn Soc 42:3–16. https://doi.org/10.1111/j.1095-8312.1991.tb00548.x

Harborne AR (2013) The ecology, behaviour and physiology of fishes on coral reef flats, and the potential impacts of climate change. J Fish Biol 83:417–447. https://doi.org/10.1111/jfb.12203

Harwood TD (2009) The circular definition of populations and its implications for biological sampling. Mol Ecol 18:765–768. https://doi.org/10.1111/j.1365-294X.2008.04066.x

Haywood MDE, Kenyon RA (2009) Habitat shifts by decapods—an example of connectivity across tropical coastal ecosystems. In: Nagelkerken I (ed) Ecological connectivity among tropical coastal ecosystems. Springer, Dordrecht, pp 229–269

Hughes TP, Baird AH, Bellwood DR et al (2003) Climate change, human impacts, and the resilience of coral reefs. Science 301:929–934. https://doi.org/10.1126/science.1085046

Huijbers CM, Nagelkerken I, Debrot AO, Jongejans E (2013) Geographic coupling of juvenile and adult habitat shapes spatial population dynamics of a coral reef fish. Ecology 94:1859–1870. https://doi.org/10.1890/11-1759.1

Hussey NE, Kessel ST, Aarestrup K et al (2015) Aquatic animal telemetry: a panoramic window into the underwater world. Science (New York, NY) 348:1255642. https://doi.org/10.1126/science.1255642

Igulu MM, Nagelkerken I, Dorenbosch M et al (2014) Mangrove habitat use by juvenile reef fish: meta-analysis reveals that tidal regime matters more than biogeographic region. PLoS One 9:e114715. https://doi.org/10.1371/journal.pone.0114715

Klautau M, Russo CAM, Lazoski C et al (1999) Does cosmopolitanism result from Overconservative systematics? A case study using the marine sponge Chondrilla nucula. Evolution 53:1414–1422

Krumme U (2009) Diel and tidal movements by fish and decapods linking tropical coastal ecosystems. In: Nagelkerken I (ed) Ecological connectivity among tropical coastal ecosystems. Springer, Dordrecht, pp 271–324

Leão ZMAN, Kikuchi RKP, Testa V (2003) Corals and coral reefs of Brazil. Latin American Coral Reefs 9–52. https://doi.org/10.1016/B978-044451388-5/50003-5

Leis J (2007) Behaviour as input for modelling dispersal of fish larvae: behaviour, biogeography, hydrodynamics, ontogeny, physiology and phylogeny meet hydrography. Mar Ecol Prog Ser 347:185–193. https://doi.org/10.3354/meps06977

Levins R (1970) Extinction. In: Gerstenhaber M (ed) Some mathematical problems in biology. American Mathematical Society, Providence, RI, pp 77–107

Lewis N, Day J, Aulani W et al (2017) Large-scale marine protected areas: guidelines for design and management. IUCN, International Union for Conservation of Nature

Liedke AMR, Pinheiro HT, Floeter SR, Bernardi G (2020) Phylogeography of the banded butterflyfish, Chaetodon striatus, indicates high connectivity between biogeographic provinces and ecosystems in the western Atlantic. Neotrop Ichthyol 18. https://doi.org/10.1590/1982-0224-2019-0054

Lima LS, Gherardi DFM, Pezzi LP et al (2021) Potential changes in the connectivity of marine protected areas driven by extreme ocean warming. Sci Rep 11. https://doi.org/10.1038/s41598-021-89192-6

Lowe WH, Allendorf FW (2010) What can genetics tell us about population connectivity? Mol Ecol 19:3038–3051. https://doi.org/10.1111/j.1365-294X.2010.04688.x

Lydersen C, Nøst OA, Lovell P et al (2002) Salinity and temperature structure of a freezing Arctic fjord-monitored by white whales (*Delphinapterus leucas*). Geophys Res Lett 29:34-1–34-4. https://doi.org/10.1029/2002GL015462

Magris RA, Treml EA, Pressey RL, Weeks R (2016) Integrating multiple species connectivity and habitat quality into conservation planning for coral reefs. Ecography 39:649–664. https://doi.org/10.1111/ecog.01507

Magris RA, Andrello M, Pressey RL et al (2018) Biologically representative and well-connected marine reserves enhance biodiversity persistence in conservation planning. Conserv Lett 11

Mantelatto MC, Póvoa AA, Skinner LF et al (2020) Marine litter and wood debris as habitat and vector for the range expansion of invasive corals (Tubastraea spp.). Mar Pollut Bull 160:111659. https://doi.org/10.1016/J.MARPOLBUL.2020.111659

