Contribution to the Theme Section 'Marine functional connectivity'

REVIEW

Corridors and barriers to marine connectivity around southern Africa

Christophe Lett[1,*], **Bernardino S. Malauene**[2,3], **Thierry B. Hoareau**[4,7],
David M. Kaplan[1,3], **Francesca Porri**[5,6]

[1]**MARBEC, Univ Montpellier, CNRS, Ifremer, IRD, 34203 Sète, France**
[2]**Instituto Oceanográfico de Moçambique, Maputo 1110, Mozambique**
[3]**Institute for Coastal and Marine Research, Nelson Mandela University, Gqeberha 6001, South Africa**
[4]**Department of Biochemistry, Genetics and Microbiology, University of Pretoria, X20, Hatfield 0028, South Africa**
[5]**South African Institute for Aquatic Biodiversity, Makhanda 6139, South Africa**
[6]**Rhodes University, Department of Ichthyology & Fisheries Science, Makhanda 6140, South Africa**

[7]***Present address:*** **Reneco International Wildlife Consultants LLC, Al Reem Island PO Box 61741,
00002 Abu Dhabi, United Arab Emirates**

ABSTRACT: Detailed knowledge on connectivity, i.e. the exchange of marine organisms among geographically separated populations, is essential for effective marine spatial planning strategies and the design of marine protected areas (MPAs) in coastal ecosystems. Coastal waters around southern Africa are characterized by complex oceanographic processes that strongly influence connectivity, challenging the design and management of marine ecosystems. Here we reviewed connectivity studies conducted across 25° of latitude on both the southeastern and southwestern sides of Africa based on biophysical modelling, ecological and molecular approaches, and identified 7 corridors and 8 barriers recognized to influence marine connectivity for a variety of vertebrate and invertebrate taxa of commercial and ecological interest. These corridors and barriers were generally consistent across studies, species and methodological approaches, and were reflected in marine bioregion breaks. Nevertheless, life history traits appear to be important to understanding why some corridors and barriers may be notable for some species and life stages and not for others. Our review underlines the value of including studies from different disciplines in order to have a broad view of marine connectivity, and, in particular, the complementarity of larval-dispersal biophysical models and seascape genetics is emphasized. The corridors and barriers to connectivity identified in this review represent baselines to critically assess existing MPAs and prioritize new spatial management efforts to mitigate human impacts on marine ecosystems.

KEY WORDS: Connectivity · Southern Africa · Barrier · Corridor · Biophysical model · Gene flow · Southern Atlantic Ocean · Western Indian Ocean

1. INTRODUCTION

Population connectivity, i.e. the exchange of individuals among geographically separated populations (Cowen et al. 2007), is central in the functioning of marine ecosystems (Beger et al. 2022), but it is partic-

ularly difficult to assess. The challenge comes from the complexity of directly observing the exchange of individuals in marine systems, particularly during the larval phase (Cowen & Sponaugle 2009), when most individuals disperse and are too small to follow *in situ*. Moreover, larval dispersal depends on several

*Corresponding author: christophe.lett@ird.fr

physical and biological processes operating simultaneously at different temporal and spatial scales (Pineda et al. 2009), making connectivity a complex integrative mechanism. Finally, multiple approaches are used to estimate marine connectivity (Leis et al. 2011) for different life history stages, which makes the studies particularly difficult to compare and to draw general conclusions on the consistency of patterns.

A major global review of >1000 marine population connectivity studies by Bryan-Brown et al. (2017) pointed at the lack of connectivity studies conducted in Africa. Although connectivity studies in Africa are unarguably lacking, a number of studies were missed in that review because of the search procedure the authors applied to identify papers dealing with marine connectivity. Papers often use geographically-specific terms (e.g. 'Benguela') instead of generic terms like 'marine', 'ocean' or 'coastal' used by Bryan-Brown et al. (2017), which could explain the exclusion of relevant papers. Such an issue is inevitable in global reviews, but this also means that there is a need to complement the work of Bryan-Brown et al. (2017) in order to provide a broader view of African research on marine connectivity.

Detailed knowledge on connectivity is essential to implement effective marine spatial planning strategies, and in particular to assess the effectiveness of existing marine protected areas (MPAs) and identify new areas to be protected (Balbar & Metaxas 2019, Popova et al. 2019, Maina et al. 2020). Waters around southern Africa support a broad range of livelihoods and include >100 declared MPAs (Kirkman et al. 2021, UNEP-Nairobi Convention & WIOMSA 2021), making this region an important area for marine connectivity research. The region is also characterized by a complex mix of eastern and western boundary current systems that strongly influence connectivity, challenging the design and management of MPAs.

There is therefore a need to review marine connectivity research around southern Africa, and, specifically, to collate existing knowledge coming from different disciplines on corridors and barriers to connectivity in the region. A number of other marine connectivity reviews have pertinence for our study, but none has specifically addressed the multiple approaches of connectivity in this region. For example, Teske et al. (2011) reviewed connectivity studies conducted in southern Africa, but used primarily a phylogeographic viewpoint. This review was also published more than a decade ago. Obura et al. (2019) did consider multiple approaches of evaluating connectivity to review barriers to dispersal, but

only for the northern Mozambique Channel. There was also a recent review of lagoon and lake connectivity in South Africa (Whitfield et al. 2017), but that study did not address marine ecosystems.

In order to identify appropriate publications in the literature, we used both Web of Science search strings and our own expert knowledge. We then selected the corridors and barriers that were repeatedly referred to in the publications. In most cases, there was wide agreement in the literature on the corridors, as these are linked to well documented oceanographic features. Some of the barriers were more difficult to interpret and had less universal support in the literature, with some being identified for certain taxa and not for others. In general, for cases where the presence of a barrier is uncertain, we included references to both literature identifying the barrier and literature indicating the absence of a barrier. Our overall aim was not to conduct a comprehensive review of biophysical modelling, ecological and molecular studies conducted in southern Africa, but to use these studies as illustrations of the effects (or absence of effects) of the identified corridors and barriers to connectivity. Importantly, biophysical modelling works focus on larval dispersal connectivity, whereas ecological and molecular studies can include other types of connectivity, such as ontogenetic movement and migration, depending on species mobility as juveniles and adults.

We first outline the ocean dynamics and marine ecosystems in our study region, and then follow with a detailed examination of corridors and barriers to marine connectivity around southern Africa, from the west to the east, as identified from biophysical modelling, ecological and molecular studies. We conclude the review by highlighting the complementarity or contrast from results derived from the different approaches considered, and also identify the lack of knowledge relative to specific regions and methodologies.

2. OCEANOGRAPHIC CONTEXT OF SOUTHERN AFRICA

Around southern Africa, the confluence of vastly different water masses and ocean circulation (Fig. 1) create potential corridors and barriers to marine connectivity. The South Equatorial Current (SEC) flows from far east towards the eastern coast of Madagascar, where it separates into the southern and northern branches of the East Madagascar Current (sEMC and nEMC, respectively) (Schott et al. 2009, Halo et
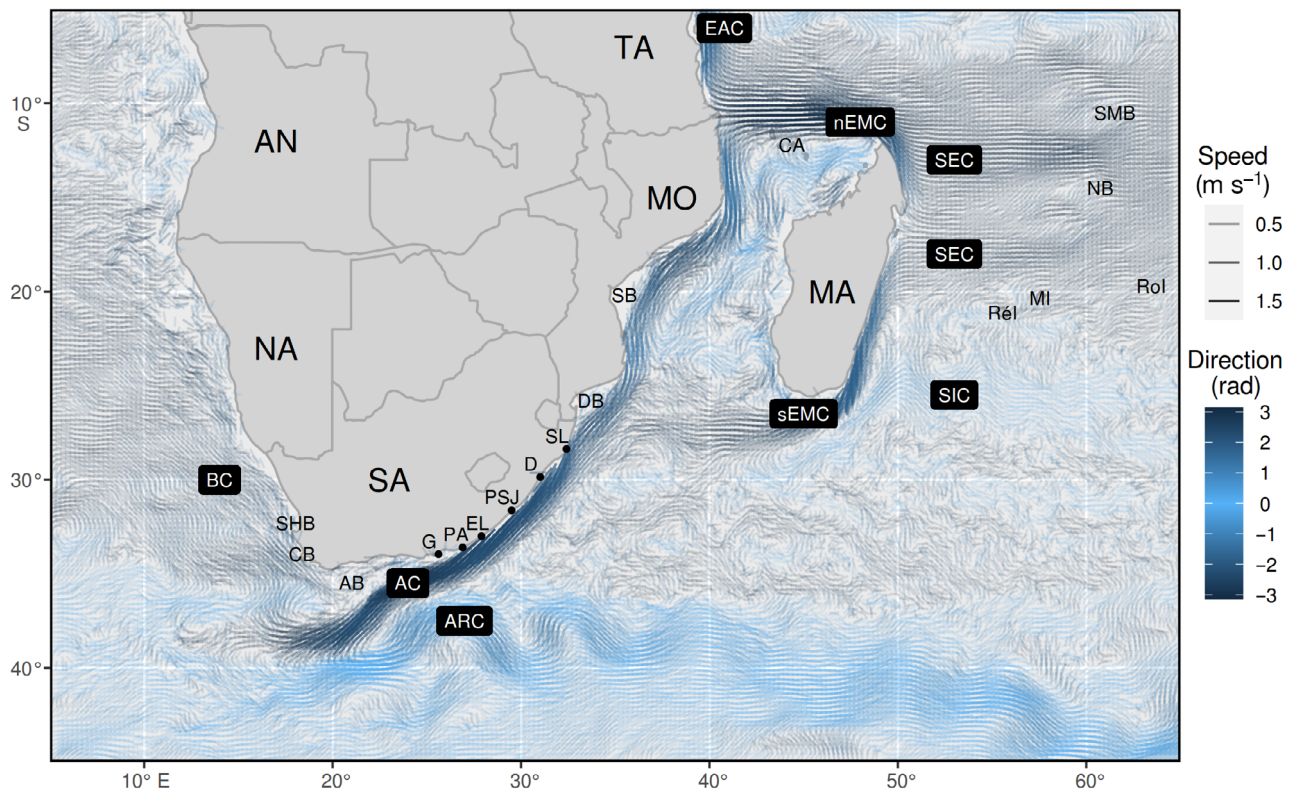
Fig. 1. Climatology of near-surface currents flowing around southern Africa as derived from oceanographic drifters of the Global Drifter Program (Laurindo et al. 2017). Colors indicate the direction of the currents (in radians; light blue flow to the east, dark blue flow to the west) and transparency the speed. White labels refer to the major currents mentioned in the text. BC: Benguela Current; AC: Agulhas Current; ARC: Agulhas Return Current; nEMC (sEMC) northern (southern) branch of the East Madagascar Current; SEC: South Equatorial Current; SIC: South Indian Countercurrent; EAC: East Africa Current. Black labels refer to the countries and locations mentioned in the text. AN: Angola; NA: Namibia; SA: South Africa; MO: Mozambique; TA: Tanzania; MA: Madagascar; SHB: St Helena Bay; CB: Camps Bay; AB: Agulhas Bank; G: Gqeberha (formerly Port Elizabeth); PA: Port Alfred; EL: East London; PSJ: Port St Johns; D: Durban; SL: St Lucia; DB: Delagoa Bight; SB: Sofala Bank; CA: Comoros Archipelago; SMB: Saya de Malha Bank; NB: Nazareth Bank; RoI: Rodrigues Island; MI: Mauritius Island; RéI: Réunion Island

al. 2014a, Voldsund et al. 2017). The nEMC flows over the northernmost tip of Madagascar merging with the northern branch of the SEC until the African mainland where it bifurcates into the East Africa Current (EAC) flowing to the north, and the northern Mozambique Channel circulation to the south (Backeberg & Reason 2010). The sEMC flows southwestwards over the southernmost tip of Madagascar, shedding mesoscale eddies towards the African mainland, while another portion of it retroflects to flow eastwards joining the South Indian Countercurrent (SIC) (Siedler et al. 2006, 2009, Halo et al. 2014a, Voldsund et al. 2017). In the Mozambique Channel, between Mozambique and Madagascar, the ocean circulation is dominated by a train of eddies propagating poleward, particularly on the western edge (Sætre & Da Silva 1984, Schouten et al. 2003, Halo et al. 2014a). These eddies, together

with those from the EMC, contribute to and influence the Agulhas Current (AC) that descends the east coast of South Africa (Lutjeharms 2006a, Beal et al. 2011). This major current travels along the southern coast of South Africa off the Agulhas Bank, moving along the edge of the southeast Atlantic Ocean before retroflecting and returning eastward into the Indian Ocean, forming the Agulhas Return Current (ARC), which flows along the northern edge of the Southern Ocean (Gordon et al. 1987, Duncombe Rae 1991, Lutjeharms & Ansorge 2001, Lutjeharms 2006a). Another portion of the Agulhas Current waters sheds into the Atlantic Ocean as large rings, i.e. the Agulhas Rings and Leakage (Lutjeharms & Gordon 1987, Richardson et al. 2003, Lutjeharms 2006a). The capes along the south coast are characterized by episodic upwelling events during periods of easterly winds, mixing cold, nutrient-rich bottom

waters with the warm waters of the Agulhas Current, producing a highly productive and dynamic environment. The western edge of the African continent is a classic eastern-boundary upwelling system characterized by the strong alongshore equatorward flow of the Benguela Current (BC), with cold and highly productive waters (Stramma & Peterson 1989). Nevertheless, upwelling is not uniform along the coast, but rather peaks in certain areas, the best known of which is the Lüderitz upwelling cell off Namibia.

