RESEARCH ARTICLE

Influence of Mozambique Channel eddies on larval loss of two shallow-water commercial shrimp species

Bernardino S. Malauene [1,2,3]*, **Christophe Lett**[4,5], **Francis Marsac**[4,5], **Pierrick Penven**[6], **Silvia Abdula**[1], **Coleen L. Moloney**[2], **Michael J. Roberts**[3,7]

1 Instituto Oceanográfico de Moçambique, Maputo, Mozambique, **2** Department of Biological Sciences, University of Cape Town, Rondebosch, Cape Town, South Africa, **3** Ocean Science and Marine Food Security, Nelson Mandela University, Gqeberha, South Africa, **4** Institut de Recherche pour le Développement (IRD), Sète Cedex, France, **5** MARBEC, University of Montpellier, CNRS, Ifremer, IRD, Sète Cedex, France, **6** University of Brest, CNRS, Ifremer, IRD, Laboratoire d'Océanographie Physique et Spatiale (LOPS), IUEM, Plouzané, France, **7** University of Southampton, Southampton, United Kingdom

* dinomalawene@yahoo.com.br

Abstract

The shallow-water shrimp fishery is an important social and economic sector in Mozambique. However, catches of shrimps have been declining over the last decades, presumably due to poor recruitment. Climate change has been proposed as a potential cause of increased mesoscale eddy activity over the Mozambique Channel, which may have played a role in poor shrimp recruitment. Indeed, stronger eddies could transport matter, including increased numbers of shrimp larvae, from the coast to unfavourable offshore areas. In this study we used a biophysical model to investigate the influence of eddies on the dispersal of larvae of two commercial shrimp species (*Penaeus indicus* and *Metapenaeus monoceros*) from their spawning areas on the Sofala Bank. We found some 5 large events of offshore or southward transport loss (>10% loss) from the Sofala Bank caused by eddies, occurring sporadically. The northern and central Sofala Bank areas were the most affected by larvae lost offshore. Simulations revealed that temperature-induced larval mortality, associated with cold-core cyclonic eddies, could also play a role in larval loss of up to 40%, which is greater than the larval transport loss associated with the eddy circulation. However, when they survived, larvae transported offshore could travel long distances (600–1600 km in 15 days), potentially promoting connectivity with other stocks in the region.

1. Introduction

Most penaeid shrimp species occur in shallow waters influenced by river estuaries [1]. They go through a complex life history comprising adults spawning in deep water in the sea (referred to hereafter as offshore), eggs floating to the sea surface offshore, and passively drifting larvae being transported into coastal estuarine brackish water [1]. Here, juveniles settle on the sea-floor and develop into sub-adults, which return to the sea [2–4]. Such a life cycle is completed in about one year [4], with the shoreward pelagic larval stage lasting 10–15 days [5, 6],

depending on ambient conditions. The passively drifting larval stages of marine organisms can be affected by environmental processes and events, such as temperature, salinity, tides, currents, and upwelling [7–9], potentially decreasing recruitment of offspring [10], with negative consequences for the adult stocks and for the fisheries that catch them [11, 12].

The Sofala Bank on the central Mozambican coast between 16 and 2˚S (Fig 1) is a key natural habitat for the largest population and stock of penaeid shrimps in the Southwestern Indian Ocean [13]. It supports the most important multi-species (six native and two recently-discovered invasive species) and multi-sectoral (artisanal, semi-industrial and industrial) shallow-water shrimp fishery in Mozambique [14–16]. Collectively, *Penaeus indicus* (H. Milne Edwards, 1837) and *Metapenaeus monoceros* (Fabricius, 1798) are the two most important commercially-targeted species, particularly for the semi-industrial and industrial sectors, contributing more than 80% of the total catch (e.g., [14, 15, 17]). The industrial and semi-industrial shallow-water shrimp fishing sectors constitute some of the main components of fisheries exports in Mozambique, providing foreign income for the country's economy [16]. The artisanal fishery is critical for sources of food and livelihoods of coastal communities [16–18]. In the last two decades, however, the Sofala Bank shallow-water shrimp catches declined to a minimum (~2000 tons) in 2012, and the stock biomass remains low [16]. The decline is suspected to be related to poor recruitment into the fishery.

