



Contribution to the Theme Section 'Marine functional connectivity'

Coastal connectivity of an abundant inshore fish species: model–data comparison along the southern coast of South Africa

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ABSTRACT: Biophysical models are often used to estimate larval dispersal patterns for the assessment of marine metapopulation spatial structure. However, comparisons of these models with field observations are relatively rare, and the extent to which models reproduce true marine connectivity patterns is unclear. We developed a biophysical model for larvae of the blacktail seabream *Diplodus capensis* (Sparidae), an abundant recreational and subsistence fishery species along the south-east coast of South Africa, and compared outputs from various configurations of that model to results from a field study conducted in a large regional embayment (Algoa Bay). Seasonal patterns of dispersal and recruitment produced by the model agreed best with field observations when thermal constraints on spawners and larvae were included. Spatial gradients in settling larvae also matched well, with the model capturing observed high settler densities within the lee of a major headland. Nevertheless, stronger spatial gradients were observed in larval densities from the field study when compared with model results, which may be explained by behavioural post-settlement processes. Model-based dispersal patterns revealed up to 5 subpopulations along the southern coast, with barriers to connectivity between subpopulations generally linked to hydrographic features. Overall, our results suggest that thermally mediated spawning behaviour, physical transport and post-settlement processes all play important roles in determining marine connectivity for the blacktail seabream. Refining physiological larval constraints may be an important component that needs to be considered going forward.

KEY WORDS: Larval dispersal · Population dynamics · Biophysical model · Seabream · *Diplodus capensis*

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1. INTRODUCTION

Many marine organisms produce planktonic offspring which may spend minutes to months in the water column as eggs or larvae before recruiting

to juvenile and/or adult habitats. These planktonic stages connect populations of sedentary or demersal species and have the potential to recruit over a wide area (White et al. 2014, Shima et al. 2018). However, the supply and settlement of larvae are extremely

variable, as they are affected by multiple factors which operate at different spatial and temporal scales (Jenkins et al. 1998, Porri et al. 2006, Pineda et al. 2010). This variability has large consequences for connectivity and population dynamics (Marshall et al. 2009, Garavelli et al. 2016). Understanding this variability in recruitment can help fisheries managers to establish sustainable exploitation levels and marine spatial managers to develop appropriate conservation measures that promote populations that are resilient to exploitation, environmental change and habitat degradation (Hutchings 2000, Miller 2007).

Apart from the initial factors controlling larval supply, such as egg production and fertilization, recruitment is largely affected by processes of dispersal and mortality. Rates of mortality may be extremely high during the planktonic period (Rumrill 1990), and dispersal may not only be determined by large-scale ocean processes but also by local, small-scale ones (Morgan et al. 2009, Nickols et al. 2015, Weidberg et al. 2019, Pattrick et al. 2021). Early work on larval dispersal highlighted the potential for larvae to disperse over large distances (Scheltema 1971), leading to populations being perceived as relatively open, i.e. having high population connectivity. While large-scale ocean processes may be disproportionately responsible for affecting the available supply of larvae (Pineda 2000), localised small-scale processes may also modify local distribution and settlement patterns (Pineda 1994, Pattrick et al. 2013, Treml et al. 2015). High rates of self-recruitment have been discovered for a range of marine species from various coastal habitats (e.g. Jones et al. 2005, Almany et al. 2007, Porri et al. 2014, Green et al. 2015, Weidberg et al. 2015), indicating that populations may have lower connectivity than previously suspected. The unknown scales of larval dispersal and population connectivity present a problem for marine ecologists, fishery managers and spatial planners, as these factors have important implications for population persistence and protection of genetic diversity (Sponaugle et al. 2002, Treml et al. 2015). Effective spacing and positioning of marine protected areas (MPAs) is critically important, but direct measurements of mean larval distribution and transport are challenging for individual species and extremely difficult for entire communities. Combinations of genetic analyses, modelling and measurement of ocean currents have therefore been advocated to elucidate larval dispersal and connectivity and assist fisheries management (Kirkman et al. 2021).

Estimating population connectivity nevertheless remains a difficult task due to the number of unknown biological and/or behavioural factors that are unique

to a species during the planktonic stage (Lowerre-Barbieri et al. 2017), but also because of the highly complex and variable hydrography of the coastal environment (Becker et al. 2007, Cowen & Sponaugle 2009). Biophysical modelling approaches allow the integration of these biological and physical processes so as to improve our understanding of these complex mechanisms and estimate possible dispersal and recruitment scenarios (Cowen et al. 2006, Gallego et al. 2007). Advances in oceanographic models have elucidated the role of hydrographic features responsible for larval transport and retention as well as its annual variability (Roberts & Mullon 2010, Garavelli et al. 2014), while coupling with individual-based models (IBMs) allows for incorporation of the biological aspects of each individual in relation to its physical environment. Here, we developed a spatially explicit biophysical model, which incorporates known early-life characteristics with a regional 3-dimensional oceanographic model, to study the dispersal and connectivity patterns of a coastal teleost species, *Diplodus capensis* (Smith, 1844), commonly known as blacktail seabream, along the southern coast of South Africa.

The blacktail seabream is an important species for recreational and subsistence fishing, contributing a large component to average catch, and is common throughout its South African distribution from Cape Point up to southern Mozambique (Heemstra & Heemstra 2004). Adults are resident to shallow surf-zone habitats associated with rocky reefs (Mann & Buxton 1992). Spawning of the pelagic eggs takes place throughout the year, predominantly during spring and summer in shallow (<30 m) coastal waters (Coetzee 1986, Mann & Buxton 1998). Incubation of the pelagic eggs typically takes 35–40 h, followed by a planktonic larval phase for a further 17–35 d (Macpherson & Raventos 2006). While no direct evidence for larval vertical migration exists for this species, eggs and early-stage larvae of the congeneric *D. sargus* and other members of the Sparidae family appear to be more commonly distributed in the surface layers (<10 m) than at greater depths (>30 m) (Olivar & Sabatés 1997, Leis et al. 2006). Shallow, subtidal rock pools and gullies function as preferred juvenile nursery habitats, particularly where rocky embayments provide shelter from the exposed South African coastline (Strydom 2008).

In this study, we modelled the effects of the physical environment (currents and temperature) on the spatial and temporal distribution of larvae of the blacktail seabream along the southern coast of South Africa. The results were compared with those from a 2 yr field study, which was conducted in a large embayment, approximately 60 km wide, to deter-

mine to what degree an ocean circulation dispersal model with temperature-based constraints on spawning and larval survival can explain the observed variance in distribution of settlement-stage blacktail. We hypothesised that temperature-based constraints on the release and survival of larvae are necessary to reproduce observed seasonal recruitment rates. Model outputs were further used to assess the potential barriers to dispersal along the southern coast of South Africa, and the resulting population structure is evaluated with regard to the existing MPA network.