3. CORRIDORS AND BARRIERS TO MARINE CONNECTIVITY

3.1. Lüderitz upwelling cell barrier

The first significant barrier on the west coast of southern Africa is the Lüderitz upwelling cell around 26° S (label 1 in Fig. 2), which splits the northern from the southern Benguela sub-systems (Boyer et al. 2000, Largier & Boyd 2001, Hutchings et al. 2009). This cold thermal barrier can also shift slightly north
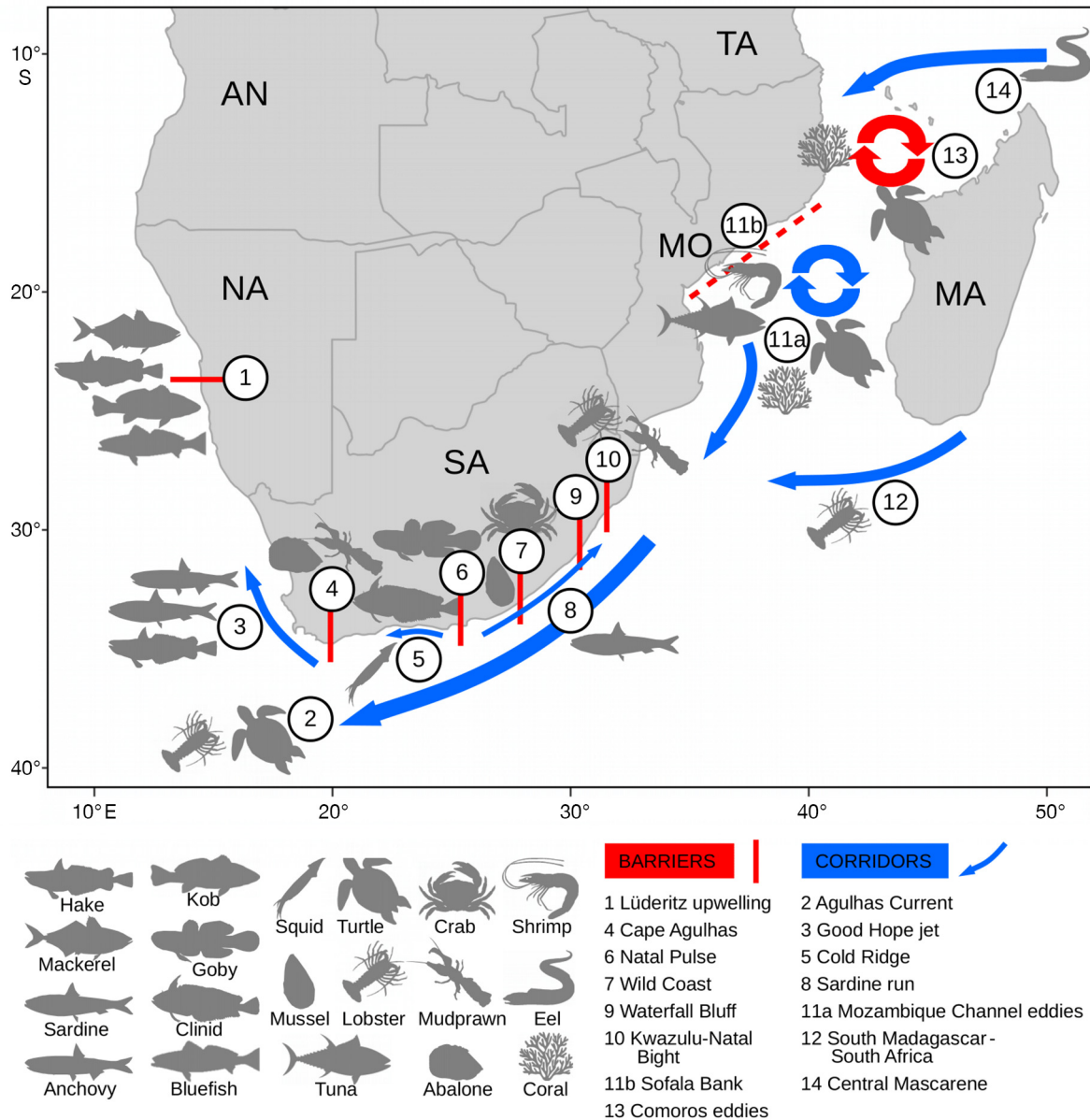

Fig. 2. Corridors (blue arrows) and barriers (red bars) to marine connectivity acting for a notable set of species in southern Africa. Barrier 11b is dashed because it was not clear where to indicate it exactly. References supporting the importance of the represented corridors and barriers are listed in Table 1 and discussed in the text. Country abbreviations as in Fig. 1

or south depending on the intensity of the upwelling (Fréon et al. 2010) and has long been identified as a potential barrier to the exchange of biota (Boyd & Cruickshank 1983, Agenbag & Shannon 1988).

Virtual larvae released close to the surface in the vicinity of the Lüderitz barrier are mostly advected offshore (Lett et al. 2007), outside habitats favourable to larval recruitment. This result is consistent with observed surface drifter trajectories (Largier & Boyd 2001). At the subsurface, however, exchanges between the northern and southern Benguela appear to be possible, although the lower temperature at depth (<14°C at 75 m) could limit larval survival (Lett et al. 2007). The Lüderitz barrier may then act as a hydrodynamic barrier to connectivity close to the surface and as a thermal barrier at the subsurface.

Several well documented examples suggest that the Lüderitz upwelling cell indeed represents a barrier to gene flow between populations along the coast. This is the case for the coastal fishes *Lichia amia* (Henriques et al. 2012) and *Atractoscion aequidens* (Henriques et al. 2014), silver kob *Argyrosomus inodorus* (Henriques et al. 2015), bluefish *Pomatomus saltatrix* (Reid et al. 2016b), kingklip *Genypterus capensis* (Schulze et al. 2020) and kelp *Laminaria pallida* (Assis et al. 2022). Furthermore, genetic differentiation (Henriques et al. 2016) and differences in otolith shapes (Shoopala et al. 2021) were found between the southern and northern Benguela stocks for the shallow-water hake *Merluccius capensis*.

Some genetic studies, however, found low or a lack of genetic differentiation along the Benguela across the Lüderitz upwelling. This would suggest that for some species, the barrier can be weak or absent due to sufficient levels of gene flow to prevent the populations from diverging. This is the case for the Cape horse mackerel *Trachurus capensis* (Boyer et al. 2000, Healey et al. 2020), the copepod *Calanoides natalis* (Höring et al. 2017) and the bearded goby *Sufflogobius bibarbatus* (Gunawickrama et al. 2020). For the copepod, the absence of genetic differences could be due to the markers used (nuclear and mtDNA sequences) that have lower resolution than microsatellite markers used in other studies. During rare periods, the Lüderitz upwelling cell can weaken, allowing the exchange of individuals and thus connecting both sides of the barrier (Boyer et al. 2000). A study evaluating the intensity and direction of gene flow in *P. saltatrix* across this barrier found that it was mostly from the south to the north (Reid et al. 2016b). Conversely, Kapula et al. (2022) demonstrated that migration in *M. capensis* was predominantly from

north to south, but that in the winter there was a small south–north migration. Overall, the studies finding weak genetic differences concerned mainly pelagic species, whereas most studies showing genetic subdivision were conducted on benthopelagic species. This suggests that the evidence of genetic isolation or lack thereof can be attributed to a combination of species life history traits and specific hydrological conditions across space and depth. The effect of markers could also play a role, as markers with low resolution like mtDNA are more prone to show a lack of genetic structure.

3.2. Agulhas Current corridor

The AC (label 2 in Fig. 2; Lutjeharms 2006a) is the strongest western boundary current in the southern hemisphere, with broad effects on water circulation and climate (Beal et al. 2011). It is a clear, unidirectional, warm current flowing southwestwards. It can therefore act as a strong corridor, but it is believed to be detrimental to early life stages of marine organisms because eggs and larvae of shelf species entrained into this current would be transported in the open ocean into areas unfavourable to settlement (Hutchings et al. 2002).

Oceanographic drifters caught in the AC drifted primarily offshore (Zardi et al. 2011), as did particles in larval dispersal simulations (Jacobs et al. 2022a, Muller et al. 2023 this Theme Section). However, Le Gouvello et al. (2020) simulated the transport of turtle hatchlings by the AC and showed that they may be transported 'back' into the Indian Ocean when trapped by the ARC, or penetrate the South Atlantic Ocean via mesoscale eddies, known as Agulhas Rings, thereby contributing to the Agulhas Leakage. The AC and Leakage were also found to connect southern Indian and Atlantic Ocean populations of rock lobsters (*Jasus tristani* and *J. paulensis*), which have a long (up to 20 mo) dispersal phase (Silva et al. 2021). Simulations showed that the transport of mangrove tree propagules from the South African coastline to the South Atlantic coastline was also possible but not far enough to the north to connect to the mangroves located in Angola (Raw et al. 2023). The Agulhas Leakage is episodic and viewed as an environmentally forced biological barrier that limits the dispersal of plankton, explaining why South Atlantic planktonic diversity is lower than that of the Indian Ocean, at least when examined at a fine taxonomic resolution and for plankton >20 µm (Villar et al. 2015).

The AC is a large-scale feature which has a major influence on the whole southern Africa region and interacts with many smaller-scale localized coastal features (Lutjeharms 2006a) that will be discussed in the following sections of our review.

3.3. Good Hope Jet corridor

The Good Hope Jet (label 3 in Fig. 2) is a northward intrusion of warm Agulhas waters from the Agulhas Bank off the Cape Peninsula (Bang & Andrews 1974, Veitch et al. 2018). This shelf-edge coastal rapid stream current flowing to the northwest forms a sharp front with the cold water upwelled on the shelf (Gordon et al. 1987).

Several modelling studies have demonstrated that ichthyoplankton can be transported by the Good Hope Jet, which is consistent with broad ecological knowledge (e.g. Hutchings et al. 2002) and trajectories of surface drifters (Lutjeharms et al. 2007). Multiple simulations have shown that the jet could connect spawning areas located on the Agulhas Bank, off the South African southern coast, to nursery areas located on the west coast north of St Helena Bay, for both the anchovy *Engraulis encrasicolus* (Huggett et al. 2003, Mullon et al. 2003, Parada et al. 2003, 2008, Koné et al. 2013) and the sardine *Sardinopos sagax* (Miller et al. 2006, McGrath et al. 2020). Simulations suggested that connectivity by the Good Hope Jet is more efficient (Huggett et al. 2003, Mullon et al. 2003) and faster (Ragoasha et al. 2019) in austral spring and summer, with interannual variability (Miller et al. 2006, McGrath et al. 2020, Ragoasha et al. 2022) and an influence of wind conditions (Blanke et al. 2009). Biological factors such as egg buoyancy (Parada et al. 2003), larval vertical migration (Parada et al. 2008) and larval growth (Koné et al. 2013) are additional factors affecting ichthyoplankton connectivity. Other simulations showed that the same jet also contributes to the transport of Cape hake ichthyoplankton from offshore spawning areas to onshore nursery grounds (Garavelli et al. 2012). The 2 hake species (shallow-water *M. capensis* and deep-water *M. paradoxus*) are presumed to interact differently with the jet, with species-specific drifting routes towards their relative nurseries; *M. capensis* follows a more inshore drift route than *M. paradoxus* (Stenevik et al. 2008).

Some species show limited genetic differentiation between Cape Point and the South African west coast, which suggest that their larvae could benefit from the Good Hope Jet to connect populations located on either side (von der Heyden et al. 2008,

Teske et al. 2014 and references therein, Bennett et al. 2017). The use of low-resolution markers is an alternative explanation for this absence of genetic structure, but if the gene flow was confirmed, then the jet could be considered as a corridor increasing marine genetic connectivity in the region. However, there are some species that show signs of restriction of gene flow or genetic structuring, including *Clinus cottoides*, *C. supercilliosus*, *Muraenoclinus dorsalis*, *Gilchristella aestuaeria*, *Exosphaeroma hylecoetes* (von der Heyden 2009) and the isopod *Excirolana latipes* (von der Heyden et al. 2020). For these species, the evidence of the Good Hope Jet acting as a corridor remains limited.

3.4. Cape Agulhas barrier

Cape Agulhas (label 4 in Fig. 2) is the southernmost tip of Africa and is often considered the point where the Atlantic and Indian Oceans divide. Two different upwelling regimes operate on either side of the cape (Chang 2009), which could therefore constitute a physical barrier to connectivity. There are indications that the region around Cape Agulhas constitutes a biogeographic boundary from a cool-temperate region to a warm-temperate zone (Harrison 2002), and a phylogeographic break (Teske et al. 2011).

Modelling studies have indeed identified Cape Agulhas as a 'dividing line', with particles released east of the Cape being largely retained there as opposed to being mostly transported to the South African west coast when released west of the Cape (Lett et al. 2006, 2015). A transport-based subsystem west of Cape Agulhas and a retention-based subsystem east of it have also been highlighted in biophysical models of sardine (Miller et al. 2006, McGrath et al. 2020), matching the 2 high-density areas for sardine separated approximately at Cape Agulhas (Teske et al. 2021).

The existence of a significant genetic break across Cape Agulhas has been reported for several species (von der Heyden 2009), although a limited level of gene flow can be observed mainly from the west to the east rather than in the opposite direction. Species characterized by genetic differences across this barrier include the abalone *Haliotis midae* (Evans et al. 2004, van der Merwe 2009), the klipfish *C. cottoides* (von der Heyden et al. 2008), the shrimp *Palaemon peringueyi* (Teske et al. 2007b), the mudprawn *Upogebia africana*, the isopod *Exosphaeroma hylecoetes* (Teske et al. 2006) and the coastal shark *Mustelus mustelus* (Maduna et al. 2016).

Other species show no genetic structure across the whole southern coast of South Africa, including the goby *Caffrogobius caffer* (Neethling et al. 2008) and the silver kob *Argyrosomus inodorus* (Mirimin et al. 2016). These contrasting results further suggest that the evidence of gene flow partly depends on the ecology of the studied species (Griffiths 1997). Alternatively, the absence of genetic differences could be due to the failure of some markers to appropriately detect more subtle genetic differences because of their resolution. This is typically the case of mtDNA markers that are well known for having lower resolution and power to detect genetic differences than microsatellite markers. To discriminate between the effect of life history traits and markers, new approaches based on whole-genome sequencing could be informative. Interestingly, 2 out of 10 drifters released on the eastern Agulhas Bank by Zardi et al. (2011) did pass off Cape Agulhas to the west coast, highlighting that this barrier is indeed permeable.

3.5. Cold Ridge corridor

The central Agulhas Bank is also characterized by the Cold Ridge (label 5 in Fig. 2; Swart & Largier 1987, Chang 2009), a quasi-permanent interannually variable tongue of cold bottom water transported to the surface. The sources of this cold water are multiple and include the Port Alfred upwelling cell (Lutjeharms 2006b), wind-driven coastal upwelling (Roberts 2005) and other localized sources along the southeastern shelf-edge of the Agulhas Bank (Schumann & van Heerden 1988, Boyd & Shillington 1994, Jackson et al. 2012). Biologically, the Cold Ridge drives high primary productivity (Mazwane et al. 2022) and copepod concentrations (Peterson et al. 1992).

Similar to the Good Hope Jet, the Cold Ridge is an important corridor for larval transport, in particular for chokka squid *Loligo reynaudii* that aggregate about 200 km upstream of the Cold Ridge for spawning (Roberts 2005), allowing westward transport of paralarvae into the ridge where maximum copepod production awaits them. This feature was first described as the 'westward transport hypothesis' by Roberts (2005) and was confirmed later by several numerical studies (Roberts & Mullon 2010, Martins et al. 2010, 2014, Downey-Breedt et al. 2016, Jacobs et al. 2022b) and drifter trajectories (Hancke et al. 2023). A minor proportion of simulated larvae of mussels (*Mytilus galloprovincialis*) could, however,

be transported eastwards by coastal counter-currents (Assis et al. 2015).