Penaeid shrimp catches depend largely on recruitment of juveniles entering the fishery [19, 20], which in turn depends on successful larval transport from spawning areas [20]. Ocean currents are important in transporting pelagic larvae [9], particularly at the sea surface where currents are stronger compared to the bottom [3]. In the absence of a permanent continuous current, the ocean circulation in the Mozambique Channel is dominated by a series of both warm-core anticyclonic and cold-core cyclonic mesoscale eddies propagating southward [21–25]. On average, about four to six large anticyclonic eddies and rings occur per year, with strong currents of up to 2 m s^{-1} at their edges [22–24]. Mozambique Channel mesoscale eddy activity has been increasing over time, as indicated by a significant eddy kinetic energy trend derived from altimetry observation during the historical period between 1993 and 2009 [26]; this trend is still present in the recently extended period from 1993 to 2022 [27]. Moreover, a projection from the past (1860) into the future (2090), based on the Coupled Model Intercomparison Project (CMIP6) framework for ongoing anthropogenic climate change, also shows an increase in mesoscale eddy activity [28]. These eddies result mainly from barotropic and baroclinic instabilities in the northern Mozambique Channel [24]. Such instability results from increasing sea temperatures and horizontal temperature gradients through the warming ocean, highlighting the impact of climate change on mesoscale eddies [29]. The highly turbulent eddy field, in particular dipole pairs with associated strong frontal currents, can strongly influence the shelf waters and circulation on the Sofala Bank [30, 31]. Previous studies showed that Mozambique Channel eddies can advect coastal production offshore [32, 33]. Eddies have been reported to control transport of oceanic fish larvae [34–38], but the impact of offshore mesoscale eddies on dispersal of shallow-water shrimp larvae is not well known.

Seawater temperature is a critical environmental factor influencing shallow-water shrimp larvae [4]. Cold water (below 25˚C [39, 40]) directly affects shrimp development and can be lethal [4, 41], as shown for *Litopenaeus vannamei* in aquaculture [42, 43]. In addition to seasonal temperature variations (range of 5˚C), with cool conditions in winter (~25˚C [32]), cold-core cyclonic eddies also decrease water column temperatures at their cores, with potential impacts on larval survival. Since mesoscale eddy activity is increasing in the highly turbulent Mozambique Channel [26, 27], shrimp larvae are likely to be exposed to greater influences of eddy-induced circulation and cooler temperatures in the future, aggravating the poor recruitment that currently occurs. Therefore, understanding patterns of shrimp larval dispersal and

survival is pivotal to appraising the depleted shallow-water shrimp stock on the Sofala Bank. This improved understanding is needed to assist in developing possible strategies of adaptation and resilience when planning sustainability of the traditional fishery under climate change.

In-situ observations of shallow-water shrimp larvae are not available in Mozambique. Using a coupled biophysical Lagrangian model based on [44], we investigated larval transport for *P. indicus* and *M. monoceros* on the Sofala Bank. We tested two main hypotheses: (i) whether shallow-water shrimp larvae are transported away from favourable estuarine ecosystems by propagating mesoscale eddies, and (ii) the extent to which cool temperatures decrease the survival of shrimp larvae. Together, these two factors could result in poor shrimp recruitment into the fishery. In the introduction section (1) we provide an overview of the life history of penaeid shrimps, and how physical factors might affect larval transport and mortality of the two species considered here. In the methods section (2) we describe the larval dispersal model for the shrimp species and how ocean circulation and temperature effects were investigated. The results section (3) describes larval dispersal from spawning areas and the impacts of eddies on offshore transport and temperature-related mortality. Finally, in the discussion section (4) we relate the set of results to existing knowledge.

2. Materials and methods

2.1. Biophysical model of larval dispersal

Biophysical models have been useful to investigate egg and larval dynamics as they consider both physical processes and biological factors, and incorporate interactions between the two at different early life-history and spatio-temporal scales [45]. In this study, we simulated larval dispersal with a biophysical model for the two most important commercial shallow-water shrimp species on the Sofala Bank, *P. indicus* and *M. monoceros*. We used the modelling tool, Ichthyop (v. 3.1, freely available at http://www.ichthyop.org), a Java package developed and described by [44], coupled to a Regional Ocean Modeling System (ROMS [46]) high-resolution configuration especially developed for the Sofala Bank [31]. The model domain is large enough to encompass the shallow waters of the entire Sofala Bank at a fine-resolution grid (~2 km, referred to as "child"), embedded into a large grid (~ 6 km, referred to as "parent") covering the adjacent offshore waters (Fig 1). Because this study focused on the influence of offshore eddies on coastal larval dispersal and export/loss, we only used the large parent domain. The lateral open boundaries were forced by the South-West Indian Ocean Model (also developed on ROMS [24]) to ensure good reproduction of Mozambique Channel eddy activity. The ROMS configuration included river discharges and tides, both of which are important processes for the Sofala Bank circulation [31]. Detailed information on the Sofala Bank oceanographic model configuration and its validation are provided by [31]. Outputs used here consisted of 3D current velocities (m s^{-1}), temperature (˚C) and salinity fields averaged every 3 days for five climatological years after the simulation reached its equilibrium stability in model year 4 (i.e. years 4, 5, 6, 7 and 8) [31].