2. MATERIALS AND METHODS

2.1. South African coastline

The southern African marine environment has been described as one of the most diverse, complex and highly variable in the world, with most of the coastline being exposed to high wave action and currents and possessing few large embayments (Lutjeharms et al. 2001, Hutchings et al. 2002). The oceanography of the eastern and southern coast is strongly influenced by the Agulhas Current (Fig. 1a), which causes retroreflections, meanders and eddies, while coastal upwelling occurs in localised areas when winds are favourable and the Agulhas Current is driven offshore by the widening continental shelf of the Agulhas Bank (Lutjeharms et al. 2001). Periodic shoreward intrusions of Agulhas Current waters onto the continental shelf may be associated with large losses of larvae as they are entrained in the current and advected from coastal regions (Porri et al. 2014). A marked seasonal change occurs on the southern coast in relation to the north–south seasonal migration of atmospheric high-pressure cells. Strong westerly winds dominate in austral winter, causing large swell and deep mixed layers. During summer, intense thermoclines develop, although frequent strong easterly winds may drive upwelling at headlands, causing abrupt changes in sea temperature of more than 10°C within a few hours (Schumann

et al. 1988, 1995, Goschen & Schumann 1995). Although deeper waters generally flow westwards, shallow layers are largely driven by winds which blow from either the west or east (Hutchings et al. 2002). The cold ridge, a feature on the central Agulhas Bank, leads to a clockwise circulation where nearshore surface waters tend to flow eastwards in the region near Mossel Bay (Hutchings et al. 2002, Roberts & van den Berg 2005). Situated towards the east of the southern coast, Algoa Bay is a large log-spiral bay with a prominent cape, Cape Recife. Nearshore currents within the bay are predominantly wind driven, alternating almost equally between eastward and westward alongshore flows, with velocities commonly ranging between 4 and 8 cm s⁻¹ for the western and eastern sectors of the bay, respectively (Schumann et al. 2005, Patrick et al. 2013). Interactions between the nearshore and offshore processes result in a dynamic environment,

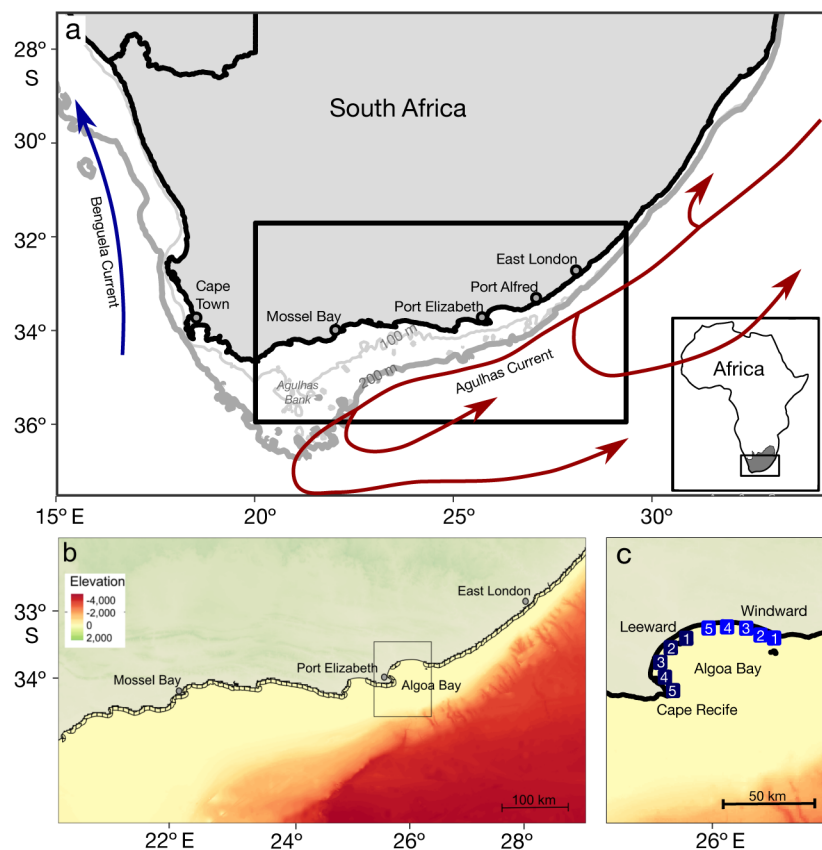


Fig. 1. (a) Geographic location of the study area (black box), showing dominant currents and retroreflections of the southern African oceans and Agulhas Bank to the south associated with a widening of the continental shelf indicated by 100 and 200 m isobaths. (b) Particle release and recruitment zones within the study area shown along the coast as gridded (~11 × 5 km) polygons. (c) Enlarged region for recruitment sites in Algoa Bay classified as leeward (western, dark blue) and windward (eastern, light blue) zones corresponding to the sites sampled by Patrick & Strydom (2014)

with periodic intrusions of Agulhas Current plumes (Schumann et al. 1988). Strong easterly winds lead to upwelling at the cape, with cold water being driven into the bay by subsequent westerly winds (Goschen & Schumann 1995).

2.2. Hydrodynamic and biophysical models

The Lagrangian particle dispersion modelling tool Ichthyop version 3.3.3 (Lett et al. 2008) was used to simulate the dispersal of eggs and larvae of the blacktail seabream *Diplodus capensis* from and to coastal habitats along the southern coast of South Africa (Fig. 1). Ichthyop uses time series of ocean current velocity and temperature fields archived from hydrodynamic model simulations to study the physical and biological factors affecting ichthyoplankton dynamics (Lett et al. 2008). We used the outputs of a 2.5 km resolution configuration of the Regional Ocean Modeling System (ROMS) covering the domain from 32 to 36°S and from 20 to 29°E (Fig. 1a,b) (Bailey et al. 2022). This configuration was developed to resolve high-resolution bay- and shelf-scale ocean processes using a multi-nested approach and validated using *in situ* instrument mooring data and remote sensing products for the period January 2011 to November 2015 (Bailey 2020) (see Figs. S1 & S2 in the Supplement at www.int-res.com/articles/suppl/m14272_supp.pdf). This period primarily incorporates a 'neutral period' but includes the end of La Niña and start of El Niño phases according to the oceanic Niño index (<https://fews.net/el-ni%C3%B1o-and-precipitation>).

Release areas were designed as coastal, alongshore sections of approximately 0.1° of longitude (~11 km). Coastal areas were chosen based on the adult habitat of blacktail seabream as shallow (<30 m) rocky coast, where spawning also takes place for this highly resident species (Mann & Buxton 1992, 1998, Cowley et al. 2002). Unsuitable habitats, such as long continuous sandy beaches (Fig. 1b), were not included as release or recruit zones in our simulations. Coastal habitat types were mapped using data from the 2011 South African National Biodiversity Assessment (<https://bgis.sanbi.org/SpatialDataset/Detail/414>, accessed 10 October 2021). Suitable habitat, defined as areas classified in the National Biodiversity Assessment as being rocky bottom, was then expanded 5 km in the offshore direction to include subtidal reef and mixed habitat, and then the large polygons were broken into 0.1° (or ~11 km) alongshore sections. Each of the resulting small zones was considered to

be both release and recruitment habitat, as settling late-stage or juvenile blacktail are found to inhabit the same shallow subtidal to intertidal rocky coastline as adults (Strydom 2008, Strydom et al. 2014). Particles ($n = 1000$) were released every day over the study region among the 102 release zones throughout the 5 yr study period with the probability of larval release within a zone being proportional to the relative area of that zone. Particles were also randomly released throughout the water column at depths between 0 and 30 m. No attempt was made to estimate the true larval output of the populations; one model particle may therefore represent many individual larvae, and ultimately, it is relative as opposed to absolute recruitment rates that are of interest in this study. A pelagic larval duration (PLD) of up to 40 d was used, and the criterion used for potential settlement was for larvae to be in recruitment areas anytime during the competency period extending from day 19 after release, which corresponds to shortly after flexion, to day 40, which corresponds to the early juvenile phase (Macpherson & Ravenstos 2006, Connell 2012). Vertical migration behaviour was not included in simulations, as this behaviour has not been resolved for this species (or genus), with studies showing a homogeneous distribution in the upper water column (<30 m) (Tilney et al. 1996, Olivar & Sabatés 1997), or evidence of reverse diel vertical migration (Trassiera 2018). Horizontal movement behaviour was not incorporated due to the predominantly pre-flexion nature and poor development of early-stage blacktail larvae. Recruitment zones, which extended up to 5 km offshore, were considered large enough to account for the potential for active or directional swimming. The full time period (2011–2015) was used to elucidate general dispersal patterns, while only 2011–2012 was used for comparisons with field observations (see Section 2.4).