3.6. Natal Pulse barrier

One of the largest hydrographic mesoscale features that influence the circulation on the entire Agulhas Bank is the intermittent Natal Pulse (label 6 in Fig. 2; Lutjeharms & Roberts 1988). Natal Pulses are linked to the nearshore intrusions and offshore displacements of the AC (Gründlingh 1979, Bryden et al. 2005). The estimated frequency of occurrence of Natal Pulses per year lies between 1.6 (Krug & Penven 2011, Krug et al. 2014, Elipot & Beal 2015) and 5 (Lutjeharms et al. 2001, Bryden et al. 2005), with considerable interannual variability (Yamagami et al. 2019). Despite the intermittent nature of these meanders, Natal Pulses can influence the temperature of the Agulhas Bank (Malan et al. 2018) and its circulation for 110 d a year (Krug et al. 2014).

Natal Pulses have been recognized as important potential barriers to the connectivity of intertidal populations due to the inshore intrusions being followed by offshore export of propagules outside suitable recruitment habitats (Porri et al. 2014, Weidberg et al. 2015). However, the intermittent nature of pulses, and a possible mismatch between the reproductive cycle of species and the occurrence of a pulse, may result in breaks in the barrier (Roberts 2010, Porri et al. 2014).

This ecological view has been largely confirmed by modelling results. Preliminary simulations showed that Natal Pulses are indeed detrimental to transport to, and retention on, the shelf (Heye 2021). Up to 50% of simulated particles were lost offshore when a pulse occurred; however, 1–2 wk after the passage of a pulse, coastal retention increased back to 90–100% (Jacobs et al. 2022a). Hence, the timing of Natal Pulses relative to particle release, i.e. species spawning, is likely crucial for successful recruitment.

Genetic breaks have been identified in the area between Gqeberha (formerly named Port Elizabeth) and Port Alfred for several species (von der Heyden 2009), supporting the potential role of the Natal Pulse as a genetic barrier. The species with genetic structure in the region include the goby *Caffrogobius caffer* (Neethling et al. 2008), the klipfish *C. cottoides* (von der Heyden et al. 2008), the cumacean *Iphinoe truncata* (Teske et al. 2006), the estuarine fish *Gilchristella aestuaria* (Norton 2005), the sandprawn *Kraussillichirus kraussi* (Golla et al. 2020) and the pill bug *Tylos capensis* (Bezuidenhout et al. 2021).

3.7. Wild Coast barrier

A thermal barrier occurs along the southeast coast of South Africa, on the steep transition from the temperate south coast water regime to the warmer-subtropical Agulhas waters, between Algoa Bay and the Wild Coast (i.e. Gqeberha to East London; label 7 in Fig. 2). This area constitutes a phylogeographic break (Teske et al. 2011) and a biogeographic boundary from a warm-temperate zone to a subtropical region (Harrison 2002). For example, it constitutes the lowest temperatures that the tropical and subtropical goatfish *Upeneus floros* can bear (Uiblein et al. 2020), with the temperate water regime preventing a westward spread of this species. By contrast, the area constitutes the highest temperature that the mussel *M. galloprovincialis* can handle, as this species does not spread farther along the coast into the warmer waters to the east (Assis et al. 2015). A mussel dispersal model, however, showed that without taking temperature into account, larval transport beyond this thermal barrier was possible (Assis et al. 2015), suggesting that the area acts as a thermal, but not as a hydrodynamic barrier.

The Wild Coast is expected to be a region of biogeographic transition, with species overlapping on the edges of their distribution ranges. This is the case for the congeneric crabs *Hymenosoma longicrure* and *H. projectum* that inhabit the temperate and tropical bioregions, respectively (Jooste et al. 2018), and for different lineages of the same mussel species (Zardi et al. 2007). This region is also characterized by populations of the estuarine sandprawn *Kraussillichirus kraussi* that are genetically unique (Golla et al. 2020), indicating that the Wild Coast can constitute a distinct bioregion for some species (Toms et al. 2014). Two species of crabs with restricted dispersal abilities also showed very contrasting genetic structures in the region. Despite its abbreviated larval phase and the importance of estuaries for its development, *H. longicrure* showed a nearly panmictic single population, whereas *Neorhynchoplax bovis,* a direct developer, showed highly structured populations (Qhaji et al. 2015). This highlights again that life history traits play a major role in the connectivity of marine species around southern Africa. In this case, the type of markers is not in question concerning the lack of genetic structure, as the authors used the same set of markers for the 2 species.

Some species show limited genetic differences along the east coast of South Africa, including the lobster *Palinurus delagoae* (Gopal et al. 2006), limpets belonging to the genus *Siphonaria* (Teske et al. 2007a), the estuarine prawn *Callianassa kraussi* (Teske et al. 2009), the coral *Pocillopora verrucosa* (Ridgway et al. 2008) and the white steenbras *Lithognathus lithognathus* (Bennett et al. 2017), whereas others do present significant population structuring, such as the mussel *Perna perna* (Zardi et al. 2007, Ntuli et al. 2020), the mudprawn *Upogebia africana* (Teske et al. 2006) and the seagrass *Zostera capensis* (Phair et al. 2019). In some of these examples, the lack of genetic structure may be due to the resolution of the markers used. The observation of east and west genetic lineages in *Perna perna* (Zardi et al. 2007) stimulated interest for possible physiological differences among the 2 distinct groups (Zardi et al. 2011), as well as for hydrographic barriers that could have determined such separation. The trajectories of drifters released at eastern and western locations of the mussel genetic break revealed little to no overlap, hence in part providing support for a physical surface barrier (Zardi et al. 2011).

3.8. Sardine run corridor and Waterfall Bluff barrier

Knowledge of the hydrodynamics of the South African eastern coast have benefited much from the analysis of the unique seasonal occurrence of the 'sardine run' (label 8 in Fig. 2). This is the term used to characterize the spectacular eastward and further northeastward movement of these fish and their predators to reach spawning grounds in southern KwaZulu-Natal (Fréon et al. 2010), against the general circulation. Temporary favourable nearshore northwestward counter currents, associated with a series of coastal upwelling cells, occur in the regions of Port Alfred, East London and Port St Johns, allowing the sardine run along this section of the coast (Roberts et al. 2010). Further northeast, however, warm waters and the prevalent southwestwards current flow function as thermal and hydrodynamic barriers to the northeastward movement of sardines, especially when the Agulhas Current encroaches on the Pondoland shelf. Roberts et al. (2010) named that barrier the 'Waterfall Bluff gateway' (label 9 in Fig. 2), which can, however, be released by countercurrents during the occurrence of a stationary and transient breakaway Durban Cyclonic eddy as well as during the intermittent generation of Natal Pulses (Roberts et al. 2010). These events allow the sardine run to pass the gateway and progress further north. Using recent genomic and transcriptomic data, Teske et al. (2021) found that sardines taking part in the run

are mostly of Atlantic origin and thus prefer cold waters. These sardines separate from the warm-temperate stock to enter temporarily favourable Indian Ocean habitats during episodic cold-water upwelling events (Beckley 1995), where they become trapped as soon as these events end.

3.9. KwaZulu-Natal Bight barrier

Moving further northeast, the Kwazulu-Natal Bight (label 10 in Fig. 2) is an oceanographically dynamic shelf region due to the influence of the AC (Schumann 1988). In this area, Natal Pulses initiate (Lutjeharms & Roberts 1988), and topographically driven upwelling occurs in the north, which at times can prevail through the entire shelf and affect nutrient composition (Lutjeharms et al. 2000). There are also the Thukela River discharges, which cause further alterations of the flow (Bosman et al. 2007), and a coastal counter-current (Heye et al. 2022). Such complex and unpredictable hydrographic features would seem an obvious barrier to biological activity.

Dispersal simulations showed that the offshore meanders of the AC govern both connectivity corridors and barriers in the region (Heye 2021). During periods where the AC is relatively stable, the upwelling cell in the north and, particularly, the Durban cyclonic lee eddy in the south, trapped simulated larvae, promoting locally inshore retention. This limits along- and cross-shelf dispersal, posing a barrier to connectivity, as previously suggested by ecological studies of ichthyoplankton distribution for coastal linefish species (Beckley 1995). On the other hand, during periods when the AC meanders and is less stable, anticyclonic eddies carried larvae offshore that entered the AC and were transported southwards (Heye 2021). These larvae could then either reach the coast downstream, retroflect into the Indian Ocean or leak into the Atlantic Ocean (Singh et al. 2018), making the barrier to dispersal permeable.

Most genetic studies focusing on the region have found little to no genetic differences relative to the neighbouring locations southwards or northwards (von der Heyden 2009). We note that the region is unique in terms of biogeography, as several broadcast spawner species from both tropical and subtropical regions overlap here (Sink et al. 2005, Gopal et al. 2006, Teske et al. 2009). It is also the distribution range edge of several species from the south and from the north, with very limited taxa that are endemic to the region (Forbes 1973, Teske et al.

2009). Therefore, this is an important transition zone that will likely increase in importance (in terms of possible shift or strength) because of climate change (Griffiths et al. 2010).

3.10. Mozambique Channel eddies corridor and Sofala Bank barrier

Ocean circulation in the Mozambique Channel (label 11a in Fig. 2) between the African mainland and Madagascar is characterized by intermittent turbulent eddies (Sætre & Da Silva 1984, Biastoch & Krauß 1999) which propagate southwards at ~3–6 km d^{-1}, with currents reaching up to 2 m s^{-1} at the edge of large anticyclonic eddies (Schouten et al. 2003, Halo et al. 2014a).

Several biophysical modelling studies showed that early life stages of several species entrained into these eddies were transported southwards mainly along the western side of the Channel into the AC system in South Africa, e.g. for shrimp from the Sofala Bank (Malauene 2015), spiny lobster (Singh et al. 2018), sea turtle (Jensen et al. 2020) and tuna (Nikolic et al. 2020). Consistently, surface drifters entering the northern Mozambique Channel moved southwards (Hancke et al. 2014). This shows that the regular presence of mesoscale eddies creates a corridor connecting the northern Mozambique Channel to southern Mozambique and northern South Africa.

Evidence from fish larval assemblages confirms the importance of this southwards corridor. Hence, the most plausible origin of larvae collected in the St Lucia region in South Africa was South Mozambique (Beckley 1995, Harris et al. 1999). The recent discovery of a new goatfish species in northern Mozambique and KwaZulu-Natal in South Africa (Uiblein et al. 2020) and the presence of a single homogeneous population throughout the region for spiny lobster *Panulirus homarus rubellus* (Singh et al. 2018, 2019) also corroborate a southwards corridor.

Within the Mozambique Channel, although the dominant mesoscale eddy field propagates southwards, drifters can occasionally move in the frontal flow field between eddies (i.e. interstitial transport) northward and across the Channel, in both eastward and westward directions, between the Mozambican and Madagascan shelves (Hancke et al. 2014). Northward dispersal was observed off Madagascar in simulations (Ramanantsoa et al. 2018, Jensen et al. 2020). Cross-channel connectivity between the coast of Mozambique and the west coast of Madagascar, i.e. connectivity eastwards,

was also evident from biophysical simulations for mangrove propagules (Van der Stocken & Menemenlis 2017), soft coral Octocorallia: Alcyonacea (Schleyer et al. 2019), fish (Reid et al. 2016a) and hypothetical reef species (Crochelet et al. 2016) larvae. Simulations also illustrated that larvae from southeast Madagascar could be advected across the Channel to the central Mozambique shelf (Singh et al. 2018, Schleyer et al. 2019), i.e. connectivity westwards. Dispersal between Madagascar and Mozambique may, however, be limited (Huyghe & Kochzius 2018) and slow.

Localized connectivity barriers can be found in the Channel. The presence of 2 genetic groups of spiny lobsters, *P. h. homarus* in the north and *P. h. rubellus* in the south of the Delagoa Bight in southern Mozambique, suggests that the strong upwelling cells in this area create a physical barrier that isolates the populations (Singh et al. 2018). A recent study on brooding corals showed the same patterns, with a divide between northern and southern populations within the Mozambique Channel (van der Ven et al. 2021). O'Donnell et al. (2017) studied 2 species of coral reef fish with contrasting dispersal capacities and found that the one with a short larval duration, *Amphiprion akallopisos*, had higher genetic differentiation among populations located in islands along the Mozambique Channel than the species with the longer pelagic larval span, *Dascyllus trimaculatus.* In other studies, genetic differentiation appears to be moderate to high within the Mozambique Channel, e.g. for green turtles (Bourjea et al. 2015), the mangrove crab *Neosarmatium meinert*i (Ragionieri et al. 2010), the reef fishes *Myripristis berndti* and *Epinephelus merra* (Muths et al. 2011, 2015), tropical brittle-stars (Hoareau et al. 2013), the mud crab *Scylla serrata* (Fratini & Vannini 2002) and the catface grouper *Epinephelus andersoni* (Coppinger et al. 2019). Environmental conditions in the Mozambique Channel can also foster the evolution of cryptic species through restriction of gene flow and diversification, as seen for reef brittle-stars (Hoareau et al. 2013). Major habitat changes along the coast of Mozambique, with mostly mangroves located between ~16 and 21° S in the Sofala Bank area (Barbosa et al. 2001), and the complexity of circulation patterns within the Mozambique Channel, could both contribute to create these phylogeographic breaks, in particular for species requiring hard substrate (label 11b in Fig. 2). However, the absence of a barrier to gene flow all along the Mozambique Channel has also been reported, for example for the mangrove tree *Avicennia marina* (Amade et al. 2021).

3.11. South Madagascar–South Africa corridor

Unidirectional flow of larvae and other biological material from south Madagascar to South Africa (label 12 in Fig. 2) driven by mesoscale eddies (Halo et al. 2014b, Marsac et al. 2014, Ockhuis 2016) is referred to as the 'suitcase hypothesis', a hypothesis supported by genetic examinations of meroplankton species composition (Ockhuis 2016, Ockhuis et al. 2017) and gene flow in spiny lobster (Singh et al. 2019). Hence, species with long-lived larvae, like lobsters, may connect south Madagascar to South Africa, but not species with short larval durations, such as barnacles and prawns, explaining the absence of genetic structure observed for lobsters (Singh et al. 2019) and the significant structures seen for barnacles (Tsang et al. 2012) and prawns (Mkare et al. 2017). One study combining biophysical modelling and genetics suggested the possibility of a connection in the opposite direction, from South Africa to Madagascar, for the dusky grouper *Epinephelus marginatus* (Reid et al. 2016a).

3.12. Comoros eddies barrier

In the Comoros Basin, local instabilities generate both anticyclonic and cyclonic eddies (Collins et al. 2014) that persist in the basin from 2 mo up to about 1 yr before they decay or move southwards into the Mozambique Channel (Collins et al. 2014, Hancke et al. 2014).

