Functional connectivity in multi-habitat marine species

Porter ES[1*], Ponchon A[1], Allgayer RL[1], Finnegan S[1], Travis JMJ[1], Layton KKS[1]

[1]School of Biological Sciences, University of Aberdeen, Aberdeen, UK

*Corresponding author email: bethporter123@gmail.com

Co-author emails: aurore.ponchon@gmail.com, r.allgayer.17@abdn.ac.uk, sfinnegan898@gmail.com, justin.travis@abdn.ac.uk, kara.layton@abdn.ac.uk

Abstract

Many marine species use different habitats at different stages of their life cycle. Functional connectivity, the degree to which the seascape facilitates or impedes movement between habitat patches, is poorly studied in marine systems. We reviewed the scientific literature to explore the various barriers preventing functional connectivity between marine habitats and how the removal of these barriers may restore connectivity. To our knowledge, this is the first systematic review to investigate functional connectivity between life cycle habitats for a range of marine species. A total of 4,499 records were identified and screened, leaving 69 publications eligible for review. The results highlighted a range of distances between nursery and adult habitats that limited functional connectivity for a number of species, predominantly reef fishes. For some species, adults were absent on reefs >9km from the closest nursery habitat, suggesting a threshold for connectivity. Similarly, increased distance between spawning and settlement habitats decreased settling success of larvae of various taxa. Pelagic larval duration, seascape topography and climate change were also shown to impact functional connectivity during the larval phase. The removal and mitigation of barriers preventing functional connectivity, including dams and habitat fragmentation, restored connectivity between disconnected life cycle habitats, but the efficacy of

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these approaches differed between species and studies. The results of this review deepen our understanding of marine functional connectivity between life cycle habitats via larval, juvenile, and adult dispersal. These findings have implications for the design and management of marine reserve networks.

Keywords: functional connectivity, structural connectivity, multihabitat, barrier, nursery, life stage

1. Introduction

Connectivity is broadly defined as the ability of the seascape to facilitate biological fluctuation (Taylor et al. 1993, Tischendorf & Fahrig 2000). Structural connectivity describes the spatial arrangement and continuity between habitat patches within the environment, irrespective of an organism's behaviour (Taylor et al. 2006). Structural connectivity is typically defined by the abundance of corridors or distance between patches (Metzger & Décamps 1997, Beier & Noss 1998). Functional connectivity on the other hand describes the degree to which the seascape facilitates or hinders an organism's movement between habitat patches (Taylor et al. 1993, 2006). It is an emergent, organism-based property, combining the physical structure of the environment with the behavioural response of the individual (Tischendorf & Fahrig 2000, Taylor et al. 2006). It depends on an individual's perception of costs and benefits associated with the habitat and how they integrate them to produce a path from one habitat to another (Bradbury et al. 2009). These costs and benefits are determined by the individual's biological characteristics, including ability to cross non-habitat patches (Greenberg 1989, Sieving et al. 1996), body size (Bakker & Van Vuren 2004), and competitive ability (Turcotte & Desrochers 2003) to name a few. Functional connectivity is also influenced by structural factors, such as distance between habitat

patches (Rothermel & Semlitsch 2002), spatial habitat distribution (Gillies & St Clair 2008), and the quality of inter-habitat matrices (Baum et al. 2004, Antongiovanni & Metzger 2005, Bender & Fahrig 2005). Therefore, changes in structural connectivity influence functional connectivity, and recent work has sought to understand this relationship (Doerr et al. 2014, Lough et al. 2017).

Most knowledge of functional connectivity is derived from terrestrial studies with comparably little information about marine systems. Connectivity is a critical criterion for the effective design of Marine Protected Areas (MPAs;Turgeon et al. 2010, Virtanen et al. 2020), but a lack of information about functional connectivity may hinder this process. This knowledge gap likely reflects the difficulty in investigating the interplay between structural and functional connectivity in marine environments (Bradbury et al. 2009). While dispersal pathways (Di Franco et al. 2012, Mori et al. 2016), dispersal estimates (Bradbury et al. 2008, Álvarez-Noriega et al. 2020), and climate change-driven changes in dispersal (Lett et al. 2010, Wilson et al. 2016) are well documented for marine systems, difficulties in conducting large-scale manipulations of marine habitats and populations (Bradbury et al. 2009, Virtanen et al. 2020) limits our knowledge of functional connectivity in particular.

Many marine species display life histories that require different habitats across life stages (Beck et al. 2001), but barriers often block migration between spawning, nursery, feeding and adult habitats (hereafter referred to as "life cycle habitats"; Jonsson et al. 1999). Diadromous species, for example, migrate between freshwater and marine habitats at different life stages and these migrations are arguably the most well-known for aquatic systems. Coral reef fishes are another well-known example of species that use different habitats throughout their life cycle. Although only 0.2% of the global seafloor is covered by coral reefs, these ecosystems provide habitat for 25%

of all marine species during at least one life cycle stage (Buddemeier et al. 2004). Many reef fishes have a life history consisting of three phases that each reside in a different habitat: planktonic larva in the water column, juveniles in coastal seagrass or mangrove nurseries, and adults on reefs (Adams & Ebersole 2002, Figure 1). In this case, a nursery habitat needs to provide conditions that support the density, growth, survival, and movement of juveniles (Beck et al. 2001), the latter of which being essential for promoting functional connectivity among juvenile and adult habitats. Larval dispersal is also a fundamental component of functional connectivity since it connects spawning and settlement habitats for species with bipartite life cycles (e.g. neon goby; Kritzer & Sale 2006, D'Aloia et al. 2015), and it contributes to gene flow among populations- a process that is especially important when considering MPA management (D'Aloia et al. 2015, Besson et al. 2017).
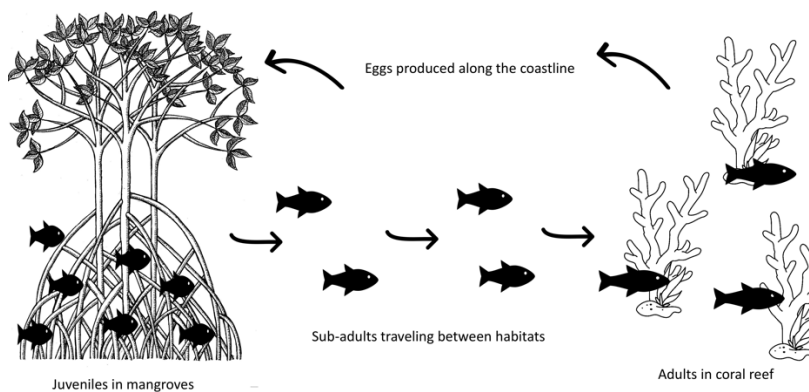

Figure 1. Illustration showing the changes in habitat use throughout the life cycle of the rainbow parrotfish (*Scarus guacamaia*). Similar life cycles are observed in many other coral reef fish species. Juveniles use mangroves as nurseries, then undertake ontogenetic migrations to coral reefs where they fulfil their adult life stage.