Margules CR, Pressey RL (2000) Systematic conservation planning. Nature 405:243–253. https://doi.org/10.1038/35012251

Marshall DJ, Morgan SG (2011) Ecological and evolutionary consequences of linked life-history stages in the sea. Curr Biol 21

Mcleod E, Anthony KRN, Mumby PJ et al (2019) The future of resilience-based management in coral reef ecosystems. J Environ Manag 233:291–301. https://doi.org/10.1016/J.JENVMAN.2018.11.034

Mooney TA, Katija K, Shorter KA et al (2015) ITAG: an eco-sensor for fine-scale behavioral measurements of soft-bodied marine invertebrates. Anim Biotelem 3:31. https://doi.org/10.1186/s40317-015-0076-1

Mora C, Sale PF (2002) Are populations of coral reef fish open or closed? Trends Ecol Evol 17:422–428. https://doi.org/10.1016/S0169-5347(02)02584-3

Nagelkerken I (ed) (2009) Ecological connectivity among tropical coastal ecosystems. Springer, Dordrecht

Nagelkerken I, Dorenbosch M, Verberk W et al (2000) Importance of shallow-water biotopes of a Caribbean bay for juvenile coral reef fishes: patterns in biotope association, community structure and spatial distribution. Mar Ecol Prog Ser 202:175–192. https://doi.org/10.3354/meps202175

Nassar JM, Khan SM, Velling SJ et al (2018) Compliant lightweight non-invasive standalone “marine skin” tagging system. npj flexible. Electronics 2:13. https://doi.org/10.1038/s41528-018-0025-1

Neves EG, Andrade SCS, da Silveira FL, Solferini VN (2008) Genetic variation and population structuring in two brooding coral species (Siderastrea stellata and Siderastrea radians) from Brazil. Genetica 132:243–254. https://doi.org/10.1007/s10709-007-9168-z

Neves JMM, Lima SMQ, Mendes LF et al (2016) Population structure of the Rockpool Blenny Entomacrodus vomerinus shows source-sink dynamics among ecoregions in the tropical Southwestern Atlantic. PLoS One 11:e0157472. https://doi.org/10.1371/journal.pone.0157472

Nielsen ES, Henriques R, Beger M et al (2020) Multi-model seascape genomics identifies distinct environmental drivers of selection among sympatric marine species. BMC Evol Biol 20:121. https://doi.org/10.1186/s12862-020-01679-4

North EW, Gallego A, Petitgas P, et al (2009) ICES Cooperative Research Report Rapport des Recherches Collectives Manual of recommended practices for modelling physical-biological interactions during fish early life International Council for the Exploration of the Sea Conseil International pour l’Exploration de la Mer

Nunes FLD, Norris RD, Knowlton N (2011) Long distance dispersal and connectivity in Amphi-Atlantic corals at regional and basin scales. PLoS One 6. https://doi.org/10.1371/journal.pone.0022298

Ogden JC, Quinn TP (1984) Migration in coral reef fishes: ecological significance and orientation mechanisms. In: McCleave JD, Arnold JP, Dodson JJ, Neill WH (eds) Mechanisms of migration in fishes. Springer, Boston, pp 293–308

Olds A, Connolly R, Pitt K, Maxwell P (2012) Primacy of seascape connectivity effects in structuring coral reef fish assemblages. Mar Ecol Prog Ser 462:191–203. https://doi.org/10.3354/meps09849

Oleksiak MF, Rajora OP (2019) Marine population genomics: challenges and opportunities. Springer, Cham, pp 3–35

Padua A, Cunha HA, Klautau M (2018) Gene flow and differentiation in a native calcareous sponge (Porifera) with unknown dispersal phase. Mar Biodivers 48:2125–2135. https://doi.org/10.1007/s12526-017-0742-z

Paludo D, Langguth A (2002) Use of space and temporal distribution of Trichechus manatus manatus Linnaeus in the region of Sagi, Rio Grande do Norte State, Brazil (Sirenia, Trichechidae). Revista Brasileira de Zoologia 19:205–215. https://doi.org/10.1590/S0101-81752002000100019

Paris C, Chérubin L, Cowen R (2007) Surfing, spinning, or diving from reef to reef: effects on population connectivity. Mar Ecol Prog Ser 347:285–300. https://doi.org/10.3354/meps06985

Peck MA, Hufnagl M (2012) Can IBMs tell us why most larvae die in the sea? Model sensitivities and scenarios reveal research needs. J Mar Syst 93:77–93. https://doi.org/10.1016/J.JMARSYS.2011.08.005