This pattern was shown to create a barrier to connectivity (label 13 in Fig. 2), with simulated larvae entrained in large eddies being trapped and isolated in the Comoros Basin, resulting in high retention for virtual coral reef larvae (Gamoyo et al. 2019), fish larvae (Maina et al. 2020) and hatchling sea turtles (Jensen et al. 2020). In some of these studies, however, larvae could eventually escape and connect to shelves along the coasts of Tanzania, Mozambique and Madagascar (Gamoyo et al. 2019, Jensen et al. 2020). This pattern is particularly important for species with a long larval duration.

A recent genetic study is consistent with the results obtained from the above simulations and illustrated how the Comoros eddies can represent a barrier to gene flow between populations of brooding coral *Seriatopora hystrix* on either side of the northern Mozambique Channel (van der Ven et al. 2021). In this specific case, the short larval stage of the species reinforced the effect of the eddies by completely restricting gene flow between locations sampled in

Madagascar and along the African coast. A similar result was obtained for the mangrove tree *Rhizophora mucronata* (Triest et al. 2021).

3.13. Central Mascarene Plateau corridor

Across the central Mascarene Plateau, between Saya de Malha and Nazareth Banks, the SEC creates a corridor (label 14 in Fig. 2) connecting central Mascarene to Madagascar and the African mainland through the nEMC and the Comoros eddies (Backeberg & Reason 2010).

Simulated eel larvae in this region were advected westward by the strong northern branch of the SEC, joining the nEMC across the northernmost tip of Madagascar into the Comoros Basin within 60 d (Pous et al. 2010). These larvae could subsequently connect to Tanzania and northern Mozambique. A small proportion of simulated larvae from central Mascarene followed the relatively weaker and slower southern branch of the SEC, merging with the sEMC and eventually reaching southeast Madagascar in 110 d (Pous et al. 2010). These results illustrate the role of this region as a corridor. In contrast, the southern Mascarene Plateau around Mauritius and Réunion islands is more isolated, with low connection to Madagascar (Pous et al. 2010, Crochelet et al. 2013, 2016, 2020) and also low connection from Rodrigues to Mauritius and then Réunion (Crochelet et al. 2013, 2016).

There is a recognized lack of *in situ* information about connectivity in the northern Mascarene Plateau (Miller et al. 2019, Fauvelot et al. 2020, Kim et al. 2022). In the southern part, genetic studies generally indicated strong genetic differentiation between populations found in the Mascarene Islands and those found in the Mozambique Channel (Hoareau et al. 2007, Muths et al. 2011, 2012, Hoareau et al. 2013, Muths et al. 2015, Borsa et al. 2016, Kiper 2019). This suggests the existence of a barrier to gene flow between these distant regions, possibly associated with the SIC flowing to the east. The genetic differentiation of populations from the Mascarene Islands has also been recently highlighted for corals (Gélin et al. 2018) and giant clams (Fauvelot et al. 2020). A study combining genetics and simulated larvae showed that specific oceanographic conditions linked to a cyclone were the most likely explanation for rare colonization events of vagrant individuals of *E. marginatus* from the east coast of Madagascar to Réunion (Reid et al. 2016a). This study illustrates that rare and extreme oceanographic conditions can explain patterns of connectivity that would seem counterintuitive at first glance.

3.14. Small-scale corridors and barriers

In addition to the corridors and barriers reported above, which have effects on marine species dispersal and connectivity at regional scales, several studies have reported smaller-scale (<10 km) corridors and barriers due to features such as bays, headlands, eddies, river plumes and fronts.

Ecological and molecular studies of invertebrate adult assemblages (especially mussels) have described contrasting patterns between bays and downstream headlands, on the south coast (Zardi et al. 2007, von der Meden et al. 2008) and the west coast (Hoffmann et al. 2012) of South Africa. The dominance of bays as the principal source populations in the region has been largely confirmed for several early life stages for invertebrates, including spawning (McQuaid & Phillips 2006), larval availability (McQuaid & Phillips 2006, Mian 2015), settlement (von der Meden 2009, Hoffmann et al. 2012) and recruitment (McQuaid & Phillips 2006, von der Meden 2009, Pfaff et al. 2011). As shown for St Helena Bay (Penven et al. 2000) and Camps Bay (Largier 2003) on the South African coast, topographic eddies could favour the retention of propagules in the lee of bays, whereas strong offshore advection prevails at the headlands, thereby creating along-shore and cross-shore discontinuities in species distributions. In Algoa Bay, a recent modelling study found higher simulated recruitment for the blacktail seabream *Diplodus capensis* on the leeward side of the bay than on the windward side (Muller et al. 2023), consistent with field data (Pattrick & Strydom 2014).

Wind forcing can also result in the formation of along-shore fronts, either as surface foam lines and slicks or below the surface (Largier & Swart 1987, Jackson et al. 2012). These small-scale fronts can both create convergence zones that delay or prevent cross-shore larval transport (Franks 1992, Pineda 1999, Shanks et al. 2000, Weidberg et al. 2014) and also facilitate final transport of larvae of coastal organisms to the shore (Lagos et al. 2008, Woodson et al. 2012). Larval behavioural shifts for active depth regulation and adaptive response to the flow dynamics may interact with these small-scale features (Weidberg et al. 2019, Pattrick et al. 2021), including the fine-scale, front-associated foam that dissipates intertidally (Porri et al. 2021). A combination of be-

havioural responses and the duration, intensity and co-occurrence with biological processes (Largier 1993) will determine the realized role of coastal fronts as barriers or corridors.

4. DISCUSSION

We identified 7 corridors and 8 barriers to marine connectivity in southern Africa from biophysical modelling, ecological and molecular studies (Fig. 2, Table 1). A variety of approaches were used in the different studies for a variety of vertebrate and invertebrate taxa of commercial and ecological interest. Different molecular techniques were developed over the years, which allowed historical results to be compared to new ones using more recent, stronger, markers. A variety of modelling platforms were also used in the reviewed works to simulate hydrodynamics (HYCOM, MITgcm, NEMO, ROMS [now CROCO]) and marine dispersal (Ariane, Ichthyop, MGET, Parcels, Pyticles). This seems to be mostly due to different research teams using different tools, but it still indicates that research on marine connectivity has been very active in the region, and it paves the way for future multi-model ensemble approaches. When corridors and barriers were investigated from different approaches, e.g. molecular and modelling, results were generally consistent. However, contrasting results obtained with different approaches may also occur, and the most striking example comes from a study where genetics and modelling were conducted together. Along the west coast of South Africa, the simulations of Mertens et al. (2018) showed that the Cape urchin *Parechinus angulosus* had a long-distance dispersal potential that was higher than that of the granular limpet *Scutellastra granularis*, as expected from its longer planktonic larval duration (70 d for the urchin vs. 10 d for the limpet). Yet the genetics revealed a strong genetic structure for the urchin population and panmixia for the limpet. As there is no known strong barrier to marine connectivity along the whole area studied by Mertens et al. (2018), the urchin genetics result is particularly puzzling and points to the importance of post-settlement processes warranting further investigation. We also identified broad knowledge gaps from particular regions and methods, in particular a lack of ecological studies conducted in the Comoros eddies region and the northern Mascarene Plateau, a lack of modelling studies investigating the south Madagascar to South Africa corridor and a lack of genetic studies specifically

designed to assess corridors and barriers within bioregions (but see Dalongeville et al. 2022) and at scales <10 km.

The identified barriers are broadly consistent with transitions between marine bioregions (i.e. transitions in coastal marine community compositions) described in studies at the global scale (i.e. studies identifying large-scale marine bioregions) and at the regional scale (i.e. studies specifically concerned with our southern African study region). At a global scale, 3 marine biogeographic regions are generally distinguished over southern Africa: the Benguela, Agulhas, and Western Indian Ocean provinces (Spalding et al. 2007, Toonen et al. 2016), separating around the Cape of Good Hope (immediately west of barrier 4 in Fig. 2) and Cape Vidal (immediately east of barrier 10). These 2 breaks were also reported at regional scales, with additional ones around St Helena Bay (Griffiths et al. 2010), Cape Agulhas (barrier 4) (Teske et al. 2011, Kirkman et al. 2016), Algoa Bay (immediately east of barrier 6) (Teske et al. 2011) and the Wild Coast (barrier 7) (Griffiths et al. 2010, Teske et al. 2011). Griffiths et al. (2010) focused on South Africa, so their study domain did not extend up to our barriers 1, 11b and 13. Teske et al. (2011) noted that the few studies conducted outside South Africa made it difficult to determine phylogeographic breaks there. Biogeographic breaks were suggested in Namibia at ~20° S and in Mozambique at ~26° S (Whitfield 2005, Potts et al. 2015), not fully matching our barriers 1 and 11b, although these breaks were based on the assessment of estuarine fauna only. However, Barrier 1 (Lüderitz upwelling) is consistent with the sub-systems proposed by Kirkman et al. (2016) for ecosystem-based management of the Benguela ecosystem, and barrier 11b (Sofala Bank) is consistent with the ecoregions of Spalding et al. (2007).

Understanding life history traits appears to be essential to explaining why a particular barrier may be important for some species and not for others. Dispersal mode and larval duration mediate the degrees and scales of connectivity, with the dispersal of long-lived broadcast spawners more likely to be dictated by shelf and pelagic oceanographic dynamics (Teske et al. 2015), whereas species with short larval duration may be more influenced by localized retention mechanisms. Given that the ability to disperse is taxon- and size-dependent, large-bodied propagules are expected to have shorter dispersal distances than small-sized plankton and hence depend less on the broad global environmental connectivity (Villarino et al. 2018), but rather on the localized spatio-temporal

Table 1. References categorized according to the main approach (biophysical modelling, ecology or genetics) used to support the reviewed corridors and barriers to marine population connectivity around southern Africa. The references listed in the oceanography column were used to set the general oceanographic context of the corresponding corridor or barrier and are only a small subset of existing references. Asterisks (*) indicate a study classified as 'Oceanography' for its use of drifters. The locations of the listed corridors and barriers are shown in Fig. 2, together with a set of species influenced by them

Corridor/Barrier	Oceanography	Biophysical modelling	Ecology	Genetics
1 Lüderitz upwelling barrier	Agenbag & Shannon (1988) Largier & Boyd (2001)	Lett et al. (2007)	Boyd & Cruickshank (1983) Boyer et al. (2000) Hutchings et al. (2009) Fréon et al. (2010)	Assis et al. (2022) Gunawickrama et al. (2020) Healey et al. (2020) Henriques et al. (2012, 2014, 2015, 2016) Höring et al. (2017) Kapula et al. (2022) Reid et al. (2016b) Schulze et al. (2020)
2 Agulhas Current corridor	Beal et al. (2012) Duncombe Rae (1991) Gordon et al. (1987) Lutjeharms (2006a) Lutjeharms & Ansorge (2001) Lutjeharms & Gordon (1987) Richardson et al. (2003) Zardi et al. (2011) (*)	Jacobs et al. (2022a) Le Gouvello et al. (2020) Muller et al. (2023) Raw et al. (2023) Silva et al. (2021)	Hutchings et al. (2002) Villar et al. (2015)	Silva et al. (2021)
3 Good Hope Jet corridor	Bang & Andrews (1974) Blanke et al. (2009) Gordon et al. (1987) Lutjeharms et al. (2007) Veitch et al. (2018)	Garavelli et al. (2012) Huggett et al. (2003) Koné et al. (2013) McGrath et al. (2020) Miller et al. (2006) Mullon et al. (2003) Parada et al. (2003, 2008) Ragoasha et al. (2019, 2022)	Hutchings et al. (2002) Stenevik et al. (2008)	Bennett et al. (2017) Teske et al. (2014) von der Heyden et al. (2008, 2020) von der Heyden (2009)
4 Cape Agulhas barrier	Chang (2009) Zardi et al. (2011) (*)	Lett et al. (2006, 2015) Miller et al. (2006) McGrath et al. (2020)	Griffiths (1997) Harrison (2002)	Evans et al. (2004) Maduna et al. (2016) Mirimin et al. (2016) Neethling et al. (2008) Teske et al. (2006, 2007b, 2011, 2021) van der Merwe (2009) von der Heyden (2009)
5 Cold Ridge corridor	Boyd & Shillington (1994) Chang (2009) Hancke et al.(2023) Jackson et al. (2012) Jacobs et al. (2022b) Lutjeharms (2006b) Roberts (2005) Schumann & van Heerden (1988) Swart & Largier (1987)	Assis et al. (2015) Downey-Breedt et al. (2016) Jacobs et al. (2022b) Martins et al. (2010, 2014) Roberts & Mullon (2010)	Mazwane et al. (2022) Peterson et al. (1992) Roberts (2005)	
6 Natal Pulse barrier	Bryden et al. (2005) Elipot & Beal (2015) Gründlingh (1979) Krug & Penven (2011)	Heye (2021) Jacobs et al. (2022a)	Porri et al. (2014) Roberts (2010) Weidberg et al. (2015)	Bezuidenhout et al. (2021) Golla et al. (2020) Neethling et al. (2008) Norton (2005)

Table 1 (continued)

Corridor/Barrier	Oceanography	Biophysical modelling	Ecology	Genetics
6 Natal Pulse barrier (continued)	Krug et al. (2014) Lutjeharms & Roberts (1988) Lutjeharms et al. (2001) Malan et al. (2018) Yamagami et al. (2019)			Teske et al. (2006) von der Heyden et al. (2008)
7 Wild Coast barrier	Zardi et al. (2011) (*)	Assis et al. (2015)	Assis et al. (2015) Harrison (2002) Jooste et al. (2018) Uiblein et al. (2020)	Bennett et al. (2017) Golla et al. (2020) Gopal et al. (2006) Ntuli et al. (2020) Qhaji et al. (2015) Phair et al. (2019) Ridgway et al. (2008) Teske et al. (2007a, 2009, 2011) Zardi et al. (2007)
8 Sardine run corridor and 9 Waterfall Bluff barrier	Roberts et al. (2010)		Beckley (1995) Fréon et al. (2010)	Teske et al. (2021)
10 Kwazulu-Natal Bight barrier	Bosman et al. (2007) Lutjeharms & Roberts (1988) Lutjeharms et al. (2000) Schumann (1988)	Heye (2021) Heye et al. (2022) Singh et al. (2018)	Beckley (1995) Forbes (1973) Griffiths et al. (2010) Sink et al. (2005)	Gopal et al. (2006) Teske et al. (2009) von der Heyden (2009)
11a Mozambique Channel eddies corridor and 11b Sofala Bank barrier	Biastoch & Krauß (1999) Halo et al. (2014a) Hancke et al. (2014a) Sætre & Da Silva (1984) Schouten et al. (2003)	Crochelet et al. (2016) Jensen et al. (2020) Malauene (2015) Nikolic et al. (2020) Ramanantsoa et al. (2018) Reid et al. (2016a) Schleyer et al. (2019) Singh et al. (2018) Van der Stocken & Menemenlis (2017)	Beckley (1995) Harris et al. (1999)	Amade et al. (2021) Bourjea et al. (2015) Coppinger et al. (2019) Fratini & Vannini (2002) Hoareau et al. (2013) Huyghe & Kochzius (2018) Muths et al. (2011, 2015) O'Donnell et al. (2017) Ragionieri et al. (2010) Singh et al. (2018, 2019) Uiblein et al. (2020) van der Ven et al. (2021)
12 South Madagascar – South Africa corridor	Halo et al. (2014b) Ockhuis (2016)		Marsac et al. (2014) Ockhuis (2016)	Mkare et al. (2017) Ockhuis et al. (2017) Reid et al. (2016a) Singh et al. (2019) Tsang et al. (2012)
13 Comoros eddies barrier	Collins et al. (2014) Hancke et al. (2014)	Gamoyo et al. (2019) Jensen et al. (2020) Maina et al. (2020)		Triest et al. (2021) van der Ven et al. (2021)
14 Central Mascarene corridor	Backeberg & Reason (2010) Schott et al. (2009) Siedler et al. (2006, 2009) Voldsund et al. (2017)	Crochelet et al. (2013, 2016, 2020) Pous et al. (2010) Reid et al. (2016a)		Borsa et al. (2016) Fauvelot et al. (2020) Gélin et al. (2018) Hoareau et al. (2007, 2013) Kiper (2019) Muths et al. (2011, 2012, 2015) Reid et al. (2016a)

configuration of barriers, relying on the local abundance to maintain and replenish populations.