Marine species commonly use coastal and estuarine habitats, including seagrasses, mangroves and macroalgae, as nurseries and settlement sites. Yet, because almost 40% of the global human population lives within 100km from the coast, these habitats

are highly susceptible to anthropogenic disturbances (Cohen et al. 1997, Millennium Ecosystem Assessment 2005). Since the start of the twentieth century, around 70% of coastal wetland cover has been lost globally (Davidson 2014), and in the last 50 years, global mangrove cover has declined by 20-35% due to degradation and deforestation (Polidoro et al. 2010). Additionally, worldwide seagrass and other submerged aquatic vegetation cover has decreased by 65% and 48%, respectively (Lotze et al. 2006). The loss and fragmentation of important settlement and juvenile habitats is likely to affect functional connectivity due to increased distances to spawning and adult habitats and patchiness between them. It is possible that functional connectivity between these habitats may cease at certain distances, but few studies have attempted to measure these thresholds (Berkström et al. 2020).

Aside from habitat fragmentation and loss, physical barriers can also affect movement between life cycle habitats for migratory species. In the North Atlantic, many diadromous fish populations are now below 10% of historical levels (Limburg & Waldman 2009) and it is likely that habitat loss and reduced connectivity from dam construction is partially responsible for this decline (Belletti et al. 2020). Climate change can also obstruct functional connectivity, with ocean acidification impairing settlement behaviour of reef fish (Munday et al. 2009a, Devine et al. 2012) and increased sea temperatures changing the pelagic larval durations (PLD) of species (Irisson 2008, Ayata et al. 2010, Huret et al. 2010). As such, marine species that use multiple habitats throughout their life cycle are impacted by a variety of barriers that limit functional connectivity and thus understanding the inter-linkages between these habitats is of central importance.

This systematic review aims to investigate the importance of functional connectivity between life cycle habitats for any marine species using multiple habitats throughout

their life cycle. Previous reviews have already been conducted on marine connectivity among habitats (e.g. Adams et al. 2006, Appeldoorn et al. 2009, Fullerton et al. 2010, Jones et al. 2009, Nagelkerken 2007), larval dispersal and movement of fishes (Almany et al. 2009, Green et al. 2015, Planes et al. 2000), and larval dispersal and its implications for connectivity (Hedgecock 2010, García-Machado et al. 2018, White et al. 2019), but this is the first systematic review of *functional* connectivity between life cycle habitats for a *range* of marine species. Here, we address the knowledge gap surrounding distance thresholds where functional connectivity ceases between life cycle habitats and we outline information about barriers to functional connectivity. We also provide recommendations on how we can use integrative tools to measure and evaluate functional connectivity more accurately and help restore it. The information gleaned here has important implications for marine spatial planning and for the preservation of biodiversity in the face of a changing climate.

2. Materials and Methods

2.1 Systematic review

2.1.1 Search strategy

A systematic literature review was conducted by collating as wide a range of publications as possible from two search databases: Scopus and Web of Science (hereafter: WOS). Other databases, including Google Scholar, JSTOR, Pubmed and Wiley, were excluded from the search as they lacked an option for bulk download, had too few characters and did not support the use of wildcards (*) or Boolean operators (e.g. AND, OR) in the search string. Records in the two databases were searched based on words and phrases in their title, abstract and keywords. The search string was based on combinations of synonyms for the key words and phrases relevant to

the topic and were grouped into three categories: (i) functional connectivity, (ii) marine species that use different habitats at different life cycle stages and (iii) terms related to the type of study/experiment. The words and phrases related to each category were contained within brackets and separated by the OR operator. The three bracketed categories were connected using the AND operator. Wildcards (*) were used to search for all possible word endings, e.g. connect* would search for connectivity, connection, connected, *etc.*

2.1.2 Testing the search string

A list of 29 publications that were especially relevant to this topic based on their titles, abstracts and keywords was compiled and used as a test set (Appendix S1). To test the search string's ability to detect these suitable publications, the search results were checked for the presence of these 29 publications. The first search string only detected 10 out of the 29 publications across the databases. As a result, missing words and phrases from the titles, abstracts, and keywords of the remaining 19 publications were incorporated into the search string. Modifying the search string was an iterative process of trial and error to achieve a balance between a sufficient number of the 29 references being detected and having too many results to screen (>3,000 per database). The words and phrases in the search strings varied slightly between the two databases because they differed in sensitivity (Supplementary Table 1). Additionally, the terms in section (ii) were split across two brackets to search in WOS as this reduced the number of results to a manageable level (<3,000; Supplementary Table 1 and Appendix S2). After each search was completed, the results were filtered to include only those records published in English and in relevant areas (e.g. marine biology, fisheries science, *etc.;* Appendix S2). In order to minimise any publication or regional biases, and to include as much secondary and grey literature as possible, the

results were not filtered by date of publication, region or publication type. The final search string detected 25 out of the 29 references and produced a total 4,499 records (1,838 from Scopus and 2,661 from WOS). This was deemed a sufficient balance between number of test references detected and number of records to screen. The final search string is presented in Appendix S2.

2.1.3 Screening

A workflow of the complete screening process is provided in Figure 2 and all records were exported to Endnote X9 to facilitate this process. First, a total of 264 duplicate records were identified and removed from the dataset using the 'Find Duplicates' tool in Endnote. The remaining 4,235 records were exported into an Excel spreadsheet for the subsequent screening phases. Second, we removed irrelevant records based on their titles, abstracts, and keywords. The final criteria (Appendix S3) were validated to ensure they were effective for screening. A set of 20 records were distributed to two independent reviewers for screening based on title, abstract, keywords and criteria. Minor discrepancies among the reviewers were discussed and resolved by the authors and the results were not modified. Next, the remaining 4,235 records were screened based on their title, abstract, keywords and criteria and a total of 254 records were retained. The full texts of these 254 records were scrutinized in the final screening phase to determine their eligibility for inclusion in this review. We did not explicitly test the validity of this screening phase because the criteria for exclusion were similar to the second screening phase that was validated. After the final screening phase, a

further 185 records were excluded (Appendix S4) and a total 69 papers were eligible
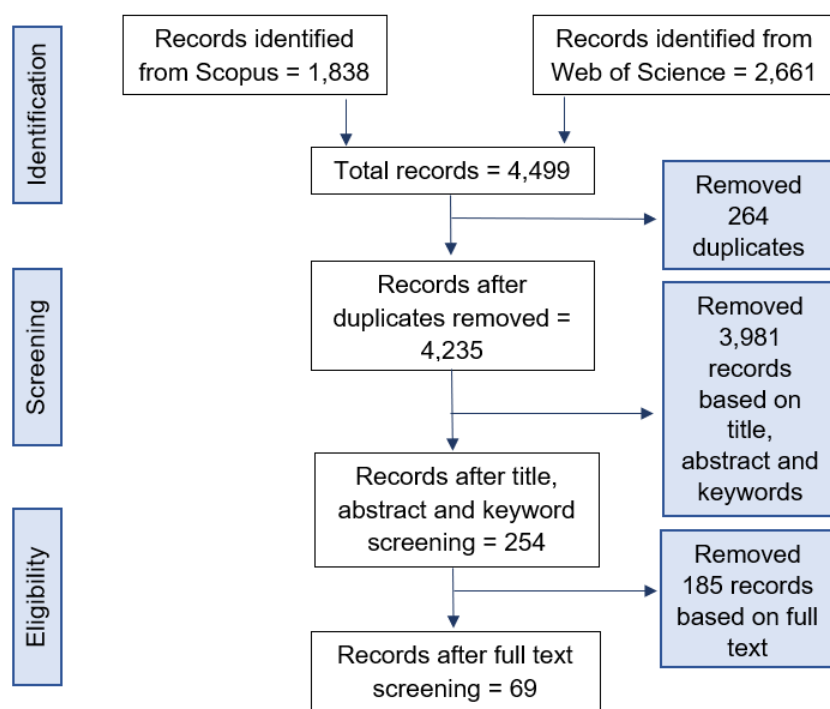
for inclusion in the review.