2.3. Model configurations

Three configurations of the biophysical model were evaluated in post-processing of simulations which were run from January 2011 to November 2015, referred to as M0–M2. The base model, M0, did not include any biological constraints on survival, i.e. recruitment was solely related to advection by currents. Model configuration M1 included thermal constraints on spawning, i.e. release of particles only occurred when temperatures within the release zones were within 16–20°C. Model configuration M2 ex-

tended the conditions of M1 to also include thermal constraints on larvae. If larvae experienced temperatures below 16°C or above 20°C anytime during the PLD (release to settlement), they were removed. This thermal range is based on average water temperatures observed along the study region during the peak period for spawning and larval recruitment (Strydom et al. 2014, Pattrick et al. 2016) and the thermal range for spawning in the *Diplodus sargus* species complex, which includes *D. capensis* (Potts et al. 2013).

Two additional model configurations were considered in preliminary tests by adding daily larval mortality rates (M) to M0 and M2, with a range of rates from $M = 0.05$ to $M = 0.43$ being tested (McGurk 1986). Survival probability to a given age was calculated using M as $(1 - M)^{\text{age}}$, with age being the number of days since the start of the competency period (day 19, mortality prior to competency having no impact on relative recruitment rates). As model outputs found that most recruitment occurred in the very first days of the competency period (90% within the first 10 d), larval mortality produced only minor changes in relative recruitment rates and simulated connectivity patterns. As such, results from these 2 additional model configurations including larval mortality are not represented here.

Model configurations M0–M2 were compared for the total number of simulated recruits and their location, dispersal distance and seasonality of recruitment. Non-parametric tests, including the Wilcoxon rank test and Kruskal-Wallis chi-squared test, were used to compare differences between model configurations. To determine if the number of particles released in simulations was sufficient to obtain statistically stable recruitment estimates, we used the approach suggested by North et al. (2009). We ran simulations using 500, 1000, 5000, 10 000 and 15 000 particles under the same model configurations for 8 release dates and compared the outputs. The difference in the numbers of particles released did not have a notable influence on the total percentage of potential settlers, with the difference never more than 6% (Table 1).

2.4. Model–data comparison

Results from M0–M2 were then compared with field observations from Pattrick & Strydom (2014), who sampled 10 surf-zone sites in Algoa Bay, South Africa (Fig. 1c). Pattrick & Strydom (2014) sampled

ichthyoplankton over a 2 yr period (January 2011–October 2012), with 2 consecutive months per season for summer (December and January), autumn (March and April), winter (June and July) and spring (September and October). Five sampling sites were positioned along each of the western (leeward, sites L1–L5) and eastern (windward, sites W1–W5) sides of the bay. Sampling was carried out using a larval seine net with a mesh aperture of 0.5 mm and a total width of 4.5 m and height of 1.5 m. The seine was pulled parallel to the shore for 25 m in shallow water of less than 1.5 m depth. Catch per unit effort was estimated as the total number of fish larvae captured per net haul, with 3 replicate hauls performed at each site. For the purposes of model–data comparison, the 10 recruitment zones sampled by Pattrick & Strydom (2014) were added to our model configurations despite these areas having only limited suitable recruitment habitat (Fig. 1c). Only simulation data which corresponded with the period of the field study (sampling dates of 2011 and 2012) were used for comparison.

2.5. Identification of subpopulations

Connectivity matrices were produced for each of the model configurations M0–M2 in order to identify potential barriers to dispersal and subpopulation structure. Subpopulations were identified using the methodology proposed by Jacobi et al. (2012) and implemented using the R package ‘ConnMatTools’ by Kaplan et al. (2017). The method identifies

Table 1. Results for simulations run on 8 dates using the same model configurations, but different numbers of released particles. Values show percentage of simulated particles that meet conditions for potential recruitment, maximum difference in recruitment rates among simulations (Max. diff.) with different particle release numbers per release date, and averaged values across all release dates

Release date	Particle number					Max. diff. (%)
	15 000	10 000	5000	1000	500	
01 Jan 2012	51.2	50.6	48.6	54.1	51.9	5.5
02 Jan 2012	51.2	51.6	52.2	52.4	55.8	4.6
01 Jun 2012	51.2	51.1	51.8	50.0	47.3	4.5
02 Jun 2012	50.7	50.2	51.3	50.0	52.3	2.3
01 Mar 2013	63.0	63.5	64.5	60.8	64.3	3.7
02 Mar 2013	64.9	65.4	65.4	62.3	59.8	5.6
01 Nov 2013	56.7	57.4	58.1	57.4	58.1	1.4
01 Nov 2013	56.4	56.5	56.7	54.5	55.2	2.2
Mean	55.7	55.8	56.1	55.2	55.6	3.7

approximately independent subpopulations by calculating a set of subpopulations that minimise connectivity between subpopulations (Jacobi et al. 2012). The method uses the mean connectivity between an area i and an area j , calculated as the average connectivity between these areas, $\frac{C_{ij}+C_{ji}}{2}$. Connectivity matrix columns were not normalised, as per Garavelli et al. (2016, 2014), as this would eliminate the effect of habitat area limitation. The level of aggregation or disaggregation in identified subpopulations is controlled by a tunable parameter, beta, with a value near 0 leading to a greater number of subpopulations (approximately 1 subpopulation per release zone), and larger, positive values leading to a single subpopulation which includes all release zones (Fig. S3). Using the formula of Jacobi et al. (2012), a set of beta values were produced which ranged from slightly greater than zero to values above one. This resulted in a set of potential subdivisions of the study domain, each having a different number of subpopulations. For each such subdivision, the percentage of self-recruitment (fraction of settlers originating in the same subpopulation), the average percentage of larvae exchanged between adjacent subpopulations and the quality or 'leakage', i.e. the percentage of exchange among all subpopulations, were calculated. The different subdivisions were then compared, and the final subpopulation arrangement was selected by finding (1) a set of subpopulations where barrier or division locations were consistent among multiple beta values, (2) no redundant subpopulations existed, i.e. where net export was greater than local retention, and (3) structure displayed low leakage values of no more than 35%. While this approach produces a reasonable set of subpopulations, given that 35% leakage was chosen somewhat arbitrarily as a cut-off, in Fig. S3 we have included subpopulation divisions for a number of different beta values, as well as how leakage between populations varies as a function of the number of subpopulations in order to illustrate the method of selection described above. All analyses were performed using R (version 3.6.3) (R Core Team 2018), and maps were created using the 'sf' (Pebesma 2018) and 'ggplot2' (Wickham 2016) packages.