Simulations consisted of the release of 30 000 combined *P. indicus* and *M. monoceros* virtual eggs within their release areas every 3 days and tracking their trajectories for 15 days, the pelagic larval duration for these species. Individuals changed stages depending on their age, from eggs through larvae to settled larvae. It was assumed that shrimp eggs hatch within a few hours (10−14 h) after spawning [5], set to 12 h in the model, and larvae drifted at the surface until they eventually settled at the bottom after 15 days.

The two shrimp species spawn all year round on the Sofala Bank [14]. To investigate seasonal variability of larval transport, simulations were run continuously for a period of five years. Individuals were characterized by their state variables: identity number, position
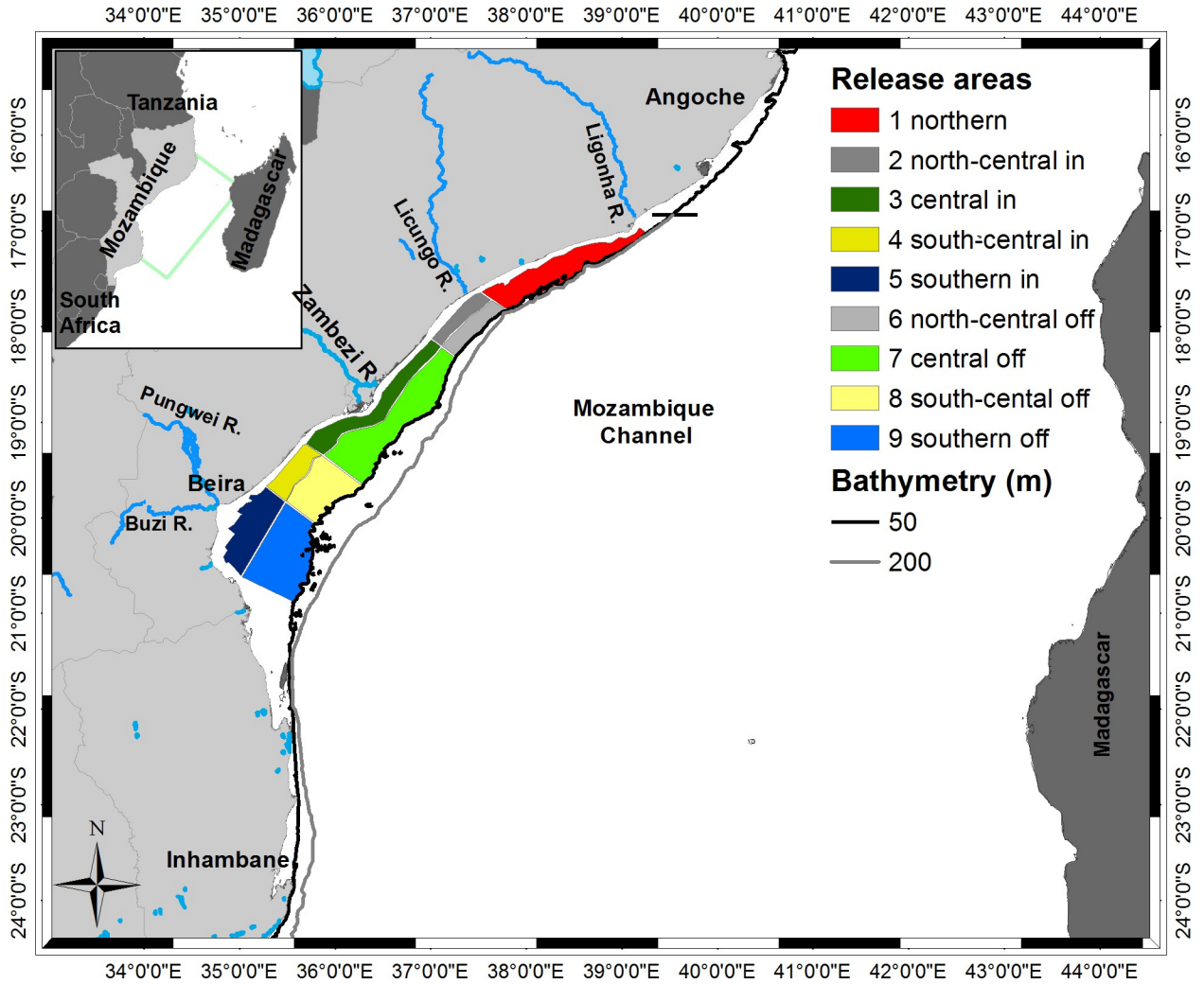
Fig 1. Map of the Sofala Bank. The green line in the top left inserted Fig shows the model domain. The nine release areas used in the simulations are indicated by the colours. Red, green, and blue are the main actual spawning zones for the two shrimp species on the Sofala Bank, whereas grey and yellow are non-spawning zones. Dark and light colours respectively indicate the inshore (in) and offshore (off) parts of the zones. Dark and light grey lines respectively indicate the 50 and 200 m isobaths. Base layers used to create this map are Diva-GIS country outlines, administrative divisions and rivers in the public domain (https://www.diva-gis.org/gdata).