Figure 2. Flowchart showing the number of records identified by two databases (Scopus and Web of Science), the number of records removed and retained at the screening phases and the number deemed eligible to include in the final review. Criteria validation was conducted as part of the screening process. Flowchart template adapted from Moher et al. (2009).

The 69 eligible records were organised using Microsoft Excel and additional metadata

was added for each, including taxa (e.g. reef fish, elasmobranchs, *etc.*) and region

(e.g. Indo-Pacific).

2.2 Case study: A population model for rainbow parrotfish

2.2.1 Model parameterization

In order to investigate the effects of anthropogenic impacts on population viability, we

designed a simplified population matrix model parameterised with demographic data

matching the rainbow parrotfish (*Scarus guacamaia*) with values taken from the

literature (Supplementary Table 2). This species was chosen because it relies heavily

on sufficient connectivity between mangrove nursery habitat and coral reefs for adult settlement. In our population model, we assumed the presence of three stages: juveniles which reside in the mangroves, subadults which undergo movements from the nursery, and adults which spend the rest of their lives on the coral reef settlement sites. The Leslie matrix used for population projection and calculation of λ, the rate of population increase, is available in Supplementary Table 3. Using this matrix, we conducted three experiments to investigate the effects of i) habitat fragmentation (increased distance between nursery and settlement site), ii) fishing pressure (increased mortality of subadults during transfer between sites), iii) nursery habitat degradation (reduction in juvenile survival rate), and a fourth experiment to reflect the combined pressure of all three.

2.2.2 Experiments

In the first experiment, we increased distance between mangrove and coral reef settlement site. Since the relationship between distance and subadult survival is unknown, we ran two simulations, one assuming a very simple negative linear and the other a negative exponential relationship. Maximum subadult survival rate was 0.65 (Kellner et al 2010) and the maximum distance away from nursery habitat was 42km (Claydon 2015). From these parameters, we created the following simple linear regression: $\sigma = -0.015d + 0.65$, where σ is the subadult survival rate and d is the distance between mangrove and coral reef sites. Using this relationship, we calculated subadult survival for a range of distances (0-40km), and the rate of population increase, λ, for the transition matrix. Population viability was defined as a population with λ=1. In the second experiment, we increased subadult mortality, reflecting greater fishing pressure over increasing distances. We tested a range of added mortality values (0.-0.15) to represent possible fishing pressures (harvest rates) that derived

from Kellner et al. (2010). In the third experiment we changed juvenile survival rate, since a reduction in nursery habitat quality impacts these rates. We used a range of juvenile survival rates (0.1-0.7) to investigate the importance of this stage on the viability of the population as a whole. In the final experiment, we tested all combinations of distance, harvest rate and juvenile survival to determine whether one pressure could be compensated for by improving another.

3. Systematic review

3.1 General trends

Although the search databases did contain records from secondary and grey literature, all eligible records in this study were published in scientific journals. Most of these records focused solely on teleost fish (n=66), with additional taxonomic coverage from elasmobranchs (n=2) and invertebrates (molluscs, crustaceans, corals) (n=69), although the later focused largely on both fish and invertebrate species. Within the teleost fish records, most were reef fish and diadromous fish (n=29 and n=17, respectively), from across a number of families. The number of articles published per year increased over a 20-year period (2000-2019), with a peak of eight articles in 2017 (Figure 3). The number of records published from 2010-2019 was two-fold higher than in 2000-2010 (Figure 3).
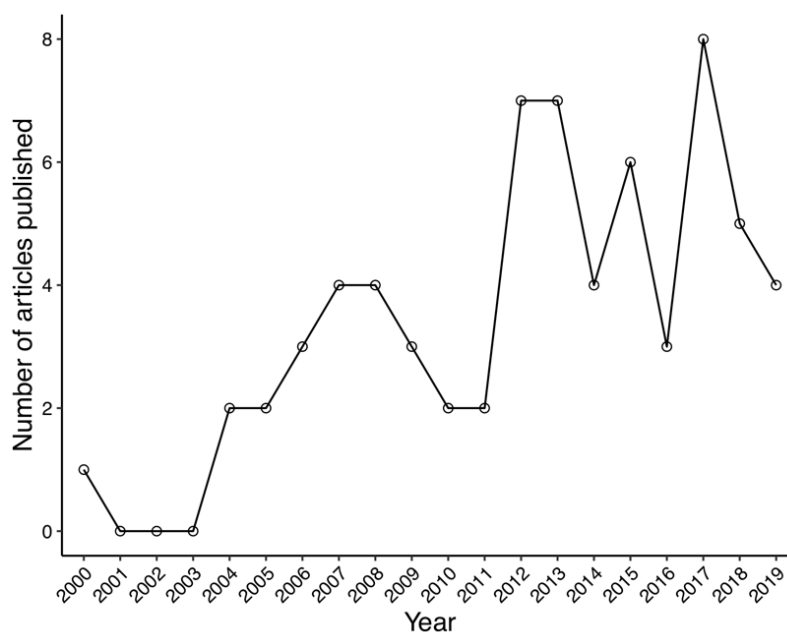
Figure 1. Number of papers published per year in scientific journals from 2000-2019 linked to multi-habitat functional connectivity in marine species.

The publications showed regional trends: 62.3% focussed on tropical and sub-tropical species, mainly in the Caribbean and Central America and the remainder on temperate species. Only five studies explicitly investigated functional connectivity and mentioned it in their titles, abstracts, and keywords, although others did discuss it in the main text (Bradbury et al. 2009, Turgeon et al. 2010, Espinoza et al. 2015, Segurado et al. 2015 and Lough et al. 2017).