3. RESULTS

3.1. Model recruitment

The base model (M0) had the highest number of recruited larvae, with 33% of all released larvae encountering recruitment habitat during the 19 to 40 d

competency period. Model configurations which included thermal thresholds on spawning (M1) or both spawning and larvae (M2) had significantly lower values of recruitment (paired Wilcoxon signed rank test, $p < 0.001$) with 18 and 12%, respectively. Recruitment was highest at the beginning of the competency period and declined rapidly up to day 40. Most larvae (56%) were within recruitment zones on the first day of competency (day 19), and nearly 80% were within recruitment zones in the first 5 d of competency (days 19 to 23). Subsequently, the addition of daily larval mortality from the onset of the competency period had a minor impact on relative patterns of potential settlement and connectivity, and models including a daily mortality rate were not considered any further. Large numbers of larvae were exported out of the domain at the western extent of the study area (20–21° E). This loss of larvae due to export out of the domain declined rapidly, as losses were less than 10% between 22 and 27° E. Recruitment success was also low for particles released from the eastern extent of the study region (27–29° E) and dispersal distances were high, suggesting that prevailing along-shore currents transported larvae mostly offshore or far from release sites along the coast (Fig. 2a,b). Recruitment varied considerably with the site of release, with clear peaks in successful recruitment occurring within embayments. Greater recruitment success was observed for larvae released between 21 and 23° E and around 26° E (Fig. 2a). Embayments were also associated with lower average dispersal distances and greater retention near the site of release (Fig. 2b). The general patterns in recruitment success did not strongly differ between model configurations, showing the same peaks and troughs (Fig. 2a). Despite a small number of individuals travelling more than 600 km, most recruitment took place near release zones, with 97% of all recruits travelling less than 200 km from release zones, 86% less than 100 km and 65% less than 50 km.

None of the model configurations displayed any significant variability in recruitment amongst years (Kruskal-Wallis chi-squared, $p > 0.1$). M0 did not show any seasonal variability in recruitment either ($p = 0.1$), but for M1 and M2 there was an expected significant variability in the seasonal recruitment ($p < 0.01$), with the lowest values obtained in austral summer or autumn and the highest in spring (Fig. 3). Dispersal distances for all models (M0–M2) exhibited significant seasonal variability ($p < 0.001$). The highest mean (\pm SD) values occurred in summer (63 ± 62 and 53 ± 45 km for M0 and M2, respectively) and the lowest in winter (43 ± 60 and 43 ± 48 km for M0 and M2,

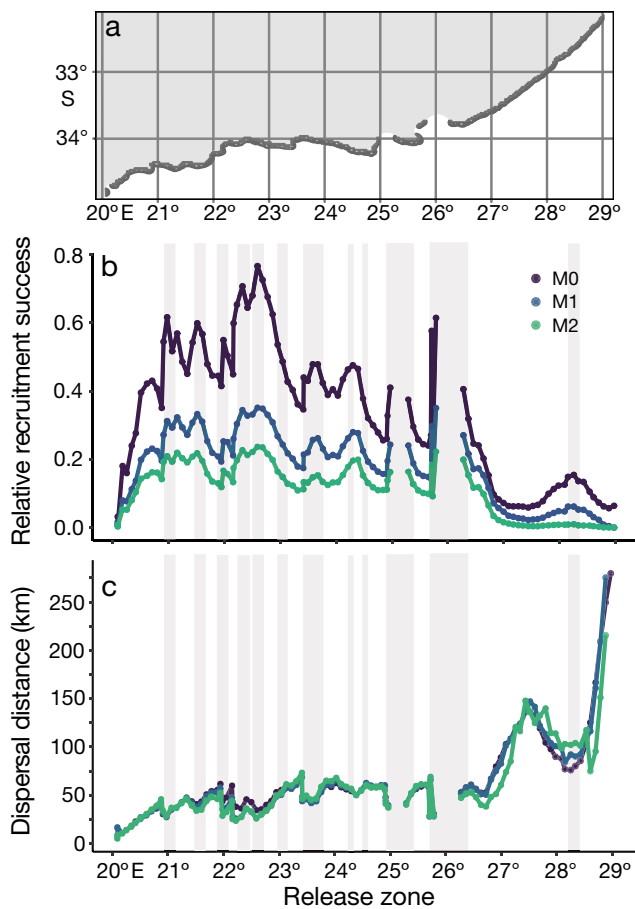


Fig. 2. (a) Gridded particle release zones along the coast, (b) recruitment success relative to the number of released particles by release zone, and (c) mean dispersal distance travelled by recruited blacktail larvae in relation to the release zone for each of the model configurations M0–M2. In panels b and c, the x-axis corresponds to the longitude of the release zones, and grey shaded bars indicate approximate locations of embayments along the coast

respectively) while autumn and spring were intermediate with 55 ± 56 and 45 ± 55 km, respectively, for M0.

3.2. Comparison with observed recruitment patterns

Field data of larval *Diplodus capensis* captures from Algoa Bay, South Africa, collected over 2 yr (Patrick & Strydom 2014) showed a strong seasonal pattern in abundance (Fig. 4). A total of 3814 *D. capensis* larvae were captured over the study duration; a significant majority of these were in the post-flexion stage of development (Patrick & Strydom 2014). The highest numbers were captured in austral spring (78% of total catch), followed by winter (14%), autumn (7%) and summer (<1%). The base

model configuration (M0) was a poor predictor of seasonal larval occurrence, with the highest values of recruitment occurring in autumn and the lowest in spring. Subsequent models (M1 and M2) produced improved seasonal patterns of larval recruitment, with the highest values in spring and the lowest in summer, which was more consistent with field data (Fig. 4).

Catches made by Patrick & Strydom (2014) from the leeward side of the bay accounted for nearly 90% of the total catch (Fig. 5). Model outputs produced similar results for all configurations, with the majority of recruitment occurring within the leeward side of the bay (86, 84 and 82% of the total Algoa Bay recruitment for M0, M1 and M2, respectively; Fig. 5). For both field and model results, a single leeward site, L5, accounted for the majority of catches. The next most abundant site was located on the windward side of the bay at W2 followed by L1 with 8 and 4% of the total catch, respectively, while remaining sites contributed 2% or less. Simulated model comparisons produced a more even recruitment among sites; site L5, as the single largest contributor to recruitment of larvae, accounted for 38% of recruitment for M0, 37% for M1 and 33% and M2. Site L4 followed with approximately 13% while remaining sites each contributed less than 8% of total recruitment.

3.3. Patterns of connectivity for Algoa Bay recruits

Simulations revealed considerable connectivity along the southern coast, with recruits in Algoa Bay originating up to 363 km from recruitment sites for the base model (M0), 351 km for M1 and 306 km for M2 (Fig. 6). For M0, more than half of the recruits originated from the bay (57%), travelling a mean haversine distance of only 32 km, though notable numbers of recruits originated from the west (22%) and east (21%) of the bay, travelling a mean distance of 103 and 155 km, respectively.

There was a considerable seasonal effect on the origin of recruits, with the greatest average distance travelled in autumn (115 ± 80 km) and the lowest in spring (88 ± 89 km). Autumn had the lowest level of recruitment for larvae originating within the bay (47%), while spring had the highest rate (68%). Recruits from outside of the bay were predominantly from the west in summer and autumn and from the east in winter and spring. For model configurations M1 and M2, high numbers of recruited larvae originated within the bay, with 56 and 59%, respectively.