We also highlighted that multiple, and at times synergistic, interactions among factors and the presence of a diverse array of drivers of dispersal indicate how the absence of strong hydrographic barriers does not necessarily result in a broad and uniform connectivity of populations. Many of the processes involved in the realized connectivity are indeed time and space dependent and operate at different scales (McQuaid et al. 2015). For example, small changes in cross-shore dispersal, mediated either by the physical environment or by the behaviour of a species, such as vertical diel migration, can have large repercussions in along-shore transport and final delivery of propagules (Largier 2003). The complexity of drivers involved in connectivity makes it difficult not only to observe and describe it, but also to project it in order to manage marine populations efficiently.

The biophysical modelling works we reviewed were mostly about larval connectivity; however, the genetics results can include any type of connectivity, not only larval connectivity, depending on species mobility as juveniles and adults. Small- (Bennett et al. 2012) to large-scale (Daly et al. 2019) connectivity has also been largely investigated for adults using acoustic telemetry, in particular for fish species of ecological and economic importance, as well as to study habitat shifts between juvenile and adult stages (Childs et al. 2015). Results from telemetry studies support the existence of corridors used by fish for large-scale movements along the south and east coasts of South Africa and identify important transboundary routes of animal migration, such as the migration at the border between South Africa and Mozambique (Cowley et al. 2017). Adult movements may contribute to overcome barriers to larval dispersal and thereby homogenize populations. Conversely, as suggested for silver kob, populations can be genetically connected by possibly overlapping or extended spawning grounds and seasons, yet hydrographic fidelity can still partially isolate populations with management and conservation repercussions (in silver kob, fish from the southeastern putative stock have a limited offshore movement in winter relative to the southern group due to the narrower Agulhas Bank) (Griffiths 1997, Mirimin et al. 2016). Recent sources of ecological and physiological barriers also come from water pollution or general anthropogenic impacts, e.g. boat traffic, spills and fisheries activities (Donaldson et al. 2014). These environmental impacts can alter the common habitat use or migration routes of estuarine-dependent and coastal species, for ex-

ample forcing individuals to find alternative spatial and trophic niches (Eggenberger et al. 2019).

Climate change may act on marine population dispersal and connectivity in many ways, including changes in ocean circulation, temperature, food availability, larval dispersal duration and shifts in habitat and/or phenology (Harley et al. 2006, Gerber et al. 2014, Llopiz et al. 2014, Wilson et al. 2016, Bashevkin et al. 2020). In southern Africa, historical changes in sea level drove changes in habitats that likely had large impacts on population connectivity, sometimes explaining the strong divergence seen today between populations of species occupying certain areas (Toms et al. 2014). On a more recent time scale, over the last decades, the AC was found to be warming (Rouault et al. 2009), broadening (Beal & Elipot 2016) and weakening (Biastoch et al. 2009), leading to increased Agulhas Leakage (Biastoch et al. 2009, van Sebille et al. 2009, Backeberg et al. 2012) and thereby to an increased connectivity between Indian and Atlantic Ocean waters. There are also indications of an intensification of the SEC and of accelerated eddy propagation in the Mozambique Channel (Backeberg et al. 2012), two of the corridors that were highlighted in this review. The western Indian Ocean has been identified as one of the fastest-warming regions in the world (Roxy et al. 2016). Modelling outputs have also highlighted that the multidecadal variability in temperature on the Agulhas shelf is driven by changes in coastal winds (Malan et al. 2019). Species tolerance to temperature is therefore another important species trait to consider, as species with a short tolerance range will be more impacted by thermal barriers than more tolerant species. Teske et al. (2019) showed that thermal selection can act as a driver of speciation along the South African coastline. We refer to Potts et al. (2015) for a thorough review of the projected impacts of climate change on coastal fishes in the different biogeographic regions composing southern Africa.

Meso- to local-scale changes in the flow can alter the delicate use of currents by organisms with repercussions on population resilience. For example, changes in currents may alter or break the connection between spawning and feeding grounds for chokka squid (Roberts 2005). Similarly, sardines may find new (unsurmountable) barriers during their 'run' to spawning areas in the east (Fréon et al. 2010, Teske et al. 2021). During the interaction between Natal Pulses and the inshore intrusions of the AC, propagules of coastal invertebrates may be more intensively transported to offshore waters and become unable to replenish and maintain the intertidal

adult populations (Porri et al. 2014). Similarly, in the KwaZulu-Natal Bight, an intensified meandering of the AC may entrain more coastal larvae offshore (Heye 2021) in areas unfavourable to recruitment. At a larger scale, given the importance of the Agulhas Rings in shaping circulation in the Atlantic and climate (Beal et al. 2011) and their influence on plankton diversity (Villar et al. 2015), alterations in the Agulhas Leakage may have important repercussions on the connectivity, functioning and resilience of communities therein. At any scale, such changes are difficult to observe, and therefore, described cases of impacts on marine populations are still limited in southern Africa (Griffiths et al. 2010). As a complement to observations, biophysical modelling using projected future environmental conditions is a promising approach to investigate and anticipate the effects of climate change on marine population dispersal and connectivity (Lett et al. 2010).

Our review underlines the value of including studies from different disciplines in order to have a broad view of marine connectivity, and in particular the complementarity of larval dispersal biophysical models and seascape genetics (Jahnke & Jonsson 2022). This multidisciplinary approach could be used in other regions where similar works on corridors and barriers to marine connectivity focused on genetics (e.g. Pascual et al. 2017, in the Mediterranean Sea) or biophysical models (e.g. Treml et al. 2015, in the Indo-West Pacific). Our review also highlights again the importance of ocean circulation to shape marine connectivity, as reported in the California Current (Checkley & Barth 2009), Canary Current (Arístegui et al. 2009) and Humboldt Current (Montecino et al. 2005, Montecino & Lange 2009) upwelling ecosystems. There are indeed similarities in the oceanographic features influencing marine connectivity in these ecosystems and in the Benguela upwelling ecosystem, such as the Lüderitz barrier in the Benguela with Point Conception in California (Chavez & Messié 2009), as well as similarities between the AC meandering corridor and the Kuroshio Current (Yasuda et al. 2009) and between the Mozambique Channel eddies and the Canary–African eddies (Landeira et al. 2017). However, the marine environment around southern Africa is truly unique in that it brings together 2 oceans in a temperate region, connecting a warm-water western boundary current to a cold-water eastern boundary upwelling system in a complex mix of flow patterns and eddies that make it an excellent place to study the impacts of connectivity on the dynamics of marine organisms.

The corridors and barriers to connectivity identified around southern Africa represent baselines to critically assess existing MPAs and prioritize future spatial management efforts to mitigate human impacts on marine ecosystems. This review should therefore contribute to improved integration of marine connectivity research into MPA design and spatial conservation planning (Balbar & Metaxas 2019, Beger et al. 2022, Fontoura et al. 2022).

LITERATURE CITED

Agenbag JJ, Shannon LV (1988) A suggested physical explanation for the existence of a biological boundary at 24°30′S in the Benguela system. S Afr J Mar Sci 6: 119–132

Amade FMC, Oosthuizen CJ, Chirwa PW (2021) Genetic diversity and contemporary population genetic structure of *Avicennia marina* from Mozambique. Aquat Bot 171: 103374

Arístegui J, Barton ED, Álvarez-Salgado XA, Santos AMP and others (2009) Sub-regional ecosystem variability in the Canary Current upwelling. Prog Oceanogr 83:33–48

Assis J, Zupan M, Nicastro KR, Zardi GI, McQuaid CD, Serrão EA (2015) Oceanographic conditions limit the spread of a marine invader along southern African shores. PLOS ONE 10:e0128124

Assis J, Neiva J, Bolton JJ, Rothman MD and others (2022) Ocean currents shape the genetic structure of a kelp in southwestern Africa. J Biogeogr 49:822–835

Backeberg BC, Reason CJC (2010) A connection between the South Equatorial Current north of Madagascar and Mozambique Channel Eddies. Geophys Res Lett 37: L04604

Backeberg BC, Penven P, Rouault M (2012) Impact of intensified Indian Ocean winds on mesoscale variability in the Agulhas system. Nat Clim Change 2:608–612

Balbar AC, Metaxas A (2019) The current application of ecological connectivity in the design of marine protected areas. Glob Ecol Conserv 17:e00569

Bang ND, Andrews WRH (1974) Direct current measurements of a shelf-edge frontal jet in the southern Benguela system. J Mar Res 32:405–417

Barbosa FMA, Cuambe CC, Bandeira SO (2001) Status and distribution of mangroves in Mozambique. S Afr J Bot 67: 393–398

Bashevkin SM, Dibble CD, Dunn RP, Hollarsmith JA, Ng G, Satterthwaite EV, Morgan SG (2020) Larval dispersal in a changing ocean with an emphasis on upwelling

regions. Ecosphere 11:e03015

Beal LM, Elipot S (2016) Broadening not strengthening of the Agulhas Current since the early 1990s. Nature 540: 570–573

Beal LM, De Ruijter WPM, Biastoch A, Zahn R, SCOR/WCRP/ IAPSO Working Group 136 (2011) On the role of the Agulhas system in ocean circulation and climate. Nature 472: 429–436

Beckley LE (1995) The Agulhas Current ecosystem with particular reference to dispersal of fish larvae. In: Okemwa E, Ntiba MJ, Sherman K (eds) Status and future of large marine ecosystems of the Indian Ocean: a report of the international symposium and workshop. International Union for Conservation of Nature (IUCN), Gland, p 74–91

Beger M, Metaxas A, Balbar AC, McGowan JA and others (2022) Demystifying ecological connectivity for actionable spatial conservation planning. Trends Ecol Evol 37: 1079–1091

Bennett R, Cowley P, Childs AR, Whitfield A (2012) Area-use patterns and diel movements of white steenbras *Lithognathus lithognathus* in a temporarily open/closed South African estuary, inferred from acoustic telemetry and long-term seine-netting data. Afr J Mar Sci 34:81–91

Bennett R, Reid K, Gouws G, Bloomer P, Cowley P (2017) Genetic stock structure of white steenbras *Lithognathus lithognathus* (Cuvier, 1829), an overexploited fishery species in South African waters. Afr J Mar Sci 39:27–41

Bezuidenhout K, Nel R, Schoeman DS, Hauser L (2021) Historic dispersal barriers determine genetic structure and connectivity in a supratidal sandy-beach brooder. Mar Ecol Prog Ser 674:1–13

Biastoch A, Krauß W (1999) The role of mesoscale eddies in the source regions of the Agulhas Current. J Phys Oceanogr 29:2303–2317

Biastoch A, Boning CW, Schwarzkopf FU, Lutjeharms JRE (2009) Increase in Agulhas leakage due to poleward shift of Southern Hemisphere westerlies. Nature 462:495–498

Blanke B, Penven P, Roy C, Chang N, Kokoszka F (2009) Ocean variability over the Agulhas Bank and its dynamical connection with the southern Benguela upwelling system. J Geophys Res Oceans 114:C12028

Borsa P, Durand JD, Chen WJ, Hubert N, Muths D, Mou-Tham G, Kulbicki M (2016) Comparative phylogeography of the western Indian Ocean reef fauna. Acta Oecol 72:72–86

Bosman C, Uken R, Leuci R, Smith AM, Sinclair D (2007) Shelf sediments off the Thukela River mouth: complex interaction between fluvial and oceanographic processes. S Afr J Sci 103:490–492

Bourjea J, Mortimer JA, Garnier J, Okemwa G and others (2015) Population structure enhances perspectives on regional management of the western Indian Ocean green turtle. Conserv Genet 16:1069–1083

Boyd AJ, Cruickshank RA (1983) An environmental basin model for West Coast pelagic fish distribution. S Afr J Mar Sci 79:150–151

Boyd AJ, Shillington FA (1994) Physical forcing and circulation patterns on the Agulhas Bank. S Afr J Sci 90:143–154

Boyer D, Cole J, Bartholomae C (2000) Southwestern Africa: Northern Benguela Current region. Mar Pollut Bull 41: 123–140

Bryan-Brown DN, Brown CJ, Hughes JM, Connolly RM (2017) Patterns and trends in marine population connectivity research. Mar Ecol Prog Ser 585:243–256

Bryden HL, Beal LM, Duncan LM (2005) Structure and transport of the Agulhas Current and its temporal variability. J Oceanogr 61:479–492

Chang N (2009) Numerical ocean model study of the Agulhas Bank and the Cool Ridge. PhD thesis, University of Cape Town

Chavez FP, Messié M (2009) A comparison of Eastern Boundary Upwelling Ecosystems. Prog Oceanogr 83:80–96

Checkley DM, Barth JA (2009) Patterns and processes in the California Current System. Prog Oceanogr 83:49–64

Childs AR, Cowley PD, Næsje TF, Bennett RH (2015) Habitat connectivity and intra-population structure of an estuary-dependent fishery species. Mar Ecol Prog Ser 537:233–245