3.2 Distance between nurseries and adult habitats

3.2.1 General trends

A study of 13 Australian estuaries reported a decline in nursery fish species richness and abundance on adult habitats with increasing distance from seagrasses, mangroves, and estuarine mouth (Gilby et al. 2018). Catch-per-unit-effort (CPUE) of nursery fishes in an Australian Gulf was highly correlated with connectivity and

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availability of coastal wetland nursery or breeding habitats (Meynecke et al. 2008). In Queensland, total area of wetland and connectedness to mangroves was positively correlated with CPUE of nursery fishes and invertebrates (Meynecke et al. 2007). For reef fishes, 19 studies demonstrated a negative relationship between distance from juvenile nurseries and adult abundance on reef habitats. Adult biomass and density of adults on reefs was higher when in proximity to nurseries, particularly large nurseries (Nagelkerken et al. 2000, Mumby et al. 2004, Dorenbosch et al. 2005, 2006a, 2006b, 2007, Grober-Dunsmore et al. 2007, Unsworth et al. 2008, McMahon et al. 2012, Nagelkerken et al. 2012, Olds et al. 2012a, 2012b, 2014, Claydon et al. 2015, Serafy et al. 2015, Harborne et al. 2016, Nagelkerken et al. 2017, Lee et al. 2019, Berkström et al. 2020). Where possible, these results are summarised in Tables 1 and 2. In Tanzania, for example, 25 species of nursery fish were absent or present in low densities on reefs far from seagrass and mangrove nurseries (~17km), compared to high abundances on reefs near nurseries (Table 1; Dorenbosch et al. 2005). In the US Virgin Islands, abundance and species richness of reef fish was higher on reefs with greater seagrass coverage and within 1km of nurseries (Table 1; Grober-Dunsmore et al. 2007). On four Caribbean islands, density and biomass of nursery-dependent fishes declined rapidly on reefs approaching 4km from nurseries and were almost entirely lost at 14km (Table 1; Nagelkerken et al. 2017). In contrast, Berkström et al. (2013) demonstrated an increase in nursery species abundance on reefs with increasing distance from mangrove nurseries. Overall, distance among nursery and adult habitats, as well as nursery size, have a significant impact on functional connectivity and below we discuss these impacts on some heavily-studied systems.

3.2.2 Trends in Parrotfishes

Parrotfishes (Family: Scaridae) were the focus of several studies examined in this review and this is likely because these grazing fish play a vital role in maintaining coral reef health (Cramer et al. 2017). For example, mean abundances of three parrotfishes (*Scarus. guacamaia, S. coeruleus* and *S. iseri)* on reefs were positively correlated with mangrove nursery area throughout the wider Caribbean (Serafy et al. 2015). Similarly, adult density and biomass of two nursery-using parrotfishes, *S. guacamaia* and *S. iserti,* were significantly higher on reefs near mangroves compared to those in mangrove-scarce areas (Table 2*;* Mumby et al. 2004). The presence of adult nursery-using parrotfish species was higher on reefs closer to seagrass and mangrove nurseries than those further away, and this pattern was not observed in non-nursery parrotfishes (Harborne et al. 2016). Finally, evidence of parrotfish grazing was higher on reefs near mangrove nursery habitats than those further away (Mumby & Hastings 2008).

3.2.3 Case study: Anthropogenic impacts on rainbow parrotfish viability

A series of experiments with our population model demonstrated that anthropogenic pressures, like habitat fragmentation and fishing, impacted population viability and functional connectivity in the rainbow parrotfish. First, we found that the maximum distance threshold between nursery and settlement site after which a population could no longer be viable was 15.58km (Figure 4a). As fishing pressure (harvest rate) increased to 5%, 10% and 15%, this maximum distance threshold decreased to 12.25km, 8.91km and 5.58km, respectively (Figure 4b). Below a juvenile survival rate of 0.3, the population could not remain viable even if the maximum distance between nursery and settlement site was just 1km (Figure 4c). Alternatively, increased juvenile survival resulted in an increase in the maximum distance threshold (Figure 4c). In the

combined experiment, a higher minimum juvenile survival rate could compensate for higher fishing pressure, but this depended on the distance between nursery and settlement site (Figure 4d). For instance, the highest harvest rate could no longer be compensated for by increased juvenile survival after 18km distance between sites (Figure 4d).
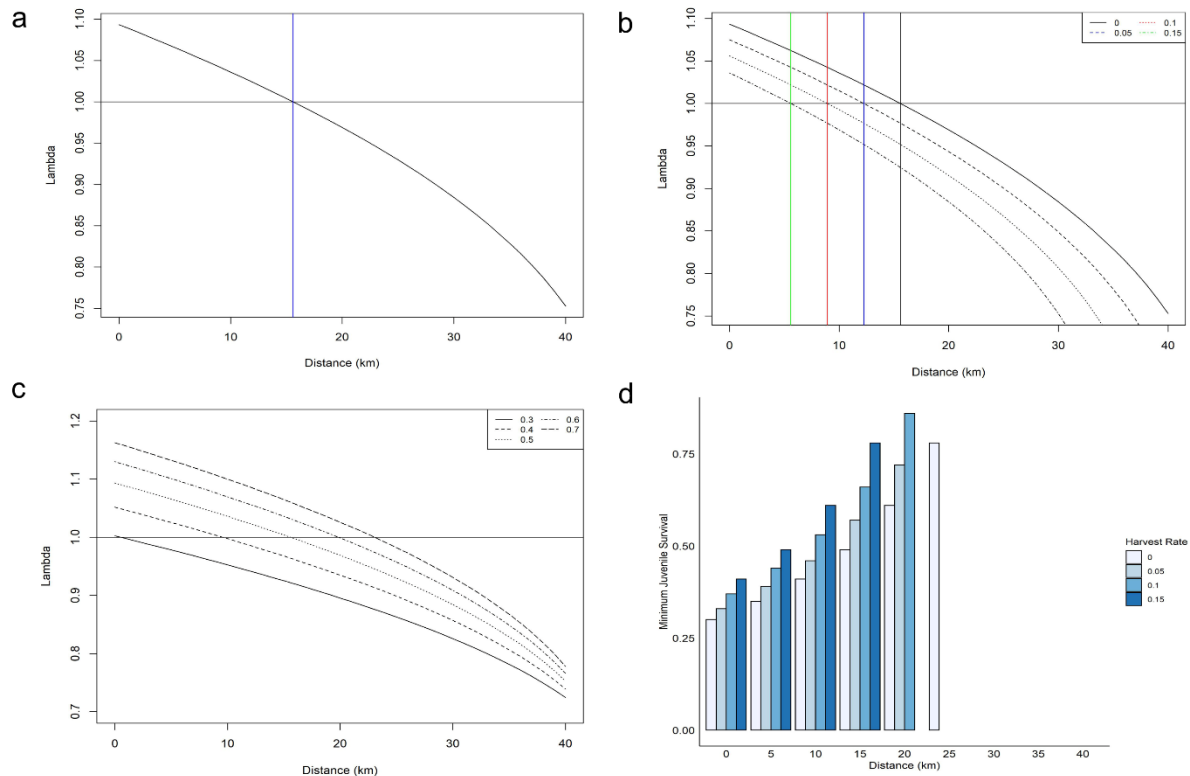

Figure 4: The impact of anthropogenic pressures on viability in the rainbow parrotfish. a) The maximum distance threshold (black horizontal line) between mangrove and coral reef sites to maintain a viable population (λ=1; red line) is 15.58km. b) The maximum distance threshold between mangrove and coral reef sites to maintain a viable population (λ=1; black horizontal line) decreases with increasing fishing pressure (harvest rate). c) Increasing juvenile survival can compensate for distance and increased fishing pressure up to a particular threshold at which the effect of habitat fragmentation stops the population from remaining viable. d) Increased juvenile survival increases the distance threshold between functional habitats.

3.2.4 Connectivity and reserve effects

Several studies demonstrated that structural connectivity between nursery and adult habitats enhanced reserve effects (e.g. higher biomass and abundance) for numerous reef fish species. Proximity to nurseries enhanced herbivorous reef fish biomass on

protected reefs in Australia, where biomass was near double that of non-protected reefs near mangroves (Olds et al. 2012b). In the Cayman Islands, proximity to nurseries and reserve protection (e.g. fishing protection) had an additive effect on biomass of large (>25cm total length) nursery species, with 139% and 203% higher biomass, respectively (Nagelkerken et al. 2012). In the Solomon Islands, structural connectivity between seagrass, mangrove and reef habitats enhanced reserve effects for 18 nursery species (Olds et al. 2014).