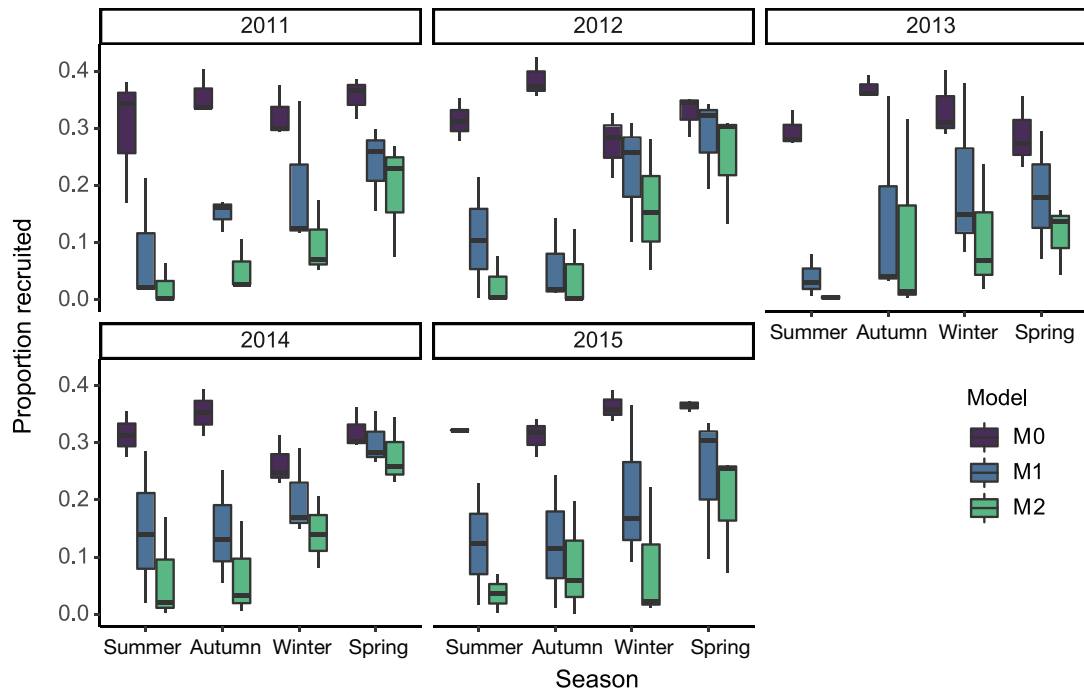


Fig. 3. Proportions of recruited larvae by season and model configuration for each year of simulation. Boxplots indicate median and 25th to 75th percentile, with whiskers showing minimum and maximum values

3.4. Barriers to dispersal

Separation of the study area into subpopulations based on their levels of connectivity produced reasonably consistent results between model configurations, although the increased seasonal effect of M1 and M2 resulted in additional barriers to larval exchange. Fig. 7 shows the most consistent separations into subpopulations for each of the model configurations based on the consistency of barrier positions and quality index (leakage). For M0, barriers to dispersal were identified at 27.5 and 24.5° E (Fig. 7a). Larval exchange from the west was minimal, with 5% or less movement from western to eastern adjacent subpopulations, while movement from the east was greater, ranging from 10 to 30% resulting in mean values of 8 and 16% exchange between subpopulations. Self-recruitment was high for all subpopulations, but lower for the easternmost subpopulation. An additional separation at 22° E was obtained with M1, where the eastward exchange between subpopulations 4 and 1 was reduced (Fig. 7b). Self-recruitment of subpopulations remained high along

the western and southern region, and overall larval exchange reduced to 30%. Finally, for M2, another additional barrier occurred at ~26° E, separating Algoa Bay from eastern regions (Fig. 7c). The barriers to exchange produced 5 subpopulations along the region of study with the lowest percentage of total larval exchange at 21%.

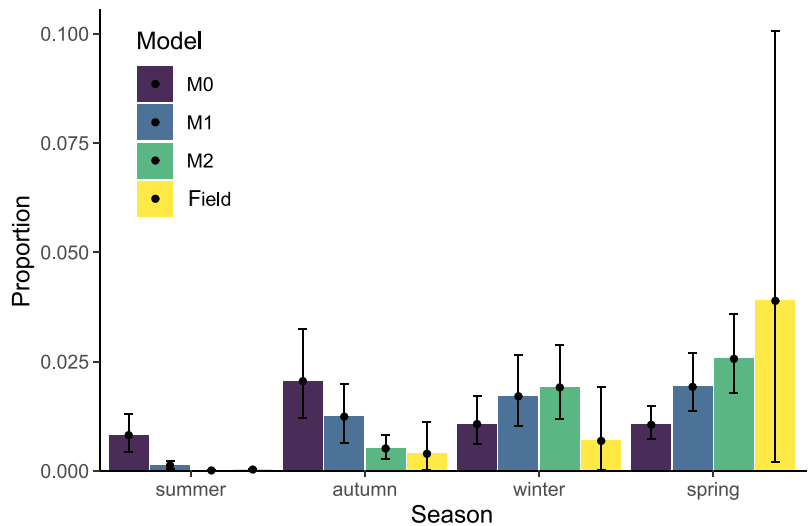


Fig. 4. Proportion of recruits by season for model configurations and field observations of Patrick & Strydom (2014) averaged over the years 2011 and 2012 and all sites. Bars indicate mean proportion of total catch and error bars indicate 95% confidence limits

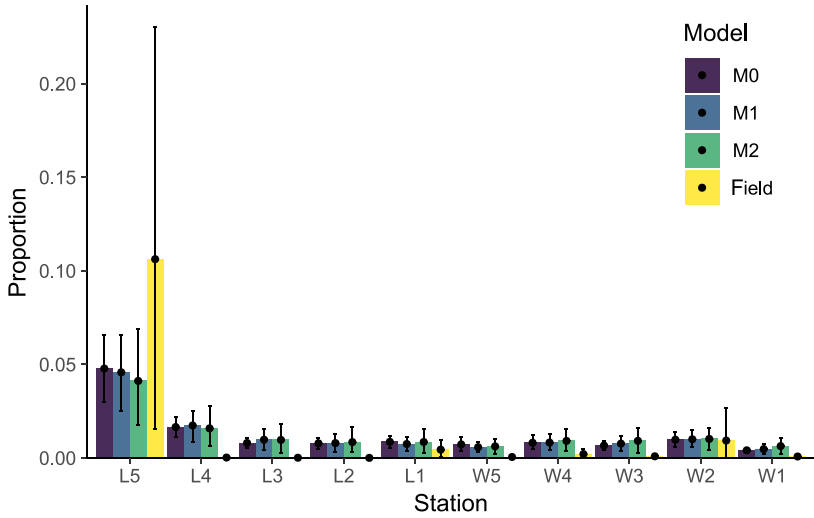


Fig. 5. Proportion of recruits by site (L1–L5: leeward sites; W1–W5: windward sites) for model configurations and field observations of Patrick & Strydom (2014) averaged over the years 2011 and 2012. Bars indicate mean proportion of total catch and error bars indicate 95% confidence limits

4. DISCUSSION

Although all model configurations tested predicted the observed spatial gradients in recruit density within Algoa Bay quite well, only models that included thermal constraints on spawners and additionally larvae predicted the observed seasonality. Including biologically relevant thermal constraints in model configurations produced seasonal recruitment patterns which more closely reflected the spring peak of spawning and recruitment of the blacktail seabream, as also indicated by gonado-somatic index data (Mann & Buxton 1998) and the presence of larvae in recruitment habitats (Strydom et al. 2014).