Peluso L, Tascheri V, Nunes FLD et al (2018) Contemporary and historical oceanographic processes explain genetic connectivity in a Southwestern Atlantic coral. Sci Rep 8:1–12. https://doi.org/10.1038/s41598-018-21010-y

Pereira PHC, Ferreira BP, Rezende SM (2010) Community structure of the ichthyofauna associated with seagrass beds (Halodule wrightii) in Formoso River estuary—Pernambuco, Brazil. An Acad Bras Cienc 82:617–628. https://doi.org/10.1590/S0001-37652010000300009

Pereira PHC, dos Santos MVB, Lippi DL et al (2017) Difference in the trophic structure of fish communities between artificial and natural habitats in a tropical estuary. Mar Freshw Res 68:473. https://doi.org/10.1071/MF15326

Pina-Amargós F, González-Sansón G (2009) Movement patterns of goliath grouper Epinephelus itajara around Southeast Cuba: implications for conservation. Endanger Species Res 7:243–247. https://doi.org/10.3354/esr00192

Pinheiro HT, Bernardi G, Simon T et al (2017) Island biogeography of marine organisms. Nature 549:82–85. https://doi.org/10.1038/nature23680

Pinheiro HT, Rocha LA, Macieira RM et al (2018) South-Western Atlantic reef fishes: zoogeographical patterns and ecological drivers reveal a secondary biodiversity Centre in the Atlantic Ocean. Divers Distrib 24:951–965. https://doi.org/10.1111/ddi.12729

Pires D d O, Castro CB, Segal B et al (2016) Reprodução de corais de águas rasas do Brasil. In: Zilberberg C, Abrantes DP, Marques JA et al (eds) Conhecendo os Recifes Brasileiros, 1st edn. Museu Nacional UFRJ, Rio de Janeiro, pp 111–128

Pittman SJ, Monaco ME, Friedlander AM et al (2014) Fish with chips: tracking reef fish movements to evaluate size and connectivity of Caribbean marine protected areas. PLoS One 9:e96028. https://doi.org/10.1371/journal.pone.0096028

Planes S, Jones GP, Thorrold SR (2009) Larval dispersal connects fish populations in a network of marine protected areas. Proc Natl Acad Sci USA 106:5693–5697. https://doi.org/10.1073/pnas.0808007106

Putman NF (2016) An ecological perspective on the migrations of marine fishes. Environ Biol Fish 99:801–804. https://doi.org/10.1007/s10641-016-0512-y

Querino LAC (2011) Composição e estrutura da comunidade de peixes recifais do Parque Estadual Marinho Areia Vermelha. Cabedelo, PB

Reis-Filho JA, Schmid K, Harvey ES, Giarrizzo T (2019) Coastal fish assemblages reflect marine habitat connectivity and ontogenetic shifts in an estuary-bay-continental shelf gradient. Mar Environ Res 148:57–66. https://doi.org/10.1016/J.MARENVRES.2019.05.004

Rodrigues RR, Rothstein LM, Wimbush M (2007) Seasonal variability of the South Equatorial Current bifurcation in the Atlantic ocean: a numerical study. J Phys Oceanogr 37:16–30

Roberts KE, Cook CN, Beher J, Treml EA (2021) Assessing the current state of ecological connectivity in a large marine protected area system. Conserv Biol 35:699–710. https://doi.org/10.1111/cobi.13580

Rudorff CAG, Lorenzzetti JA, Gherardi DFM, Lins-Oliveira JE (2009) Modeling spiny lobster larval dispersion in the tropical Atlantic. Fish Res 96:206–215. https://doi.org/10.1016/J.FISHRES.2008.11.005

Russo CAM, Solé-Cava AM, Thorpe JP (1994) Population structure and genetic variation in two tropical sea anemones (Cnidaria, Actinidae) with different reproductive strategies. Mar Biol 119:267–276. https://doi.org/10.1007/BF00349566

Salas EM, Bernardi G, Berumen ML et al (2019) RADseq analyses reveal concordant Indian Ocean biogeographic and phylogeographic boundaries in the reef fish *Dascyllus trimaculatus*. R Soc Open Sci 6:172413. https://doi.org/10.1098/rsos.172413

Sale PF, Kritzer JP (2003) Determining the extent and spatial scale of population connectivity: decapods and coral reef fishes compared. Fish Res 65:153–172. https://doi.org/10.1016/J.FISHRES.2003.09.013

Sale PF, van Lavieren H, Ablan Lagman MC et al (2010) Preserving reef connectivity: a handbook for marine protected area managers. Connectivity Working Group, Coral Reef Targeted Research & Capacity Building for Management Program, UNU-INWEH, Melbourne