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(longitude, latitude in degrees east and south respectively, and water depth in meters), age (days) and status (settled, lost or dead for the temperature experiment). Model outputs contained all the state variables recorded every 4 hours.

2.1.1. Simulated Release and loss areas. Nine release areas were defined for all simulations (Fig 1). These areas fell within the three actual spawning zones identified for the two species on the Sofala Bank [47]: the northern zone (area 1), the central zone (split into areas 3 inshore and 7 offshore), and the southern zone (areas 5 and 9). In addition, two non-spawning zones were defined: the north-central zone (areas 2 and 6) and the south-central zone (areas 4 and 8). These nine release areas were used to test the hypothesis that natural selection would cause organisms to spawn in locations most favourable to their fate, here being locations leading to highest coastal retention of larvae.

Since *P. indicus* tend to spawn more inshore and *M. monoceros* more offshore [47], the release areas were divided into a shallow inshore area (between the 10 and 35 m isobaths) and

a deeper offshore area (between the 35 to 50 m isobaths), except for the northernmost area (area 1) which is too narrow (Fig 1).

Because these spawning areas are assumed to be the same as the recruitment areas [14], simulated larvae found outside the release areas at the end of the simulation were considered lost from the Sofala Bank coastal stock or population. The mean percentages of larvae lost are available in [48].

2.1.2. Movement of eggs and larvae. Movements of eggs and larvae included horizontal and vertical advection using a forward-Euler time-stepping scheme [44]. The model time step (Δt) was set to 2400 s (40 min), which meets the CFL criterion defined as $\Delta t << L/U_{max}$, where L is the ROMS grid size (6200 m; the parent domain to cover the Sofala Bank and adjacent waters) and U_{max} is the maximum recorded current velocity ($\sim$ 2 m s−1), hence Δt <3100 s. At each time step Ichthyop interpolates the information from ROMS (current velocities, temperatures, and salinities) and calculates the updated larval state variables. Egg buoyancy was set at 1 g cm−3 and larvae were forced to drift at the surface. Horizontal diffusion was implemented following [49].

2.1.3. Cool temperature mortality simulations. To investigate the potential effect of cool water temperature on larval mortality, we tested six values of lethal temperature thresholds from 20 to 25˚C for one of the simulated years. Only one year (model year 5) was used because it was too costly in terms of computations required to run all six temperature simulations for each of the five model years. Low temperature tolerance for the two species is not well defined in the literature. We assumed lethal temperatures might occur from 25˚C, the middle to low optimum range for most reared and wild penaeid species around the world (e.g., [1, 12]), to 20˚C, the low temperature tolerance [1, 12, 50]. For each simulation (20, 21, 22, 23, 24 and 25˚C) it was assumed that larvae died when exposed to water temperatures cooler than the threshold values. Mean larval mortality from each of the six temperatures are available in [48].

2.2. Analysis of model outputs

2.2.1. Calculation of travel distances. We calculated the distance travelled by the simulated larvae between two points using the R function distHaversine of the package geosphere [51], based on the Haversine function. The total distance travelled was obtained by summing up all distances between consecutive points along the trajectory for all larvae. The linear distance from origin to final location, i.e. displacement, was also computed. Distances travelled data alongside with R code to plot them can be found in [48].