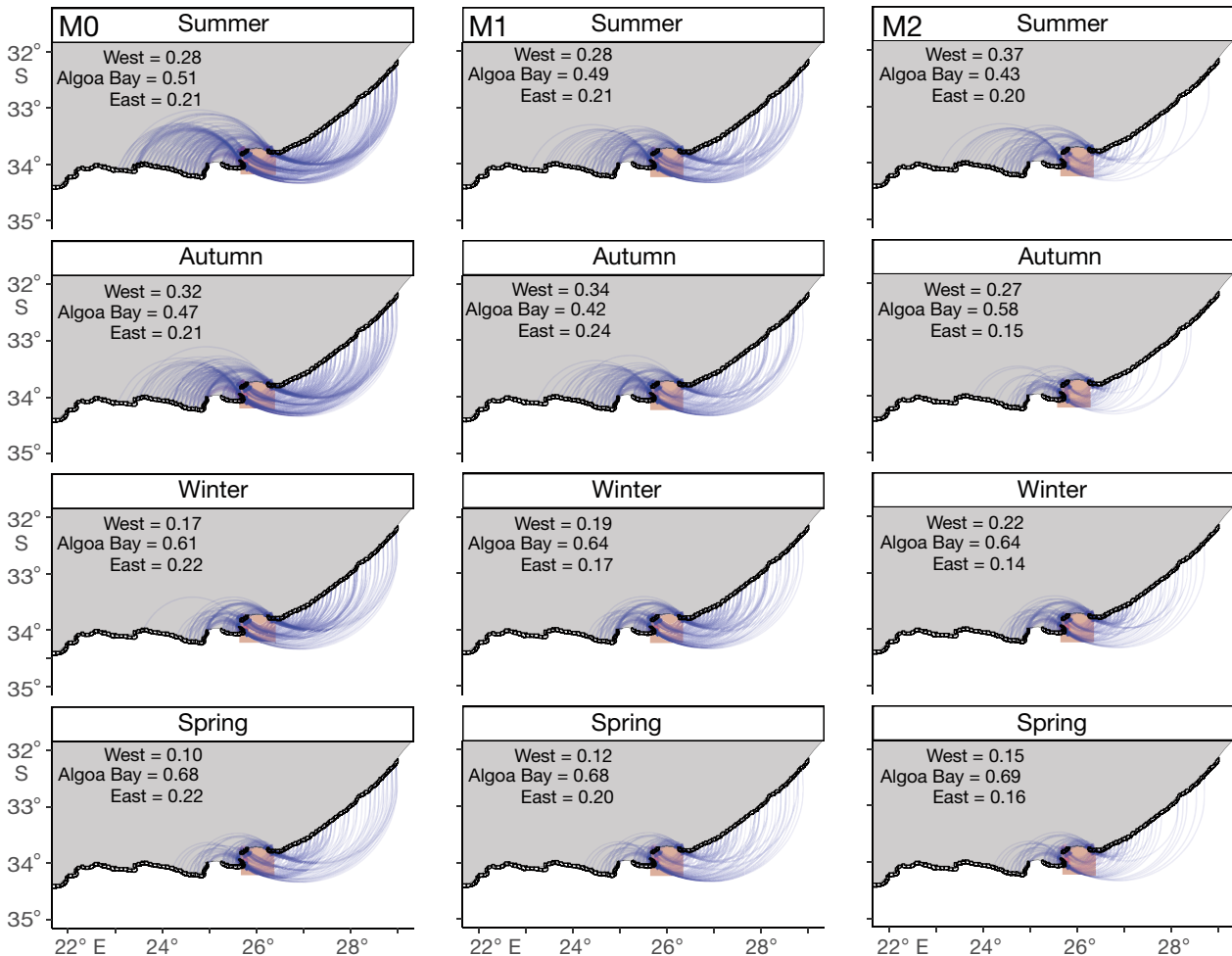


Fig. 6. Origins of larvae that recruited in Algoa Bay (location shown by red square) by season for model configurations M0 (left), M1 (centre) and M2 (right). Larvae recruited from the west are represented with upward arcs, recruits from the east with downward arcs and proportions of recruits which originated from the west, east or within Algoa Bay are shown in each panel

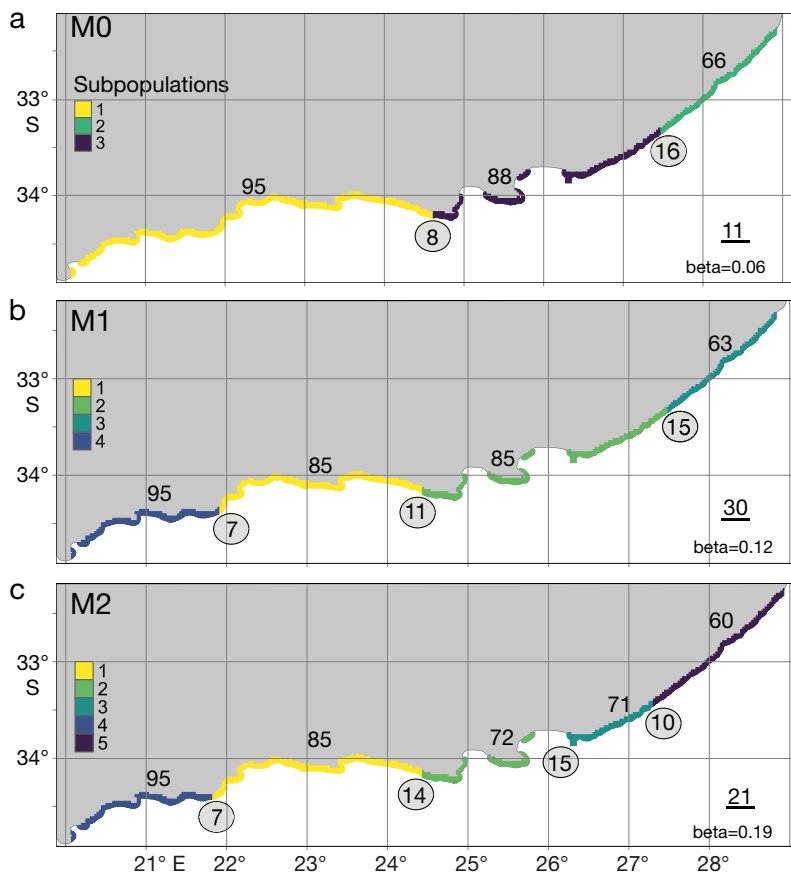


Fig. 7. Partitioning of the southern coast blacktail population into subpopulations based on their levels of simulated connectivity for model configurations M0 (top), M1 (middle) and M2 (bottom). Underlined values indicate the percentage of exchange between all subpopulations (also referred to as leakage), encircled values indicate the mean percentage exchange between 2 adjacent subpopulations, and the percentage of self-recruitment within each subpopulation is indicated by the open value above colored regions. The optimal partitioning is shown for each model configuration based on the consistency of barrier positions and low leakage.

In particular, M2 displayed a seasonal recruitment pattern in Algoa Bay which most closely resembled the findings of Patrick & Strydom (2014). Nevertheless, whereas the seasonal proportion of recruits agreed with field data in summer, autumn and spring, winter recruitment values from M2 were considerably greater than the field results. This discrepancy may be related to the effect of photoperiod on gonad maturation, as Mann & Buxton (1998) suggested that the spawning season of blacktail along the southern coast is correlated with photoperiod and water temperature. However, peak spawning occurs in late winter at the species' eastern extent of distribution and in summer at the western edge (Coetzee 1986, Connell 2012). This suggests that while photoperiod may be a contributing factor, temperature and its variability may more directly

influence peak spawning activity, together with a suite of other possible factors such as phenological adaptations to local conditions along the coastline.