Santos S, Hrbeck T, Faris IP et al (2006) Population genetic structuring of the king weakfish, Macrodon ancylodon (Sciaenidae), in Atlantic coastal waters of South America: deep genetic divergence without morphological change. Mol Ecol 15:4361–4373. https://doi.org/10.1111/j.1365-294X.2006.03108.x

Selkoe K, D'Aloia C, Crandall E et al (2016) A decade of seascape genetics: contributions to basic and applied marine connectivity. Mar Ecol Prog Ser 554:1–19. https://doi.org/10.3354/meps11792

Sexton JP, Hangartner SB, Hoffmann AA (2014) Genetic isolation by environment or distance: which pattern of gene flow is most common? Evolution 68:1–15. https://doi.org/10.1111/evo.12258

Sherman K (1991) The large marine ecosystem concept: research and management strategy for living marine resources. Ecol Appl 1:349–360. https://doi.org/10.2307/1941896

Shinzato C, Mungpakdee S, Arakaki N, Satoh N (2016) Genome-wide SNP analysis explains coral diversity and recovery in the Ryukyu archipelago. Sci Rep 5:18211. https://doi.org/10.1038/srep18211

Siegel DA, Mitarai S, Costello CJ et al (2008) The stochastic nature of larval connectivity among nearshore marine populations. Proc Natl Acad Sci USA 105:8974–8979. https://doi.org/10.1073/pnas.0802544105

Soeth M, Spach HL, Daros FA et al (2020) Use of otolith elemental signatures to unravel lifetime movement patterns of Atlantic spadefish, Chaetodipterus faber, in the Southwest Atlantic Ocean. J Sea Res 158:101873. https://doi.org/10.1016/J.SEARES.2020.101873

Spalding MD, Fox HE, Allen GR, et al. (2007) Marine ecoregions of the world: a bioregionalization of coastal and shelf areas. BioScience 57(7):573–583. https://doi.org/10.1641/B570707

Sturm AB, Eckert RJ, Méndez JG et al (2020) Population genetic structure of the great star coral, Montastraea cavernosa, across the Cuban archipelago with comparisons between microsatellite and SNP markers. Sci Rep 10:15432. https://doi.org/10.1038/s41598-020-72112-5

Sundby S, Kristiansen T (2015) The principles of buoyancy in marine fish eggs and their vertical distributions across the world oceans. PLoS One 10:e0138821. https://doi.org/10.1371/journal.pone.0138821

Sunnucks P (2000) Efficient genetic markers for population biology. Trends Ecol Evol 15:199–203. https://doi.org/10.1016/S0169-5347(00)01825-5

Treml EA, Halpin PN, Urban DL, Pratson LF (2008) Modeling population connectivity by ocean currents, a graph-theoretic approach for marine conservation. Landsc Ecol 23:19–36. https://doi.org/10.1007/s10980-007-9138-y

van Nouhuys S (2016) Metapopulation ecology. In: eLS. John Wiley & Sons, Ltd, Chichester, pp 1–9

Vila-Nova DA, Bender MG, Carvalho-Filho A et al (2011) The use of non-reef habitats by Brazilian Reef Fish species: considerations for the design of marine protected areas. Natureza & Conservação 9:79–86. https://doi.org/10.4322/natcon.2011.010

Virtanen EA, Moilanen A, Viitasalo M (2020) Marine connectivity in spatial conservation planning: analogues from the terrestrial realm. Landsc Ecol 35:1021–1034. https://doi.org/10.1007/s10980-020-00997-8

Volk DR, Konvalina JD, Floeter SR et al (2021) Going against the flow: barriers to gene flow impact patterns of connectivity in cryptic coral reef gobies throughout the western Atlantic. J Biogeogr 48:427–439. https://doi.org/10.1111/jbi.14010

White CF, Lin Y, Clark CM, Lowe CG (2016) Human vs robot: comparing the viability and utility of autonomous underwater vehicles for the acoustic telemetry tracking of marine organisms. J Exp Mar Biol Ecol 485:112–118. https://doi.org/10.1016/J.JEMBE.2016.08.010

Whoriskey F, Hindell M (2016) Developments in tagging technology and their contributions to the protection of marine species at risk. Ocean Dev Int Law 47:221–232. https://doi.org/10.1080/00908320.2016.1194090

Xavier JH d A, Cordeiro CAMM, Tenório GD et al (2012) Fish assemblage of the Mamanguape environmental protection area, NE Brazil: abundance, composition and microhabitat availability along the mangrove-reef gradient. Neotrop Ichthyol 10:109–122. https://doi.org/10.1590/S1679-62252012000100011