Table 1. The change (Δ) in density of adult nursery-using reef fish on reefs based on distance from nursery habitat. The nursery habitats are seagrasses or coastal wetlands, such as mangroves, or a combination, while adult habitats are represented by reefs. Change in adult density is represented by either a numerical value (e.g. <0.5/100m^2 = density of adults is less than 0.5 individuals per 100m^2) or general trend ('lower', 'decrease') when exact values were not presented in the paper. All data were extracted from publications included in this review.

Taxa	Distance from nursery	Δ in adult density	Region: Country	Reference
Barracuda *Sphyraena barracuda*	>9km	<0.03/100m^2	Caribbean: Aruba	Dorenbosch, et al. 2007
Butterflyfishes *Chaetodon capistratus*	>9km	Significantly lower	Caribbean: Aruba	Dorenbosch, et al. 2007
	14km	2/100m^2	Caribbean: Aruba, Bermuda, Cayman Islands and Curaçao	Nagelkerken et al. 2017
Goatfishes *Parupeneus spp.*	17km	Decreased	Africa: Tanzania	Dorenbosch, et al. 2005
Grunts *Haemulon flavolineatum*	2-4km 14km	Rapid decrease <5/100m^2	Caribbean: Aruba, Bermuda, Cayman Islands and Curaçao	Nagelkerken et al. 2017
Haemulon parra	>9km	Absent	Caribbean: Aruba	Dorenbosch, et al. 2007
Haemulon sciurus,	>9km	Significantly lower	Caribbean: Aruba	Dorenbosch, et al. 2007
	2-4km 14km	Rapid decrease <0.1/100m^2	Caribbean: Aruba, Bermuda, Cayman Islands and Curaçao	Nagelkerken et al. 2017
Haemulon spp.	>80km	Absent	Africa: Mozambique	Berkström et al. 2020
	1km	Decreased	Caribbean: US Virgin Islands	Grober-Dunsmore et al. 2007
Mojarra *Gerres cinereus*	>9km	Absent	Caribbean: Aruba	Dorenbosch, et al. 2007

Parrotfishes *Chlorurus strongylocephalus*	17km	Decreased	Africa: Tanzania	Dorenbosch, et al. 2005
Scarus ghobban	17km	Decreased	Africa: Tanzania	Dorenbosch, et al. 2005
Scarus guacamaia	>42km	Absent	Caribbean: Bonaire	Claydon et al. 2015
	>17km	Absent	Caribbean: Aruba	Dorenbosch et al. 2006b
	>9km	<0.03/100m^2	Caribbean: Aruba	Dorenbosch, et al. 2007
Scarus iserti	>9km	Significantly lower	Caribbean: Aruba	Dorenbosch, et al. 2007
	2-4km 14km	Rapid decrease <2/100m^2	Caribbean: Aruba, Bermuda, Cayman Islands and Curaçao	Nagelkerken et al. 2017
Scarus spp.	8km 12km	Declined Absent	Africa: Mozambique	Berkström et al. 2020
Snappers *Lutjanus apodus*	>9km	Significantly lower	Caribbean: Aruba	Dorenbosch, et al. 2007
	2-4km 14km	Rapid decrease <0.25/100m^2	Caribbean: Aruba, Bermuda, Cayman Islands and Curaçao	Nagelkerken et al. 2017
Lutjanus ehrenbergii	16km 50km	Four-fold decrease <1/100m^2	Red Sea	McMahon et al. 2012
Lutjanus griseus	>9km	Absent	Caribbean: Aruba	Dorenbosch, et al. 2007
Lutjanus mahogoni	>9km	Significantly lower	Caribbean: Aruba	Dorenbosch, et al. 2007
	2-4km 14km	Rapid decrease <0.1/100m^2	Caribbean: Aruba, Bermuda, Cayman Islands and Curaçao	Nagelkerken et al. 2017
Lutjanus spp.	8km 12km	Declined Absent	Africa: Mozambique	Berkström et al. 2020
	17km	Decreased	Africa: Tanzania	Dorenbosch, et al. 2005
	>1km	Decreases	Caribbean: US Virgin Islands	Grober-Dunsmore et al. 2007
Ocyurus chrysurus	9km	Significantly lower	Caribbean: Aruba	Dorenbosch, et al. 2007

	2-4km 14km	Rapid decrease <0.25/100m^2	Caribbean: Aruba, Bermuda, Cayman Islands and Curaçao	Nagelkerken et al. 2017
Wrasses *Cheilinus spp.*	17km	Decreased	Africa: Tanzania	Dorenbosch, et al. 2005
Cheilinus undulates	Far reefs	0.05/100m^2	Africa: Tanzania	Dorenbosch et al. 2006b

Table 2. The change (Δ) in biomass of adult fish on reefs based on increased distance from nurseries and represented by grams per 100m^2 (Nagelkerken et al. 2012) or based on reefs in mangrove-scarce areas compared to areas with higher mangrove cover and represented by percentage (Mumby et al. 2004). The fish are nursery species using coastal habitats, including seagrasses and mangroves, as nurseries and reefs as adult habitats. The studies were conducted in the Cayman Islands (Nagelkerken et al 2012) or Belize (Mumby et al. 2004) and are denoted by a and b, respectively.

Taxa	Δ in adult biomass
Grunts	
Haemulon flavolineatum	-672g[a]
Haemulon plumierii	-344g[a]
Haemulon sciurus	-414g[a]
	-2667%[b]
Parrotfish	
Scarus guacamaia	-160g[a]
Scarus iseri	-177g[a]
	-42%[b]
Lutjanus apodus	-563g[a]
Lutjanus mahogoni	-163g[a]
Ocyurus chrysurus	-337g[a]
	-50%[b]

3.3 Physical barriers to functional connectivity

3.3.1 General trends

The following nine studies demonstrated the effects of physical barriers and habitat fragmentation on functional connectivity between habitats for various fish species. In Mozambique, abundance of adult reef fish was very low on reefs that were separated from nurseries by deep water and large stretches of sand, despite the reefs being moderate distances from nurseries (Berkström et al. 2020). Similarly, a continental shelf break in the Red Sea acted as a barrier for juvenile snapper (*Lutjanus ehrenbergii*) dispersal from inshore nurseries to oceanic reefs beyond the break

(McMahon et al. 2012). Structural connectivity between an isolated fjord and the adjacent North Atlantic Ocean was limited to the few weeks a year when a manmade channel was opened. There was high genetic differentiation between rainbow smelt (*Osmerus mordax*) populations within and outside the fjord, suggesting the channel prevents access to spawning and nursery grounds outside the fjord (Bradbury et al. 2009). On a smaller scale, sand patches acted as a barrier to movement for longfin damselfish (*Stegastes diencaeus;* Turgeon et al. 2010). Probability of crossing sand barriers dropped sharply as sand width increased, falling below 50% when they were between 1.85-3.9m wide (Turgeon et al. 2010). Laboratory experiments on juvenile cod (*Gadus morhua*) observed a 37% reduction in gap crossing behaviour between eelgrass patches 7.5m apart, compared to 3m apart (Ryan et al. 2012). At the greater patch distance, juveniles delayed leaving the patch when in smaller groups, and gap crossing was 75% lower when predators were present (Ryan et al. 2012).