Recruitment success and dispersal distance were strongly influenced by the area of release. Larvae released within embayments along the southern coast were twice as likely to successfully recruit when compared with those released outside of these areas. Additionally, larvae released in embayments typically exhibited lower dispersal distances indicating settlement closer to their site of release. Sheltered marine environments, such as bays, commonly exhibit greater retention of eggs and larvae than open coastlines (Wing et al. 2003, Breheny et al. 2012, von der Meden et al. 2012), and even small embayments in the lee of headlands may provide retention opportunities (Roughan et al. 2005, Morgan et al. 2011). The value of these areas along the southern coast, where nearshore flows are broken by topographic features, cannot be understated for a coastline which has been described as one of the smoothest and least convoluted in the world (Hutchings et al. 2002).

When comparing recruitment values between the western (leeward) and eastern (windward) side of Algoa Bay, there was considerable agreement between model results and field data, with most recruitment occurring on the leeward side. This is predominantly due to the overwhelmingly high catches from a single site, L5 (Fig. 5). There was little variation in the relative spatial pattern of recruitment at the various sites across model configurations, suggesting that seasonality, due to thermal constraints, had limited effect on dispersal patterns at the small scale of Algoa Bay. Slightly higher values of recruitment on the windward side with M2 compared to M0 may be attributed to the predominance of eastward flow in the Bay over spring compared to predominantly westward flow over autumn (Roberts 2010). Elevated values at station L5, for both simulated and field results, may be related to topographical features where eggs and larvae are retained in the lee of a headland (Morgan et al. 2011), although habitat

availability may also play a role for field results. Stations L5 and L1 were unique among the other sampling sites, offering mixed rocky shore-associated surf zones, compared with all other sites, which were noted as sandy beach surf zones (Patrick & Strydom 2014). These mixed shore habitats offer advantages to early recruits in terms of reduced wave action and current flow and better feeding opportunities. As such, these areas have been identified as preferred nursery habitats for newly settled blacktail larvae and/or early juveniles (Strydom 2008). High densities of postflexion/early-settled blacktail at L5 collected by Patrick & Strydom (2014) may in part be driven by active behavioural processes and habitat selection. For example, larval fish may be choosing not to settle in other sandy-bottom portions of the bay, thereby resulting in an accumulation of recruits at L5 with its extensive rocky-bottom habitat. Indeed, blacktail settlement-stage larvae are capable swimmers, able to cover large distances, up to 6 km, without food or rest at swimming speeds up to 19 cm s^{-1} , which exceeds the modal current velocity in the Algoa Bay nearshore of 8 cm s^{-1} (Patrick & Strydom 2009). This may explain the consistently stronger spatial gradients in settler density in observations than in our simulations. Nevertheless, our results

demonstrate that dispersal models based exclusively on ocean circulation are capable of reproducing to a large extent spatial gradients in Algoa Bay. This was similarly shown by Teske et al. (2016), whose relatively simple circulation models were able to explain high levels of genetic structure and self-recruitment along the southern Australian coastline.

The identification of blacktail subpopulations from the connectivity matrices highlighted robust patterns of connectivity and barriers to dispersal along the southern coast. For all model configurations, 2 common major separations were identified at 27.5 and 24.5° E (Fig. 7a). Subsequent barriers were identified for M1 and M2 at approximately 22 and 26° E , suggesting that up to 5 relatively isolated subpopulations may exist along the southern coast when thermal constraints on spawning or larval survival are included and seasonality of settlement is affected. The first major barrier at 27.5° E is consistent with the transition from the subtropical Natal province bioregion on the east to the warm-temperate Agulhas region on the west (Spalding et al. 2007). The transition of these bioregions is related to the position of the gradual deflection of the southward-flowing Agulhas Current from the coast (Fig. S2). This leads to divergent upwelling near the coast (Fig. 8), which

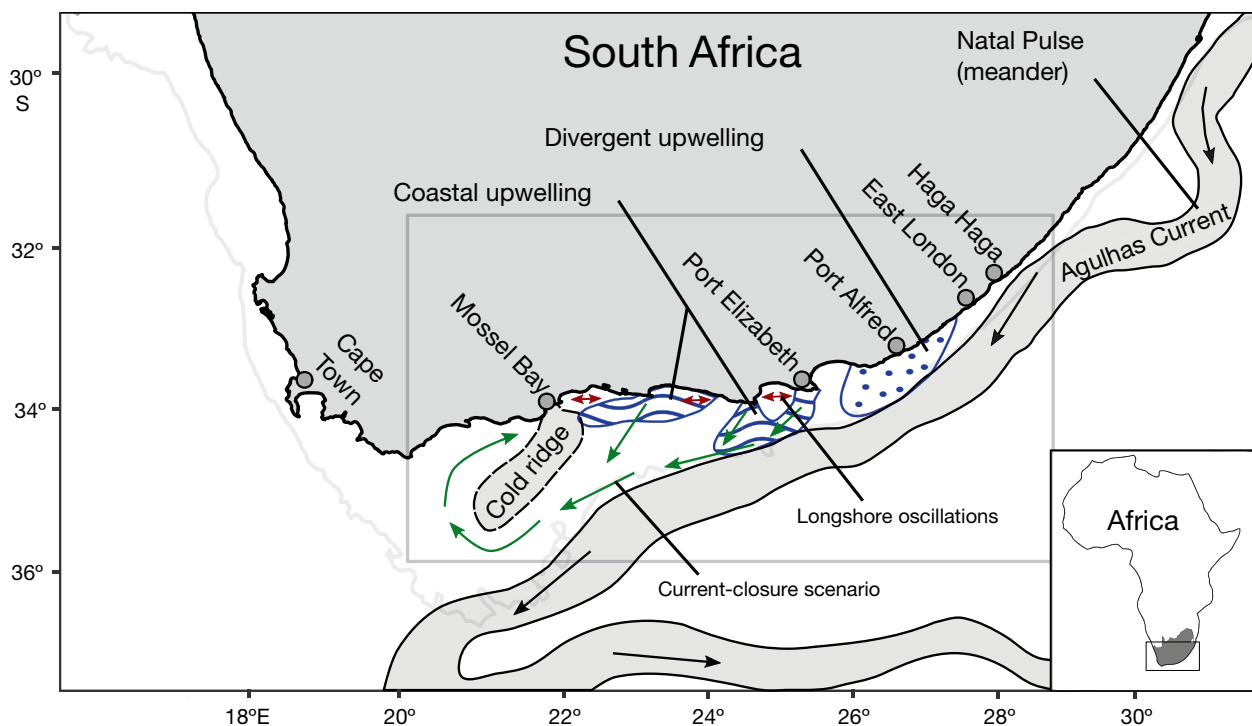


Fig. 8. Common oceanographic processes and features of the southern African marine environment showing locations of prominent wind-driven (blue striped areas) and divergent upwelling (blue dotted area) cells and current-closure (green arrows) and longshore oscillations (double red arrows) for the south coast as proposed by Tilney et al. (1996) (adapted from Roberts 2005)

most likely prevents further eastward transport, while the prevailing nearshore current drives larvae southwards and offshore, thus reducing settlement to the west (Hutchings et al. 2002). There is further support for the role of this mechanism in shaping the connectivity of coastal fish populations with Golla et al. (2020) and Von der Heyden (2009) using genetic techniques, finding that this region forms a barrier to the genetic connectivity of a range of coastal marine species.