Collins C, Hermes JC, Reason CJC (2014) Mesoscale activity in the Comoros Basin from satellite altimetry and a high-resolution ocean circulation model. J Geophys Res Oceans 119:4745–4760

Coppinger CR, James N, Gouws G, Mann BQ, Guissamulo A, Mwale M (2019) Assessing the genetic diversity of catface grouper *Epinephelus andersoni* in the subtropical Western Indian Ocean. Fish Res 218:186–197

Cowen RK, Sponaugle S (2009) Larval dispersal and marine population connectivity. Annu Rev Mar Sci 1:443–466

Cowen RK, Gawarkiewicz G, Pineda J, Thorrold SR, Werner FE (2007) Population connectivity in marine systems: an overview. Oceanography 20:14–21

Cowley P, Bennett R, Childs AR, Murray T (2017) Reflection on the first five years of South Africa's Acoustic Tracking Array Platform (ATAP): status, challenges and opportunities. Afr J Mar Sci 39:363–372

Crochelet E, Chabanet P, Pothin K, Lagabrielle E and others (2013) Validation of a fish larvae dispersal model with otolith data in the Western Indian Ocean and implications for marine spatial planning in data-poor regions. Ocean Coast Manag 86:13–21

Crochelet E, Roberts J, Lagabrielle E, Obura D, Petit M, Chabanet P (2016) A model-based assessment of reef larvae dispersal in the Western Indian Ocean reveals regional connectivity patterns—potential implications for conservation policies. Reg Stud Mar Sci 7:159–167

Crochelet E, Barrier N, Andrello M, Marsac F, Spadone A, Lett C (2020) Connectivity between seamounts and coastal ecosystems in the Southwestern Indian Ocean. Deep Sea Res II 176:104774

Dalongeville A, Nielsen ES, Teske PR, von der Heyden S (2022) Comparative phylogeography in a marine biodiversity hotspot provides novel insights into evolutionary processes across the Atlantic–Indian Ocean transition. Divers Distrib 28:2622–2636

Daly R, Filmalter JD, Daly CAK, Bennett RH and others (2019) Acoustic telemetry reveals multi-seasonal spatiotemporal dynamics of a giant trevally *Caranx ignobilis* aggregation. Mar Ecol Prog Ser 621:185–197

Donaldson MR, Hinch SG, Suski CD, Fisk AT, Heupel MR, Cooke SJ (2014) Making connections in aquatic ecosystems with acoustic telemetry monitoring. Front Ecol Environ 12:565–573

Downey-Breedt NJ, Roberts MJ, Sauer WHH, Chang N (2016) Modelling transport of inshore and deep-spawned chokka squid (*Loligo reynaudi*) paralarvae off South Africa: the potential contribution of deep spawning to recruitment. Fish Oceanogr 25:28–43

Duncombe Rae CM (1991) Agulhas retroflection rings in the South Atlantic Ocean: an overview. S Afr J Mar Sci 11: 327–344

Eggenberger CW, Santos RO, Frankovich TA, James WR, Madden CJ, Nelson JA, Rehage JS (2019) Coupling telemetry and stable isotope techniques to unravel movement: snook habitat use across variable nutrient environments. Fish Res 218:35–47

Elipot S, Beal LM (2015) Characteristics, energetics, and origins of Agulhas Current meanders and their limited influence on ring shedding. J Phys Oceanogr 45: 2294–2314

Evans BS, Sweijd NA, Bowie RCK, Cook PA, Elliott NG (2004) Population genetic structure of the perlemoen *Haliotis midae* in South Africa: evidence of range expansion and founder events. Mar Ecol Prog Ser 270:163–172

Fauvelot C, Zuccon D, Borsa P, Grulois D and others (2020) Phylogeographical patterns and a cryptic species provide new insights into Western Indian Ocean giant clams phylogenetic relationships and colonization history. J Biogeogr 47:1086–1105

Fontoura L, D'Agata S, Gamoyo M, Barneche DR and others (2022) Protecting connectivity promotes successful biodiversity and fisheries conservation. Science 375:336–340

Forbes AT (1973) An unusual abbreviated larval life in the estuarine burrowing prawn *Callianassa kraussi* (Crustacea: Decapoda: Thalassinidea). Mar Biol 22:361–365

Franks PJS (1992) Sink or swim: accumulation of biomass at fronts. Mar Ecol Prog Ser 82:1–12

Fratini S, Vannini M (2002) Genetic differentiation in the mud crab *Scylla serrata* (Decapoda: Portunidae) within the Indian Ocean. J Exp Mar Biol Ecol 272:103–116

Fréon P, Coetzee JC, van der Lingen CD, Connell AD and others (2010) A review and tests of hypotheses about causes of the KwaZulu-Natal sardine run. Afr J Mar Sci 32:449–479

Gamoyo M, Obura D, Reason CJC (2019) Estimating connectivity through larval dispersal in the Western Indian Ocean. J Geophys Res Biogeosci 124:2446–2459

Garavelli L, Grüss A, Grote B, Chang N and others (2012) Modeling the dispersal of Cape hake ichthyoplankton. J Plankton Res 34:655–669

Gélin P, Pirog A, Fauvelot C, Magalon H (2018) High genetic differentiation and low connectivity in the coral *Pocillopora damicornis* type β at different spatial scales in the Southwestern Indian Ocean and the Tropical Southwestern Pacific. Mar Biol 165:167

Gerber LR, Mancha-Cisneros MDM, O'Connor MI, Selig ER (2014) Climate change impacts on connectivity in the ocean: implications for conservation. Ecosphere 5:33

Golla TR, Pieterse L, Jooste CM, Teske PR (2020) Discovery of populations endemic to a marine biogeographical transition zone. Divers Distrib 26:1825–1832

Gopal K, Tolley KA, Groeneveld JC, Matthee CA (2006) Mitochondrial DNA variation in spiny lobster *Palinurus delagoae* suggests genetically structured populations in the southwestern Indian Ocean. Mar Ecol Prog Ser 319: 191–198

Gordon AL, Lutjeharms JRE, Gründlingh ML (1987) Stratification and circulation at the Agulhas Retroflection. Deep Sea Res A Oceanogr Res Pap 34:565–599

Griffiths MH (1997) The life history and stock separation of silver kob, *Argyrosomus inodorus*, in South African waters. Fish Bull 95:47–67

Griffiths CL, Robinson TB, Lange L, Mead A (2010) Marine biodiversity in South Africa: an evaluation of current states of knowledge. PLOS ONE 5:e12008

Gründlingh ML (1979) Observation of a large meander in the Agulhas Current. J Geophys Res Oceans 84: 3776–3778

Gunawickrama KBS, Delaval A, Johansen T, van der Plas AK, Salvanes AGV (2020) Genetic structure of *Sufflogobius bibarbatus* in the Benguela upwelling ecosystem using microsatellite markers. J Appl Ichthyol 36:168–182

Halo I, Backeberg B, Penven P, Ansorge I, Reason C, Ullgren JE (2014a) Eddy properties in the Mozambique Channel: a comparison between observations and two numerical ocean circulation models. Deep Sea Res II 100: 38–53

Halo I, Penven P, Backeberg B, Ansorge I, Shillington F, Roman R (2014b) Mesoscale eddy variability in the southern extension of the East Madagascar Current: seasonal cycle, energy conversion terms, and eddy mean properties. J Geophys Res Oceans 119:7324–7356

Hancke L, Roberts MJ, Ternon JF (2014) Surface drifter trajectories highlight flow pathways in the Mozambique Channel. Deep Sea Res II 100:27–37

Hancke L, Roberts MJ, Smeed D, Jebri F (2023) Cold ridge formation mechanisms on the Agulhas Bank (South Africa) as revealed by satellite-tracked drifters. Deep Sea Res II 208:105245

Harley CDG, Hughes AR, Hultgren KM, Miner BG and others (2006) The impacts of climate change in coastal marine systems. Ecol Lett 9:228–241

Harris SA, Cyrus DP, Beckley LE (1999) The larval fish assemblage in nearshore coastal waters off the St Lucia Estuary, South Africa. Estuar Coast Shelf Sci 49:789–811

Harrison TD (2002) Preliminary assessment of the biogeography of fishes in South African estuaries. Mar Freshw Res 53:479–490

Healey AJE, Farthing MW, Nunoo FKE, Potts WM and others (2020) Genetic analysis provides insights into species distribution and population structure in East Atlantic horse mackerel (*Trachurus trachurus* and *T. capensis*). J Fish Biol 96:795–805

Henriques R, Potts W, Sauer W, Shaw P (2012) Evidence of deep genetic divergence between populations of an important recreational fishery species, *Lichia amia* L. 1758, around southern Africa. Afr J Mar Sci 34:585–591

Henriques R, Potts WM, Santos CV, Sauer WHH, Shaw PW (2014) Population connectivity and phylogeography of a coastal fish, *Atractoscion aequidens* (Sciaenidae), across the Benguela Current region: evidence of an ancient vicariant event. PLOS ONE 9:e87907

Henriques R, Potts WM, Sauer WHH, Shaw PW (2015) Incipient genetic isolation of a temperate migratory coastal sciaenid fish (*Argyrosomus inodorus*) within the Benguela Cold Current system. Mar Biol Res 11:423–429

Henriques R, von der Heyden S, Lipinski MR, du Toit N, Kainge P, Bloomer P, Matthee CA (2016) Spatio-temporal genetic structure and the effects of long-term fishing in two partially sympatric offshore demersal fishes. Mol Ecol 25:5843–5861

Heye S (2021) Surface circulation in the KwaZulu-Natal Bight and its impact on the connectivity of marine protected areas. MSc thesis, University of Cape Town

Heye S, Krug M, Penven P, Hart-Davis M (2022) The Natal Bight coastal counter-current: a modeling study. Cont Shelf Res 249:104852

Hoareau TB, Lecomte-Finiger R, Grondin HP, Conand C, Berrebi P (2007) Oceanic larval life of La Réunion 'bichiques', amphidromous gobiid post-larvae. Mar Ecol Prog Ser 333:303–308

Hoareau TB, Boissin E, Paulay G, Bruggemann JH (2013) The Southwestern Indian Ocean as a potential marine evolutionary hotspot: perspectives from comparative phylogeography of reef brittle-stars. J Biogeogr 40: 2167–2179

Hoffmann V, Pfaff MC, Branch GM (2012) Spatio-temporal patterns of larval supply and settlement of intertidal invertebrates reflect a combination of passive transport and larval behavior. J Exp Mar Biol Ecol 418–419:83–90

Höring F, Cornils A, Auel H, Bode M, Held C (2017) Population genetic structure of *Calanoides natalis* (Copepoda, Calanoida) in the eastern Atlantic Ocean and Benguela upwelling system. J Plankton Res 39:618–630

Huggett J, Fréon P, Mullon C, Penven P (2003) Modelling the transport success of anchovy *Engraulis encrasicolus* eggs and larvae in the southern Benguela: the effect of spatio-temporal spawning patterns. Mar Ecol Prog Ser 250:247–262

Hutchings L, Beckley LE, Griffiths MH, Roberts MJ, Sundby S, van der Lingen C (2002) Spawning on the edge: spawning grounds and nursery areas around the southern African coastline. Mar Freshw Res 53:307–318

Hutchings L, van der Lingen CD, Shannon LJ, Crawford RJM and others (2009) The Benguela Current: an ecosystem of four components. Prog Oceanogr 83:15–32

Huyghe F, Kochzius M (2018) Sea surface currents and geographic isolation shape the genetic population structure of a coral reef fish in the Indian Ocean. PLOS ONE 13: e0193825

Jackson JM, Rainville L, Roberts MJ, McQuaid CD, Lutjeharms JRE (2012) Mesoscale bio-physical interactions between the Agulhas Current and the Agulhas Bank, South Africa. Cont Shelf Res 49:10–24

Jacobs Z, Kelly S, Jebri F, Roberts M and others (2022a) Retention properties of the Agulhas bank and their relevance to the chokka squid life cycle. Deep Sea Res II 202: 105151

Jacobs Z, Roberts M, Jebri F, Srokosz M and others (2022b) Drivers of productivity on the Agulhas Bank and the importance for marine ecosystems. Deep Sea Res II 199: 105080

Jahnke M, Jonsson PR (2022) Biophysical models of dispersal contribute to seascape genetic analyses. Philos Trans R Soc B 377:20210024

Jensen MP, Dalleau M, Gaspar P, Lalire M and others (2020) Seascape genetics and the spatial ecology of juvenile green turtles. Genes 11:278

Jooste CM, Oliver J, Emami-Khoyi A, Teske PR (2018) Is the Wild Coast in eastern South Africa a distinct marine bioregion? Helgol Mar Res 72:6

Kapula V, Ndjaula HON, Schulze M, Durholtz D and others (2022) Genetic assessment of seasonal alongshore migration in *Merluccius capensis* in the Benguela region. Fish Res 250:106293

Kim M, Kang JH, Rho T, Kang HW, Kang DJ, Park JH, Son P (2022) Mesozooplankton community variability in the Seychelles–Chagos Thermocline Ridge in the western Indian Ocean. J Mar Syst 225:103649

Kiper I (2019) DNA barcoding and phylogeography of rabbitfishes (Teleostei: Siganidae): addressing challenges in a marine fish family with introgressive taxa using a multilocus approach. PhD thesis, University of Pretoria

Kirkman SP, Blamey L, Lamont T, Field JG and others (2016) Spatial characterisation of the Benguela ecosystem for ecosystem-based management. Afr J Mar Sci 38:7–22

Kirkman S, Mann B, Sink K, Adams R and others (2021) Evaluating the evidence for ecological effectiveness of South Africa's marine protected areas. Afr J Mar Sci 43: 389–412

Koné V, Lett C, Fréon P (2013) Modeling the effect of food availability on recruitment success of Cape anchovy ichthyoplankton in the southern Benguela upwelling system. Afr J Mar Sci 35:151–161

Krug M, Penven P (2011) New perspectives on Natal Pulses from satellite observations. J Geophys Res Oceans 116: C07013

Krug M, Tournadre J, Dufois F (2014) Interactions between the Agulhas Current and the eastern margin of the Agulhas Bank. Cont Shelf Res 81:67–79

Lagos NA, Castilla JC, Broitman BR (2008) Spatial environmental correlates of intertidal recruitment: a test using barnacles in northern Chile. Ecol Monogr 78:245–261

Landeira JM, Brochier T, Mason E, Lozano-Soldevilla F, Hernández-León S, Barton ED (2017) Transport pathways of decapod larvae under intense mesoscale activity in the Canary–African coastal transition zone: implications for population connectivity. Sci Mar 81:299–315

Largier JL (1993) Estuarine fronts: How important are they? Estuaries 16:1–11

Largier JL (2003) Considerations in estimating larval dispersal distances from oceanographic data. Ecol Appl 13: 71–89