Two studies highlighted the negative effects of habitat fragmentation for Bahamian nursery species. Unfragmented, mangrove-lined creeks had higher abundance of nursery reef fishes than fragmented, mangrove-lined creeks, and some species, such as snappers, were smaller in the fragmented creeks compared to the unfragmented (Valentine-Rose et al. 2007). Minimally and unfragmented estuaries contained higher abundances of reef species (such as damselfish, parrotfish, snappers, grunts, and wrasses) than fragmented estuaries, while damselfishes and grunts were completely absent in totally fragmented estuaries (Layman et al. 2004). Habitat fragmentation also affected the grey reef (*Carcharhinus amblyrhynchos*), silvertip (*C. albimarginatus*), and bull shark (*C. leucas;* Espinoza et al. 2015). Network analysis revealed that removing reefs reduced the size and number of inter-reef movements, and several dispersal corridors between closely spaced reefs were identified (Espinoza et al.

2015). Similarly, fragmentation of nursery habitat is likely to be detrimental for the scalloped hammerhead shark (*Sphyrna lewini*), as the species has low oceanic dispersal for breeding (Duncan et al. 2006). Together, these studies demonstrate that small and large-scale habitat fragmentation can affect the movement of species between habitats.

3.3.2 Trends in Diadromous species

3.3.2.1 Barrier removal

The following 16 studies investigated physical barriers, such as dams, on the functional connectivity between life cycle habitats in diadromous species. In Australia's Hunter River, six diadromous species were only detected, or in higher abundances in an unrestricted tributary, compared to one restricted by human infrastructure (Rolls 2011). For the Australian grayling (*Prototroctes maraena*), an obligate migrant, dams blocked 44.5% of suitable habitat in New South Wales and 34-36% in Tasmania (Lin et al. 2017). Similarly, dams in the Tagus basin river network in Portugal reduced habitat availability to 58% and 72% and reduced structural and functional connectivity to 52% and 50% for sea lamprey (*Petromyzon marinus*) and allis shad (*Alosa alosa*), respectively (Segurado et al. 2015). In Maine, the removal of a dam blocking access to *P. marinus* nesting sites resulted in 400% more nests and a fourfold increase in the abundance of spawners (Hogg et al. 2013). Similarly, in France, the number of *P. marinus* nests in a river was 2.8 times higher following dam removal (Lasne et al. 2015). Dam removal has also had positive effects on salmonid species. Density of young brown trout (*Salmo trutta)* increased by 20.6k% upstream of dam removal and by 417% downstream while density of older *S. trutta* increased by 47% upstream and 39% downstream (Birnie-Gauvin et al. 2017). Similarly, abundances of *S. trutta* and

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rainbow trout (*Oncorhynchus mykiss*) increased more than twofold following removal of a dam in Michigan (Burroughs et al. 2010). Forget et al. (2018) also predicted that dam removal on the Sélune River would increase suitable habitat area for Atlantic salmon (*Salmo salar*) by 124%. Bull trout (*Salvelinus confluentus*) rapidly resumed their anadromous life cycle following removal of impassable dams that had landlocked a population for nearly 100 years (Quinn et al. 2017). Overall, these studies demonstrate that removing barriers can increase structural and functional connectivity between diadromous life cycle habitats.

3.3.2.2 Fish passes

Where barriers are not removed, fish passes can allow migrating species to navigate over barriers. In Australia, a navigation lock allowed nearly 15,000 congolli (*Pseudaphritis urvillii*) to pass dams blocking migration to downstream spawning grounds, resulting in a 180-fold increase in juvenile abundance (Bice et al. 2018). However, Australian bass (*Percalates novemaculeata*) were unable to locate fish pass entrances and could only migrate downstream to estuarine spawning grounds at high river-flow levels (Hardin et al. 2017). A laboratory experiment demonstrated that bristle passes on weirs significantly increased passage success for large eels (*Anguilla anguilla*) but were only marginally successful for river lamprey (*Lampetra fluviatilis;* Kerr et al. 2015), aligning with previous work (Foulds & Lucas, 2013). For Scottish Atlantic salmon (*S. salar*), even a 3% reduction in passability of passable manmade barriers had the same impact on connectivity as impassable manmade barriers (Buddendorf et al. 2019), however passage efficacy differed within and between species. In an English river, only 25% of freshwater-resident brown trout (*S. trutta*) were able to use a fish pass compared to 63% of anadromous *S. trutta,* despite having the same level of attraction to the pass (Lothian et al. 2020).

3.4 Larval dispersal and connectivity

In species with relatively sedentary adults, functional connectivity between larval and juvenile habitats is essential to maintain gene flow. This was observed in cod (*G. morhua*) and emperor (*Lethrinus nebulosus*) populations (Berry et al. 2012, Rogers et al. 2014). In red mullet (*Mullus barbatus*), connectivity between larval and settlement habitats across the Western Mediterranean region is weakened by substantial loss of larvae to unsuitable settlement sites (Gargano et al. 2017). For the flounder (*Platichthys solemdali*), larval drift close to the surface (<10m) resulted in nearly 76% being lost to the open sea, whilst deeper drift >10m resulted in retention of 69-94% along the coast, increasing the chances of successfully settling in nursery habitats (Corell & Nissling 2019). Similarly, for Chilean loco (*Concholepas concholepas*) connectivity between spawning and settlement habitats is twice as high when spawning occurs in water 40-60m deep, compared to 0-20m (Garavelli et al. 2014).

Once drifting, pelagic larvae and eggs might not survive high transport distances. In plaice (*Pleuronectes platessa*), recruitment negatively correlated with distance over which eggs and larvae were transported (Bolle et al. 2009). In North Sea plaice, offshore spawning habitats were poorly connected to coastal nursery grounds with only 5-30% of larvae reaching nurseries compared to 40-80% of larvae from coastal spawning sites (Hufnagl et al. 2013). Similarly, larval retention was high in the flounder, *P. solemdali*, due to close proximity of nursery and spawning grounds (Corell & Nissling 2019). Brown rockfish (*Sebastes auriculatus*) larval settlement success decreased with increasing distance from spawning habitat (Buonaccorsi et al. 2005) and for multiple reef fish in the Bahamas, larval retention was up to 60% higher in reefs connected to nursery habitat compared to unconnected reefs (Brown et al. 2016). In a Caribbean goby (*Elacatinus lori*), larval dispersal declined rapidly with increasing

distance from spawning grounds, where oceanic breaks of up to 20km acted as a barrier and resulted in high genetic differentiation between separated habitats (D'Aloia et al. 2013, 2014). Similarly, topographic features act as a barrier for Baltic flounder (*Platichthys flesus*) eggs and larvae, limiting connectivity between larval and settlement habitats (Hinrichsen et al. 2017).