The addition of the dispersal barrier at 24.5° E, which leads to the study region being separated into a western, central and eastern part, may be explained by coastal alongshore current dynamics. Due to the influence of the Agulhas Current, westward flow dominates on the Agulhas Bank, although a counter-current retroflexion occasionally leads to nearshore eastward flows opposing the greater shelf flow (Roberts 2005, Roberts & van den Berg 2005). A 'current-closure scenario' cell has been proposed for this region (Fig. 8), where coastal upwelling causes offshore displacement of surface layers (Fig. 8), followed by westward drift on the mid-shelf and return to the coast with subsequent nearshore eastward drift (Tilney et al. 1996). While this scenario is only applicable to spring/summer circulation, due to the prevalence of upwelling over this period, Tilney et al. (1996) also suggested that coastal longshore oscillations (Fig. 8) caused by coastal trapped waves would predominate during winter, reducing alongshore dispersal. The 'current-closure scenario' is also expected to be bounded in the west by the cool-water ridge off the coast at Mossel Bay (22° E) (Tilney et al. 1996), which forms the third barrier to exchange identified in models M1 and M2 where recruitment was predominantly in spring. The mollusc *Turbo sarmaticus* has genetic breaks near this location (Von der Heyden 2009), suggesting that transport from the east is also inhibited for this species.

The final barrier to transport, identified for M2, occurs in Algoa Bay seemingly bisecting the embayment itself. Turpie et al. (2000) identified a discontinuity in coastal fish distributions in this area, suggesting this region forms the edge of the core distribution for a number of coastal fish species. A large, semi-permanent upwelling cell (Fig. 8) lies to the East of Algoa Bay near Port Alfred (~26° E), commonly causing colder water to move onto the eastern parts of the Agulhas Bank and into Algoa Bay (Lutjeharms et al. 2000, Roberts 2010). Upwelling events in this region and other headlands along the south coast can lead to dramatic changes in temperature of up to

10°C or more in less than a day and affect the distributions of marine organisms (Schumann et al. 1988), potentially providing barriers to gene flow. Indeed, Von der Heyden et al. (2008) found that populations of *Clinus cottoides* were effectively isolated between Port Alfred and Haga Haga (26.8–28.2° E), exhibiting low connectivity with populations to the west or east of this range. However, upwelling-related barriers are fluid in nature and commonly display spatial and temporal variability, particularly when wind regime shifts, such as occurs during La Niña conditions, increase both the frequency and intensity of coastal upwelling (Duncan et al. 2019). Thus, these variable and 'soft' barriers may not always limit connectivity. For example, Neethling et al. (2008) and Teske et al. (2010) failed to observe any genetic structuring along the southern coast for coastal and resident fishes.

Knowledge of larval dispersal and connectivity patterns is vital information for management of fishery stocks and the design of marine reserves. Decisions based on incorrect assumptions of larval dispersal and population connectivity may lead to the implementation of ineffective conservation measures (Cowen et al. 2000). The current South African MPA network appears to show some coverage for all of the identified subpopulations along the southern coast (Fig. 9). Considering how the observed barriers to dispersal were supported by oceanographic features and genetic barriers, the current network likely facilitates the conservation of many coastal species to some extent. However, while movement patterns and dispersal abilities are highly variable, the general spacing of reserves has previously been recommended to be less than 15–20 km (Green et al. 2015, Mann et al. 2016). Along the southern coast of South Africa, 20–40 km spacings for reserves has been suggested as optimal based on tag-recapture and modelling studies (Attwood & Bennett 1995, Griffiths & Wilke 2002).

The current South African MPA network shows an average nearest-neighbour distance of 35 km (SD 39.5) (Kirkman et al. 2021). However, within the study region, this distance is higher (46.8 ± 16 km) and exceeds the modelled dispersal distance found for many zones along the coast (Fig. 2b). Behavioural processes such as active swimming are believed to increase local retention (Leis 2006, Leis et al. 2011, Lett et al. 2019), thereby enhancing local population persistence in individual MPAs but reducing exchanges between protected areas and therefore weakening network resilience to shocks or popula-

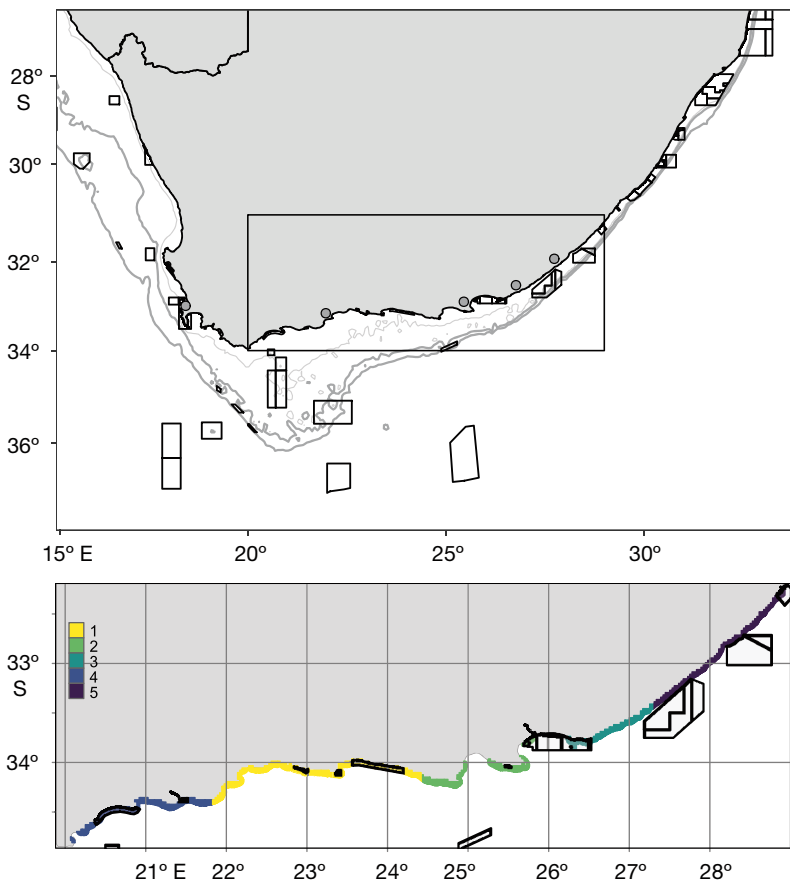


Fig. 9. Marine protected area (MPA) network of South Africa (excluding the Prince Edward Islands MPA to the south) (top); below is the MPA network within the study region (in black) overlapped with subpopulations obtained from M2 (in colour). Top map shows 100, 200 and 300 m isobaths in grey

tion failures in individual MPAs. This may be particularly relevant for the subpopulation identified between 24.5 and 26° E, where a single small MPA is located (Fig. 9), which may be insufficient to be either self-persistent or contribute to an MPA network effect.

Though biophysical dispersal models have contributed to our understanding of large-scale dispersal patterns, recruitment and connectivity (Miller 2007), limitations of oceanographic models and implemented larval behaviour prevent these models from replacing empirical methods (Kaplan et al. 2017). For instance, biophysical models can fail to reproduce fine-scale coastal hydrodynamic processes, such as those which occur along jagged coasts or headlands (Briton et al. 2018). Poor knowledge on the behaviour and biology of larvae, particularly with regards to how these characteristics change during early ontogeny (Leis 2007, Leis et al. 2007), also impedes the production of realis-

tic outputs. As such, a combination of approaches has been suggested where, for example, biophysical models, genetic analyses, physical sampling methods and biological and behavioural studies could be used as complementary methods in order to determine dispersal and connectivity (Kirkman et al. 2021). Although weaknesses in any approach should be acknowledged and even genetic methods may provide little clarification with regards to gene flow and population connectivity (Teske et al. 2015), a combination of methods can indeed improve agreement of estimates (Skogen et al. 2021).

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