Largier J, Boyd AJ (2001) Drifter observations of surface water transport in the Benguela Current during winter 1999. S Afr J Sci 97:223–229

Largier JL, Swart VP (1987) East–west variation in thermocline breakdown on the Agulhas Bank. S Afr J Mar Sci 5: 263–272

Laurindo LC, Mariano AJ, Lumpkin R (2017) An improved near-surface velocity climatology for the global ocean from drifter observations. Deep Sea Res I 124:73–92

Le Gouvello DZM, Hart-Davis MG, Backeberg BC, Nel R (2020) Effects of swimming behaviour and oceanography on sea turtle hatchling dispersal at the intersection of two ocean current systems. Ecol Model 431:109130

Leis JM, Van Herwerden L, Patterson HM (2011) Estimating connectivity in marine fish populations: What works best? Oceanogr Mar Biol Annu Rev 49:193–234

Lett C, Roy C, Levasseur A, van der Lingen CD, Mullon C (2006) Simulation and quantification of enrichment and retention processes in the southern Benguela upwelling ecosystem. Fish Oceanogr 15:363–372

Lett C, Veitch J, van der Lingen CD, Hutchings L (2007) Assessment of an environmental barrier to transport of ichthyoplankton from the southern to the northern Benguela ecosystems. Mar Ecol Prog Ser 347:247–259

Lett C, Ayata SD, Huret M, Irisson JO (2010) Biophysical modelling to investigate the effects of climate change on marine population dispersal and connectivity. Prog Oceanogr 87:106–113

Lett C, van der Lingen C, Loveday BR, Moloney CL (2015) Biophysical models of larval dispersal in the Benguela Current ecosystem. Afr J Mar Sci 37:457–465

Llopiz J, Cowen R, Hauff M, Ji R and others (2014) Early life history and fisheries oceanography: new questions in a changing world. Oceanography 27:26–41

Lutjeharms JRE (2006a) The Agulhas Current. Springer, Berlin

Lutjeharms JRE (2006b) The ocean environment off southeastern Africa: a review. S Afr J Sci 102:419–426

Lutjeharms JRE, Ansorge IJ (2001) The Agulhas Return Current. J Mar Syst 30:115−138

Lutjeharms JRE, Gordon AL (1987) Shedding of an Agulhas ring observed at sea. Nature 325:138−140

Lutjeharms JRE, Roberts HR (1988) The Natal pulse: an extreme transient on the Agulhas Current. J Geophys Res Oceans 93:631−645

Lutjeharms JRE, Valentine HR, Van Ballegooyen RC (2000) The hydrography and water masses of the Natal Bight, South Africa. Cont Shelf Res 20:1907−1939

Lutjeharms JRE, Boebel O, van der Vaart PCF, de Ruijter WPM, Rossby T, Bryden HL (2001) Evidence that the Natal Pulse involves the Agulhas Current to its full depth. Geophys Res Lett 28:3449−3452

Lutjeharms JRE, Durgadoo JV, Ansorge IJ (2007) Surface drift at the western edge of the Agulhas Bank. S Afr J Sci 103:63−67

Maduna SN, da Silva C, Wintner SP, Roodt-Wilding R, Bester-der Merwe AE (2016) When two oceans meet: regional population genetics of an exploited coastal shark, *Mustelus mustelus*. Mar Ecol Prog Ser 544:183−196

Maina JM, Gamoyo M, Adams VM, D'agata S, Bosire J, Francis J, Waruinge D (2020) Aligning marine spatial conservation priorities with functional connectivity across maritime jurisdictions. Conserv Sci Pract 2:e156

Malan N, Backeberg B, Biastoch A, Durgadoo JV, Samuelsen A, Reason C, Hermes J (2018) Agulhas Current meanders facilitate shelf−slope exchange on the Eastern Agulhas Bank. J Geophys Res Oceans 123: 4762−4778

Malan N, Durgadoo JV, Biastoch A, Reason C, Hermes J (2019) Multidecadal wind variability drives temperature shifts on the Agulhas Bank. J Geophys Res Oceans 124: 3021−3035

Malauene B (2015) Environmental influences on banana shrimps of the Sofala Bank, Mozambique Channel. PhD thesis, University of Cape Town

Marsac F, Barlow R, Ternon JF, Ménard F, Roberts M (2014) Ecosystem functioning in the Mozambique Channel: synthesis and future research. Deep Sea Res II 100: 212−220

Martins RS, Roberts MJ, Chang N, Verley P, Moloney CL, Vidal EAG (2010) Effect of yolk utilization on the specific gravity of chokka squid (*Loligo reynaudii*) paralarvae: implications for dispersal on the Agulhas Bank, South Africa. ICES J Mar Sci 67:1323−1335

Martins RS, Roberts MJ, Lett C, Chang N, Moloney CL, Camargo MG, Vidal EAG (2014) Modelling transport of chokka squid (*Loligo reynaudii*) paralarvae off South Africa: reviewing, testing and extending the 'Westward Transport Hypothesis.' Fish Oceanogr 23:116−131

Mazwane SL, Poulton AJ, Hickman AE, Jebri F, Jacobs Z, Roberts M, Noyon M (2022) Spatial and temporal variability of net primary production on the Agulhas Bank, 1998−2018. Deep Sea Res II 199:105079

McGrath AM, Hermes JC, Moloney CL, Roy C, Cambon G, Herbette S, van der Lingen CD (2020) Investigating connectivity between two sardine stocks off South Africa using a high-resolution IBM: retention and transport success of sardine eggs. Fish Oceanogr 29:137−151

McQuaid CD, Phillips TE (2006) Mesoscale variation in reproduction, recruitment and population structure of intertidal mussels with low larval input: a bay/open coast comparison. Mar Ecol Prog Ser 327:193−206

McQuaid CD, Porri F, Nicastro KR, Zardi GI (2015) Simple, scale-dependent patterns emerge from very complex effects—an example from the intertidal mussels *Mytilus galloprovincialis* and *Perna perna*. Oceanogr Mar Biol Annu Rev 53:127−156

Mertens LEA, Treml EA, von der Heyden S (2018) Genetic and biophysical models help define marine conservation focus areas. Front Mar Sci 5:268

Mian SI (2015) Mesoscale mechanisms of larval transport and settlement in relation to physical factors off the south coast of South Africa: a topographic approach. MSc thesis, Rhodes University, Grahamstown

Miller DCM, Moloney CL, van der Lingen CD, Lett C, Mullon C, Field JG (2006) Modelling the effects of physical−biological interactions and spatial variability in spawning and nursery areas on transport and retention of sardine eggs and larvae in the southern Benguela ecosystem. J Mar Syst 61:212−229

Miller MJ, Wouthuyzen S, Feunteun E, Aoyama J and others (2019) Contrasting biodiversity of eel larvae across the central Indian Ocean subtropical gyre. Deep Sea Res II 161:120−131

Mirimin L, Kerwath S, Macey B, Lamberth SJ and others (2016) Genetic analyses of overfished silver kob *Argyrosomus inodorus* (Scieanidae) stocks along the southern African coast. Fish Res 176:100−106

Mkare TK, Groeneveld JC, Teske PR, Matthee CA (2017) Comparative genetic structure in two high-dispersal prawn species from the south-west Indian Ocean. Afr J Mar Sci 39:467−474

Montecino V, Lange CB (2009) The Humboldt Current System: ecosystem components and processes, fisheries, and sediment studies. Prog Oceanogr 83:65−79

Montecino V, Strub PT, Chavez F, Thomas A, Tarazona J, Baumgartner T (2005) Bio-physical interactions off Western South America. In: Robinson AR, Brink K (eds) The sea. Harvard University Press, Cambridge, MA, p 329−390

Muller C, Lett C, Porri F, Pattrick P and others (2023) Coastal connectivity of an abundant inshore fish species, model−data comparison along the southern coast of South Africa. Mar Ecol Prog Ser https://doi.org/10.3354/meps14272

Mullon C, Fréon P, Parada C, van der Lingen C, Huggett J (2003) From particles to individuals: modelling the early stages of anchovy (*Engraulis capensis/encrasicolus*) in the southern Benguela. Fish Oceanogr 12: 396−406

Muths D, Tessier E, Gouws G, Craig M and others (2011) Restricted dispersal of the reef fish *Myripristis berndti* at the scale of the SW Indian Ocean. Mar Ecol Prog Ser 443: 167−180

Muths D, Gouws G, Mwale M, Tessier E, Bourjea J (2012) Genetic connectivity of the reef fish *Lutjanus kasmira* at the scale of the western Indian Ocean. Can J Fish Aquat Sci 69:842−853

Muths D, Tessier E, Bourjea J (2015) Genetic structure of the reef grouper *Epinephelus merra* in the West Indian Ocean appears congruent with biogeographic and oceanographic boundaries. Mar Ecol 36:447−461

Neethling M, Matthee CA, Bowie RC, von der Heyden S (2008) Evidence for panmixia despite barriers to gene flow in the southern African endemic, *Caffrogobius caffer* (Teleostei: Gobiidae). BMC Evol Biol 8:325

Nikolic N, Montes I, Lalire M, Puech A and others (2020) Connectivity and population structure of albacore tuna across southeast Atlantic and southwest Indian Oceans

inferred from multidisciplinary methodology. Sci Rep 10: 15657

Norton OB (2005) The population structure of two estuarine fish species, *Atherina breviceps* (Pisces: Atherinidae) and *Gilchristella aestuaria* (Pisces: Clupeidae), along the Southern African coastline. MSc thesis, Rhodes University, Grahamstown

Ntuli NN, Nicastro KR, Zardi GI, Assis J, McQuaid CD, Teske PR (2020) Rejection of the genetic implications of the 'Abundant Centre Hypothesis' in marine mussels. Sci Rep 10:604

O'Donnell JL, Beldade R, Mills SC, Williams HE, Bernardi G (2017) Life history, larval dispersal, and connectivity in coral reef fish among the Scattered Islands of the Mozambique Channel. Coral Reefs 36:223–232

Obura DO, Bandeira SO, Bodin N, Burgener V and others (2019) The Northern Mozambique Channel. In: Sheppard C (ed) World seas: an environmental evaluation, 2nd edn. Academic Press, p 75–99

Ockhuis SAN (2016) The 'suitcase hypothesis' – Can eddies provide a pathway for gene flow between Madagascar and KwaZulu-Natal? MSc thesis, Cape Peninsula University of Technology, Cape Town

Ockhuis S, Huggett JA, Gouws G, Sparks C (2017) The 'suitcase hypothesis': Can entrainment of meroplankton by eddies provide a pathway for gene flow between Madagascar and KwaZulu-Natal, South Africa? Afr J Mar Sci 39:435–451

Parada C, van der Lingen CD, Mullon C, Penven P (2003) Modelling the effect of buoyancy on the transport of anchovy (*Engraulis capensis*) eggs from spawning to nursery grounds in the southern Benguela: an IBM approach. Fish Oceanogr 12:170–184

Parada C, Mullon C, Roy C, Fréon P, Hutchings L, van der Lingen CD (2008) Does vertical migratory behaviour retain fish larvae onshore in upwelling ecosystems? A modelling study of anchovy in the southern Benguela. Afr J Mar Sci 30:437–452

Pascual M, Rives B, Schunter C, Macpherson E (2017) Impact of life history traits on gene flow: a multispecies systematic review across oceanographic barriers in the Mediterranean Sea. PLOS ONE 12:e0176419

Pattrick P, Strydom NA (2014) The effects of exposure in sandy beach surf zones on larval fishes. J Fish Biol 84: 1354–1376

Pattrick P, Weidberg N, Goschen WS, Jackson JM, McQuaid CD, Porri F (2021) Larval fish assemblage structure at coastal fronts and the influence of environmental variability. Front Ecol Evol 9:684502

Penven P, Roy C, Colin de Verdière A, Largier J (2000) Simulation of a coastal jet retention process using a barotropic model. Oceanol Acta 23:615–634

Peterson WT, Hutchings L, Huggett JA, Largier JL (1992) Anchovy spawning in relation to the biomass and the replenishment rate of their copepod prey on the western Agulhas Bank. S Afr J Mar Sci 12:487–500

Pfaff MC, Branch GM, Wieters EA, Branch RA, Broitman BR (2011) Upwelling intensity and wave exposure determine recruitment of intertidal mussels and barnacles in the southern Benguela upwelling region. Mar Ecol Prog Ser 425:141–152

Phair NL, Toonen RJ, Knapp I, von der Heyden S (2019) Shared genomic outliers across two divergent population clusters of a highly threatened seagrass. PeerJ 7: e6806

Pineda J (1999) Circulation and larval distribution in internal tidal bore warm fronts. Limnol Oceanogr 44: 1400–1414

Pineda J, Reyns NB, Starczak VR (2009) Complexity and simplification in understanding recruitment in benthic populations. Popul Ecol 51:17–32

Popova E, Vousden D, Sauer WHH, Mohammed EY and others (2019) Ecological connectivity between the areas beyond national jurisdiction and coastal waters: safeguarding interests of coastal communities in developing countries. Mar Policy 104:90–102

Porri F, Jackson JM, Von der Meden CEO, Weidberg N, McQuaid CD (2014) The effect of mesoscale oceanographic features on the distribution of mussel larvae along the south coast of South Africa. J Mar Syst 132: 162–173

Porri F, Puccinelli E, Pattrick P (2021) Lack of match between nutrient-enriched marine seafoam and intertidal abundance of long-lived invertebrate larvae. J Sea Res 170:102009

Potts WM, Götz A, James N (2015) Review of the projected impacts of climate change on coastal fishes in southern Africa. Rev Fish Biol Fish 25:603–630

Pous S, Feunteun E, Ellien C (2010) Investigation of tropical eel spawning area in the South-Western Indian Ocean: influence of the oceanic circulation. Prog Oceanogr 86: 396–413

Qhaji Y, van Vuuren BJ, Papadopoulos I, McQuaid C, Teske P (2015) A comparison of genetic structure in two low-dispersal crabs from the Wild Coast, South Africa. Afr J Mar Sci 37:345–351

Ragionieri L, Cannicci S, Schubart CD, Fratini S (2010) Gene flow and demographic history of the mangrove crab *Neosarmatium meinerti*: a case study from the western Indian Ocean. Estuar Coast Shelf Sci 86:179–188

Ragoasha N, Herbette S, Cambon G, Veitch J, Reason C, Roy C (2019) Lagrangian pathways in the southern Benguela upwelling system. J Mar Syst 195:50–66

Ragoasha MN, Herbette S, Veitch J, Cambon G, Reason CJC, Roy C (2022) Inter-annual variability of the alongshore Lagrangian transport success in the Southern Benguela Current Upwelling System. J Geophys Res Oceans 127:e2020JC017114