Additionally, pelagic larval duration (PLD) and swimming ability are important intrinsic drivers of connectivity between habitats. The relatively short PLD (58 days) of the catadromous fish, *Kuhlia rupestris,* was found to maintain genetic connectivity on a small scale but was unable to prevent genetic divergence across the species' extensive range in the Indo-Pacific (Feutry et al. 2013). Damselfish larvae with high swimming ability were able to disperse a similar distance as coral larvae with low swimming ability, despite having a PLD three times shorter (Treml et al. 2012). Where possible, data on PLD and maximum dispersal distance has been summarised in Table 3.

Larval dispersal and connectivity are also relevant to marine spatial planning. For species where larval dispersal connects habitats, the spacing between MPAs is of critical importance because it ensures that these networks are seeding nearby unprotected areas. However, several studies show that many MPAs are still poorly connected. For instance, a network of nearly 100 coastal Mediterranean MPAs is not well-connected for dusky grouper (*Epinephelus marginatus*) larvae (Andrello et al. 2013). The varied dispersal distances (Table 3), coupled with the patchy distribution of MPAs in some areas, leaves 20% of settlement habitats with no larval supply (Andrello et al. 2013). In the barnacle, *Semibalanus balanoides,* and whelk, *Nucella lapillus,* larval connectivity within mainland MPA habitats is higher than between island

and mainland MPA habitats, due to lower distances within mainland MPA habitats (Bell

2008).

Table 3. Maximum pelagic larval duration (PLD) (days) and maximum larval dispersal distances (km) for various taxa extracted from publications in this review. Nursery and/or settlement habitats are provided. Contents marked with an asterisk (*) were sourced out with the 69 publications in the review in order to complete sections of the table. Contents marked with a ^ are from modelled species.

Taxa	Max PLD (days)	Larval swimming ability	Max larval dispersal (km)	Nursery or settlement habitats	Reference
Anemonefish (*Amphiprion melanopus*)	11	Strong	28	Anemones on coral reefs	Dixson et al. 2011, Bonin et al. 2016,
Anemonefish^	10	Strong	28	Anemones on coral reefs	Booth 1992*, Leis & Carson-Ewart
Damselfish^	20	Strong	155	Coral reefs*	2002*, Treml et al. 2012
Coral larva^	60	Poor	147	Coral reefs	
Gastropod mollusc (*Concholepas concholepas*)	80 140		170 220	Rocky, shallow intertidal habitats*	Manríquez et al. 2008*, 2009*, Garavelli et al. 2014
Grouper (*Ephinephelus marginatus*)	~30		906 (median 120)	Coastal areas, bays, & estuaries*	Andrello et al. 2013, Condini et al. 2016*
Catadromous fish (*Kuhlia rupestris*)	58	Moderate	Multiple 100s	Various freshwater habitats*	Feutry et al. 2012*, Feutry et al. 2013

3.5 Effects of climate change: Ocean acidification and sea temperature rise

Climate change, specifically rising sea surface temperatures and acidification, impacts

several aspects of connectivity in our oceans. In laboratory experiments, two clownfish

(*Amphiprion percula* and *A. melanopus*) demonstrated an ontogenetic shift in olfactory

cue preferences throughout their 11-day PLD and became attracted to cues from

appropriate settlement sites near the end of this duration (Dixson et al. 2011). Orange

clownfish (*A. percula*) reared in more acidic seawater (pH7.8) were unable to

distinguish between cues from their parents or from other adults, or respond to

olfactory cues in general, while those reared in natural conditions (pH8.15) could do

so (Munday et al. 2009b). As such, ocean acidification has the potential to disrupt functional connectivity between clownfish larval and settlement habitats.

Increased sea temperatures also impact connectivity by affecting PLD. In the Gulf of California, increased sea temperatures are predicted to decrease PLD of leopard grouper (*Mycteroperca rosacea*), blue crab (*Callinectes bellicosus*) and rock scallop (*Spondylus limbatus*) (Álvarez-Romero et al. 2018). Coupled with changes in wind patterns, rising sea temperatures could increase or decrease PLD of common sole (*Solea solea*) larvae by ~20% and increase dispersal distance by 70% (Lacroix et al. 2018). Throughout the North Sea, larval recruitment at nurseries could decrease by 58% in some areas and increase by 36% in others (Lacroix et al. 2018). However, sea temperature rise also influences the availability of copepods, the primary prey for cod (*G. morhua*) larvae and juveniles (Lough et al. 2017). In a warm year, increased abundance of *Centropages* copepod species was consistent with greater potential growth of juveniles and recruitment survival, ultimately affecting functional connectivity between juvenile and adult cod habitats (Lough et al. 2017).

4. Discussion

4.1 Barriers to functional connectivity

The publications in this review demonstrated that functional connectivity between life cycle habitats is impacted by multiple barriers, including distance, obstruction, and habitat fragmentation. First, 22 publications demonstrated that biomass and presence of adults on adult habitats decreased with increasing distance from nurseries for coastal and reef species, while this pattern was absent in non-nursery species (Olds et al. 2014, Harborne et al. 2016, Nagelkerken et al. 2017). This was further supported by publications demonstrating reduced functional connectivity between life cycle

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habitats due to physical barriers, habitat fragmentation and altered larval dispersal. Physical barriers, such as dams, were particularly detrimental for diadromous species, by preventing migration between marine and freshwater life cycle habitats. In other taxa, barriers and habitat fragmentation affected functional connectivity between habitats through reduced gap crossing behaviour (Turgeon et al. 2010, Espinoza et al. 2015, Ryan et al. 2020), reduced nursery availability (Layman et al. 2004, Duncan et al. 2006, Valentine-Rose et al. 2007), reduced juvenile dispersal (McMahon et al. 2012, Berkström et al. 2020) and increased heterogeneity either side of barriers (Bradbury et al. 2019). Overall, increased distances between habitats exposes individuals to lower quality intermittent substrata, with reduced food availability, higher predation risk and fewer refuges (Sweatman & Robertson 1994, Turgeon et al. 2010). Individuals may perceive these risks to be too great, thereby reducing functional connectivity.

Functional connectivity between spawning and settlement habitats during the larval stage was affected by various barriers, including topography (D'Aloia et al. 2014, Brown et al. 2016, Hinrichsen et al. 2017), larval loss to unsuitable sites (Munday et al. 2009b, Garavelli et al. 2014, Gargano et al. 2017, Corell & Nissling 2019), swimming ability (Treml et al. 2012), PLD (Feutry et al. 2013, Álvarez-Romero et al. 2018, Lacroix et al. 2018) and distance between spawning and settlement habitats (Buonaccorsi et al. 2005, Bell 2008, Bolle et al. 2009, Andrello et al. 2013, D'Aloia et al. 2013, Hufnagl et al. 2013, Corell & Nissling 2019). A species' maximum dispersal distance is typically proportional to its PLD (Shanks et al. 2003). Therefore, increased dispersal distance, due to fragmentation or poorly spaced MPAs, ultimately results in loss of larvae to unsuitable sites and increased mortality (Cowen & Sponaugle 2009). Larval retention (*i.e.* self-recruitment) occurs when there are large distances between

spawning and settlement habitats and/or when species have low PLD (Bolle et al. 2009, Treml et al. 2012). High larval retention, coupled with high larval import, can increase population resilience, however this resilience will quickly decline in fragmented and degraded habitats (Jones et al. 2009). This review demonstrated various barriers to larval dispersal between spawning and settlement habitats, which would likely reduce immigration to self-recruiting populations and limit functional connectivity. The population model developed here for the rainbow parrotfish further demonstrates the effects of increased habitat fragmentation on functional connectivity. It shows that increased distance between sites can be mitigated by improving the quality of nursery habitats that in turn increases juvenile survival. However, even with highest possible connectivity between sites, populations will not be viable without sufficient juvenile survival in the nursery. This demonstrates the importance of maintaining both high quality nursery habitat and connectivity between nursery (e.g. mangroves) and settlement habitats (e.g. coral reefs) in order to ensure continued survival of the rainbow parrotfish and species with similar life history strategies.