Ramanantsoa JD, Krug M, Penven P, Rouault M, Gula J (2018) Coastal upwelling south of Madagascar: temporal and spatial variability. J Mar Syst 178:29–37

Raw JL, Van der Stocken T, Carroll D, Harris LR, Rajkaran A, Van Niekerk L, Adams JB (2023) Dispersal and coastal geomorphology limit potential for mangrove range expansion under climate change. J Ecol 111:139–155

Reid K, Crochelet E, Bloomer P, Hoareau TB (2016a) Investigating the origin of vagrant dusky groupers, *Epinephelus marginatus* (Lowe, 1834), in coastal waters of Réunion Island. Mol Phylogenet Evol 103:98–103

Reid K, Hoareau TB, Graves JE, Potts WM, dos Santos SMR, Klopper AW, Bloomer P (2016b) Secondary contact and asymmetrical gene flow in a cosmopolitan marine fish across the Benguela upwelling zone. Heredity 117: 307–315

Richardson PL, Lutjeharms JRE, Boebel O (2003) Introduction to the 'Inter-ocean exchange around southern Africa.' Deep Sea Res II 50:1–12

Ridgway T, Riginos C, Davis J, Hoegh-Guldberg O (2008) Genetic connectivity patterns of *Pocillopora verrucosa* in

southern African Marine Protected Areas. Mar Ecol Prog Ser 354:161−168

Roberts MJ (2005) Chokka squid (*Loligo vulgaris reynaudii*) abundance linked to changes in South Africa's Agulhas Bank ecosystem during spawning and the early life cycle. ICES J Mar Sci 62:33−55

Roberts MJ (2010) Coastal currents and temperatures along the eastern region of Algoa Bay, South Africa, with implications for transport and shelf−bay water exchange. Afr J Mar Sci 32:145−161

Roberts MJ, Mullon C (2010) First Lagrangian ROMS-IBM simulations indicate large losses of chokka squid *Loligo reynaudii* paralarvae from South Africa's Agulhas Bank. Afr J Mar Sci 32:71−84

Roberts MJ, van der Lingen CD, Whittle C, van den Berg M (2010) Shelf currents, lee-trapped and transient eddies on the inshore boundary of the Agulhas Current, South Africa: their relevance to the KwaZulu-Natal sardine run. Afr J Mar Sci 32:423−447

Rouault M, Penven P, Pohl B (2009) Warming in the Agulhas Current system since the 1980's. Geophys Res Lett 36: L12602

Roxy MK, Modi A, Murtugudde R, Valsala V and others (2016) A reduction in marine primary productivity driven by rapid warming over the tropical Indian Ocean. Geophys Res Lett 43:826−833

Sætre R, Da Silva AJ (1984) The circulation of the Mozambique channel. Deep-Sea Res A Oceanogr Res Pap 31: 485−508

Schleyer MH, Downey-Breedt NJ, Benayahu Y (2019) Species composition of Alcyonacea (Octocorallia) on coral reefs at Europa Island and associated connectivity across the Mozambique Channel. Mar Biodivers 49:2485−2491

Schott FA, Xie SP, McCreary JP (2009) Indian Ocean circulation and climate variability. Rev Geophys 47:RG1002

Schouten MW, de Ruijter WPM, van Leeuwen PJ, Ridderinkhof H (2003) Eddies and variability in the Mozambique Channel. Deep Sea Res II 50:1987−2003

Schulze MJ, von der Heyden S, Japp D, Singh L and others (2020) Supporting fisheries management with genomic tools: a case study of kingklip (*Genypterus capensis*) off southern Africa. Front Mar Sci 7:557146

Schumann EH (1988) Physical oceanography off Natal. In: Schumann EH (ed) Coastal ocean studies off Natal, South Africa. Lecture Notes on Coastal and Estuarine Studies Vol 26. American Geophysical Union (AGU), p 101−130

Schumann EH, van Heerden IL (1988) Observations of Agulhas Current frontal features south of Africa, October 1983. Deep Sea Res A Oceanogr Res Pap 35:1355−1362

Shanks AL, Largier J, Brink L, Brubaker J, Hooff R (2000) Demonstration of the onshore transport of larval invertebrates by the shoreward movement of an upwelling front. Limnol Oceanogr 45:230−236

Shoopala E, Wilhelm M, Paulus S (2021) Stock separation of the shallow-water hake *Merluccius capensis* in the Benguela ecosystem using otolith shape analysis. Afr J Mar Sci 43:1−14

Siedler G, Rouault M, Lutjeharms JRE (2006) Structure and origin of the subtropical South Indian Ocean Countercurrent. Geophys Res Lett 33:L24609

Siedler G, Rouault M, Biastoch A, Backeberg B, Reason CJC, Lutjeharms JRE (2009) Modes of the southern extension of the East Madagascar Current. J Geophys Res Oceans 114:C01005

Silva CNS, Young EF, Murphy NP, Bell JJ and others (2021) Climatic change drives dynamic source−sink relationships in marine species with high dispersal potential. Ecol Evol 11:2535−2550

Singh SP, Groeneveld JC, Hart-Davis MG, Backeberg BC, Willows-Munro S (2018) Seascape genetics of the spiny lobster *Panulirus homarus* in the Western Indian Ocean: understanding how oceanographic features shape the genetic structure of species with high larval dispersal potential. Ecol Evol 8:12221−12237

Singh SP, Groeneveld JC, Willows-Munro S (2019) Between the current and the coast: genetic connectivity in the spiny lobster *Panulirus homarus rubellus*, despite potential barriers to gene flow. Mar Biol 166:36

Sink K, Branch G, Harris J (2005) Biogeographic patterns in rocky intertidal communities in KwaZulu-Natal, South Africa. Afr J Mar Sci 27:81−96

Spalding MD, Fox HE, Allen GR BS, Davidson N and others (2007) Marine ecoregions of the world: a bioregionalization of coastal and shelf areas. Bioscience 57:573−583

Stenevik EK, Verheye HM, Lipinski MR, Ostrowski M, Stromme T (2008) Drift routes of Cape hake eggs and larvae in the southern Benguela Current system. J Plankton Res 30:1147−1156

Stramma L, Peterson RG (1989) Geostrophic transport in the Benguela Current region. J Phys Oceanogr 19: 1440−1448

Swart VP, Largier JL (1987) Thermal structure of Agulhas Bank water. S Afr J Mar Sci 5:243−252

Teske PR, McQuaid CD, Froneman PW, Barker NP (2006) Impacts of marine biogeographic boundaries on phylogeographic patterns of three South African estuarine crustaceans. Mar Ecol Prog Ser 314:283−293

Teske PR, Barker NP, McQuaid CD (2007a) Lack of genetic differentiation among four sympatric southeast African intertidal limpets (Siphonariidae): phenotypic plasticity in a single species? J Molluscan Stud 73:223−228

Teske PR, Froneman P, Barker N, McQuaid C (2007b) Phylogeographic structure of the caridean shrimp *Palaemon peringueyi* in South Africa: further evidence for intraspecific genetic units associated with marine biogeographic provinces. Afr J Mar Sci 29:253−258

Teske PR, Winker H, McQuaid CD, Barker NP (2009) A tropical/subtropical biogeographic disjunction in southeastern Africa separates two Evolutionarily Significant Units of an estuarine prawn. Mar Biol 156:1265−1275

Teske PR, von der Heyden S, McQuaid CD, Barker NP (2011) A review of marine phylogeography in southern Africa. S Afr J Sci 107:43−53

Teske PR, Papadopoulos I, Barker NP, McQuaid CD, Beheregaray LB (2014) Mitonuclear discordance in genetic structure across the Atlantic/Indian Ocean biogeographical transition zone. J Biogeogr 41:392−401

Teske PR, Sandoval-Castillo J, van Sebille E, Waters J, Beheregaray LB (2015) On-shelf larval retention limits population connectivity in a coastal broadcast spawner. Mar Ecol Prog Ser 532:1−12

Teske PR, Sandoval-Castillo J, Golla TR, Emami-Khoyi A, Tine M, von der Heyden S, Beheregaray LB (2019) Thermal selection as a driver of marine ecological speciation. Proc R Soc B 286:20182023

Teske PR, Emami-Khoyi A, Golla TR, Sandoval-Castillo J and others (2021) The sardine run in southeastern Africa is a mass migration into an ecological trap. Sci Adv 7: eabf4514

Toms JA, Compton JS, Smale M, von der Heyden S (2014) Variation in palaeo-shorelines explains contemporary population genetic patterns of rocky shore species. Biol Lett 10:20140330

Toonen RJ, Bowen BW, Iacchei M, Briggs JC (2016) Biogeography, marine. In: Kliman RM (ed) Encyclopedia of evolutionary biology. Academic Press, Oxford, p 166−178

Treml EA, Roberts J, Halpin PN, Possingham HP, Riginos C (2015) The emergent geography of biophysical dispersal barriers across the Indo-West Pacific. Divers Distrib 21:465−476

Triest L, Van der Stocken T, De Ryck D, Kochzius M and others (2021) Expansion of the mangrove species *Rhizophora mucronata* in the Western Indian Ocean launched contrasting genetic patterns. Sci Rep 11:4987

Tsang LM, Achituv Y, Chu KH, Chan BKK (2012) Zoogeography of intertidal communities in the West Indian Ocean as determined by ocean circulation systems: patterns from the *Tetraclita* barnacles. PLOS ONE 7:e45120

Uiblein F, Gouws G, Lisher M, Malauene BS (2020) *Upeneus floros*, a new goatfish from South Africa and Mozambique, with updated taxonomic accounts for *U. guttatus* and *U. pori* and a key to Western Indian Ocean *Upeneus* species (Mullidae). Zootaxa 4834:523−555

UNEP-Nairobi Convention, WIOMSA (2021) Western Indian Ocean marine protected areas outlook: towards achievement of the Global Biodiversity Framework Targets. UNEP and WIOMSA, Nairobi

van der Merwe AE (2009) Population genetic structure and demographic history of South African abalone, *Haliotis midae*, in a conservation context. PhD thesis, Stellenbosch University

Van der Stocken T, Menemenlis D (2017) Modelling mangrove propagule dispersal trajectories using high-resolution estimates of ocean surface winds and currents. Biotropica 49:472−481

van der Ven RM, Flot JF, Buitrago-López C, Kochzius M (2021) Population genetics of the brooding coral *Seriatopora hystrix* reveals patterns of strong genetic differentiation in the Western Indian Ocean. Heredity 126:351−365

van Sebille E, Biastoch A, van Leeuwen PJ, de Ruijter WPM (2009) A weaker Agulhas Current leads to more Agulhas leakage. Geophys Res Lett 36:L03601

Veitch J, Hermes J, Lamont T, Penven P, Dufois F (2018) Shelf-edge jet currents in the southern Benguela: a modelling approach. J Mar Syst 188:27−38

Villar E, Farrant GK, Follows M, Garczarek L and others (2015) Environmental characteristics of Agulhas rings affect interocean plankton transport. Science 348:1261447

Villarino E, Watson JR, Jönsson B, Gasol JM and others (2018) Large-scale ocean connectivity and planktonic body size. Nat Commun 9:142

Voldsund A, Aguiar-González B, Gammelsrød T, Krakstad JO, Ullgren J (2017) Observations of the East Madagascar Current system: dynamics and volume transports. J Mar Res 75:531−555

von der Heyden S (2009) Why do we need to integrate population genetics into South African marine protected area planning? Afr J Mar Sci 31:263−269

von der Heyden S, Prochazka K, Bowie RCK (2008) Significant population structure and asymmetric gene flow patterns amidst expanding populations of *Clinus cottoides* (Perciformes, Clinidae): application of molecular data to marine conservation planning in South Africa. Mol Ecol 17:4812−4826

von der Heyden S, Mbongwa N, Hui C (2020) Supporting sandy beach conservation through comparative phylogeography: the case of *Excirolana* (Crustacea: Isopoda) in South Africa. Estuar Coast Shelf Sci 242:106841

von der Meden CEO (2009) Intertidal patterns and processes: tracking the effects of coastline topography and settlement choice across life stages of the mussels *Perna perna* and *Mytilus galloprovincialis*. PhD thesis, Rhodes University, Grahamstown

von der Meden CEO, Porri F, Erlandsson J, McQuaid CD (2008) Coastline topography affects the distribution of indigenous and invasive mussels. Mar Ecol Prog Ser 372:135−145

Weidberg N, Lobón C, López E, Flórez LG, del Pino Fernández Rueda M, Largier JL, Acuña JL (2014) Effect of nearshore surface slicks on meroplankton distribution: role of larval behaviour. Mar Ecol Prog Ser 506:15−30

Weidberg N, Porri F, Von der Meden CEO, Jackson JM, Goschen W, McQuaid CD (2015) Mechanisms of nearshore retention and offshore export of mussel larvae over the Agulhas Bank. J Mar Syst 144:70−80

Weidberg N, Goschen W, Jackson JM, Pattrick P, McQuaid CD, Porri F (2019) Fine scale depth regulation of invertebrate larvae around coastal fronts. Limnol Oceanogr 64:785−802

Whitfield A (2005) Preliminary documentation and assessment of fish diversity in sub-Saharan African estuaries. Afr J Mar Sci 27:307−324

Whitfield AK, Weerts SP, Weyl OLF (2017) A review of the influence of biogeography, riverine linkages, and marine connectivity on fish assemblages in evolving lagoons and lakes of coastal southern Africa. Ecol Evol 7:7382−7398

Wilson LJ, Fulton CJ, Hogg AM, Joyce KE, Radford BTM, Fraser CI (2016) Climate-driven changes to ocean circulation and their inferred impacts on marine dispersal patterns. Glob Ecol Biogeogr 25:923−939

Woodson CB, McManus MA, Tyburczy JA, Barth JA and others (2012) Coastal fronts set recruitment and connectivity patterns across multiple taxa. Limnol Oceanogr 57:582−596

Yamagami Y, Tozuka T, Qiu B (2019) Interannual variability of the Natal Pulse. J Geophys Res Oceans 124:9258−9276

Yasuda N, Nagai S, Hamaguchi M, Okaji K, Gérard K, Nadaoka K (2009) Gene flow of *Acanthaster planci* (L.) in relation to ocean currents revealed by microsatellite analysis. Mol Ecol 18:1574−1590

Zardi GI, McQuaid CD, Teske PR, Barker NP (2007) Unexpected genetic structure of mussel populations in South Africa: indigenous *Perna perna* and invasive *Mytilus galloprovincialis*. Mar Ecol Prog Ser 337:135−144

Zardi GI, Nicastro KR, McQuaid CD, Hancke L, Helmuth B (2011) The combination of selection and dispersal helps explain genetic structure in intertidal mussels. Oecologia 165:947−958