Functional connectivity between larval habitats was also affected by climate change in several of the reviewed publications. Ocean acidification impaired olfaction, preventing location of suitable settlement sites in clownfish (Munday et al. 2009b, Dixson et al. 2011). As a result, a tendency to settle on anemones near parents may render populations prone to inbreeding (Munday et al. 2009b). Increased sea temperature decreased PLD of various species, affecting functional connectivity as settlement habitats previously connected by larval dispersal, would be unreachable with lower PLDs (Álvarez-Romero et al. 2018, Lacroix et al. 2018). This result is consistent with studies included in our review (Irisson 2008, Ayata et al. 2010, Huret

et al. 2010) and emphasises the need to conserve functional connectivity between life cycle habitats under climate change.

4.2 Restoring functional connectivity

Several publications in this review documented increased reproductive output, population densities and resumption of diadromous migrations following dam removal. Removal of barriers was more effective than installing fish passes, as passage efficacy varied substantially between species and apparatus type, consistent with the wider literature (Noonan et al. 2012, Linnansaari et al. 2015, Bunt et al. 2016). Salmonids were more successful than non-salmonids at passing fish passes upstream (61.7% vs. 21.1%) and downstream (74.6% vs. 39.6%; Noonan et al. 2012), and thus future work is needed to improve passage success and maintain functional connectivity in non-salmonid species (Noonan et al. 2012, Linnansaari et al. 2015). Similarly, even in structurally connected ecosystems, 59% of bull trout (*Salvelinus confluentus*) were freshwater-resident and did not migrate to marine habitats (Austin et al. 2019). Although not fully understood, freshwater residency is believed to be influenced by complex interactions between genetic and environmental factors (Pulido 2011, Dodson et al. 2013, Ferguson et al. 2019). As freshwater residency is common in many salmonid populations (Dodson et al. 2013), functional connectivity between diadromous life cycle habitats may be influenced by a wider range of factors than those highlighted in this review.

A number of species depend on coastal habitats during part of their life cycle. However, these habitats are particularly vulnerable to human activity and destruction (Millennium Ecosystem Assessment 2005, Nagelkerken et al. 2017). To effectively mitigate disturbance and manage seascapes, it is essential to understand connectivity

between habitats and establish thresholds where connectivity diminishes (Berkström et al. 2020). This is particularly relevant in the design and management of MPAs since protecting highly connected seascapes can enhance reserve effects and can benefit multiple species simultaneously (Beger et al. 2010, Edwards et al. 2010, Nagelkerken et al. 2012, Olds et al. 2014, Berkström et al. 2020). Functional connectivity among habitats can be conserved in a number of ways. First, by conserving MPA spacing and designating reserve boundaries that account for species' dispersal distances, thereby ensuring adequate settlement and recruitment (Underwood et al. 2009, Jonsson et al. 2016, Magris et al. 2016). Next, functional connectivity through ontogenetic dispersal in the juvenile and sub-adult life stages can be maintained by protecting required habitats and dispersal corridors (Mumby 2006, White 2015). Finally, functional connectivity during adult life stages (e.g., seasonal migration to spawning grounds) can be conserved by establishing temporary MPAs at spawning habitats and scaling MPAs to encompass species' dispersal distances and migration corridors (Sadovy & Domeier 2005, Moffitt et al. 2009, Pendoley et al. 2014, Metcalfe et al. 2015). Overall, MPAs should be spaced within 15km of each other and MPA area should be double the species' home range and encompass all life cycle habitats (Green et al. 2015, D'Aloia et al. 2017).

4.3 Advancing functional connectivity

The increase in number of relevant studies published over the last 20 years suggests growing interest in this topic. However, most publications in this review focused on shallow and/or coastal tropical and sub-tropical systems, with polar, sub-polar and deep-sea systems entirely lacking. Several polar and sub-polar species are known to utilise multiple habitats throughout their life cycle, including the Scotia Sea icefish (*Chaenocephalus aceratus;* Ashford et al. 2010), Patagonian toothfish (*D. eleginoides;*

Mori et al. 2016), Antarctic toothfish (*Dissostichus mawsoni;* La Mesa et al. 2019), and sablefish (*Anoplopoma fimbria;* Gibson et al. 2019)- species that are exposed to high fishing pressure and climate change in the Southern Ocean. Studying functional connectivity and habitat use is challenging in marine systems, especially in polar, sub-polar and deep-sea areas that are isolated and difficult to access (e.g., Bradbury et al. 2009, Barnes & Clarke 2011). Nonetheless, the absence of publications from these ecosystems presents a significant knowledge gap in this review and the wider scientific literature. Where possible, future research should focus on these ecosystems to broaden our understanding of marine functional connectivity at high latitudes and low depths.

New methods can also help advance our understanding of functional connectivity. First, because functional connectivity depends on species-specific movement and dispersal, accurate population modelling is essential for reliably estimating this. Modelling platforms that integrate both the ecological and evolutionary dynamics of populations will be particularly useful for this work (e.g., RangeShifter platform, Bocedi et al. 2014). Second, genetic data provides valuable information about gene flow and genetic structure that is directly relevant to functional connectivity and can help to identify barriers to dispersal (Row et al. 2018). This information can also be incorporated into population models to produce a more holistic understanding of dispersal among life cycle habitats. Although much of the existing literature focuses on landscape genomics, the field of seascape genomics is rapidly expanding and will provide valuable tools and resources for future work in marine functional connectivity (e.g., Selmoni et al. 2020). Lastly, understanding the functional linkages between nursery and settlement habitats would not only enhance understanding of functional connectivity but also provide important information about ecosystem health and

function (McMahon et al. 2012).   Stable isotype analysis is particularly helpful for this work and can be used to quantify movements in individuals among habitats and within seascapes (McMahon et al. 2010, 2011a, 2011b, 2012).

4.4 Conclusions

This systematic review summarised the available literature on functional connectivity in marine systems and provides novel insight into an understudied branch of marine ecology. Several studies identified distance thresholds between life cycle habitats where functional connectivity ceased above these thresholds, although these may vary with juvenile survival rate and fishing pressure. Functional connectivity was significantly impacted by habitat fragmentation and physical barriers, but the removal or bypass of these barriers restored functional connectivity in some species. Finally, larval connectivity between spawning and settlement habitats was affected by distance, PLD, seascape topography and climate change. The results presented here have implications for the design and management of MPA networks and deepen our understanding of marine functional connectivity the face of habitat loss and fragmentation.

5. Acknowledgments

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