2.2.2. Self-organizing map (SOMs). We used self-organizing maps (SOMs), an artificial neural network classification method, and a non-linear cluster analysis [52] to identify and extract the main patterns of mesoscale eddy activity off the Sofala Bank from the ROMS Sea Surface Height Anomalies following [31]. A small 2x2 SOM map, i.e. 4 SOM patterns, was extracted using the R package Kohonen [53] to represent dominant modes of the Mozambique Channel eddy fields. The probability of occurrence of each pattern was defined by the Euclidean distance.

2.2.3. Statistical analyses. Cross-correlation analyses, with a maximum lag of 15 days, were conducted between time series of simulated larval loss and each Euclidian distance to eddy activity patterns retrieved from SOMs. A similar approach was used in previous biophysical dispersal modelling studies [54]. Euclidian distance to a particular eddy SOM pattern is interpreted as a probability of having that pattern in the eddy field at that time. Because the Euclidian distances were not normally distributed, the Spearman's rank correlation at a 95% confidence level was used. When there were positive correlations to a particular SOM pattern,

eddy pattern was interpreted as having a positive effect on loss of simulated larval, i.e. more loss, and vice versa.

One-way analysis of variance (ANOVA) was performed to investigate factors determining the percentage of simulated larvae lost by comparing all nine release areas and six low-lethal temperatures at $\alpha = 0.05$ using R software. Where there were significant differences, the post-hoc Tukey test was conducted to assess whether the difference was among all groups. Prior to performing the ANOVA, the assumptions of normality and homogeneity of variances were verified for the simulation outputs. For normality, a visual inspection was conducted on the frequency distributions of loss for all release areas and all temperatures by plotting both histograms and probability plots (Q-Q plots). For equal variance, both visual inspection of the residuals and Levene's test at $\alpha = 0.05$ were conducted.

3. Results

3.1. Simulated larval dispersal

The highest densities of simulated larvae within the 5-year period were observed on the Sofala Bank inner shelf (Fig 2A), corresponding to the larval release areas. There were relatively high densities elsewhere in the domain, with lowest densities in the northern part. There were no clear dominant larval pathways; however, when looking at trajectories in more detail, three general larval dispersal patterns were apparent: (i) shelf retention, with nearly all simulated larvae from all release areas retained on the Sofala Bank shelf for the entire pelagic larval duration of 15 days (e.g., Fig 2B); (ii) southward drift, with most larvae from the northern and central release areas traveling southwards along the shore throughout the extent of the Sofala Bank and then exiting at the southernmost limit of the model near Inhambane, whereas larvae released from the southern areas stayed mostly on the shelf (e.g., Fig 2C); and (iii) offshore drift, when larvae, also mostly from the northern and central release areas, crossed the shelf edge into offshore waters (e.g., Fig 2D).

Simulated larvae transported offshore exited the Sofala Bank (referred to as "the Bank") from several locations. For instance, in Fig 2D larvae exited the Bank from its central part, whereas in Fig 2E larvae were advected offshore along two distinct pathways, one in the north and the other in the center, depending on their release area. In Fig 2F, larvae originating from the northern release area exited the Bank from its northernmost part, whereas larvae from the central area travelled southwards and exited to the south. Overall, most larvae from the southern release areas did not move much, being retained on the shelf up to the end of the simulations (Fig 2B–2F).

3.1.1. Simulated larval loss. Time series of simulated loss of larvae originating from all nine release areas are strongly correlated with loss from only five actual spawning areas (r = 0. 87; $p > 0.05$), with the same peaks and troughs (Fig 3). There were four to six pulses of elevated percentage ($> 10\%$) of simulated larvae transported away from the Sofala Bank each year throughout the time series (Fig 3), with no clear seasonality.

Simulated larvae that were transported away from the Sofala Bank, and therefore considered lost, came from seven of the nine release areas; the inner shelf of the southern areas off Beira (areas 4 and 5) had no losses (Fig 4). There were significant differences in mean simulated larval loss among the originating release areas (ANOVA: $F_{8,1017} = 27.1$; $p < 0.001$). The northernmost release area 1 yielded the highest simulated larval loss, only comparable to the adjacent offshore release area 6. In the north and central Sofala Bank, larval loss was significantly higher when originating from offshore release areas (6 and 7) than from inshore release areas (2 and 3; Fig 4). In the south-central areas (4 and 8) there was little difference in the
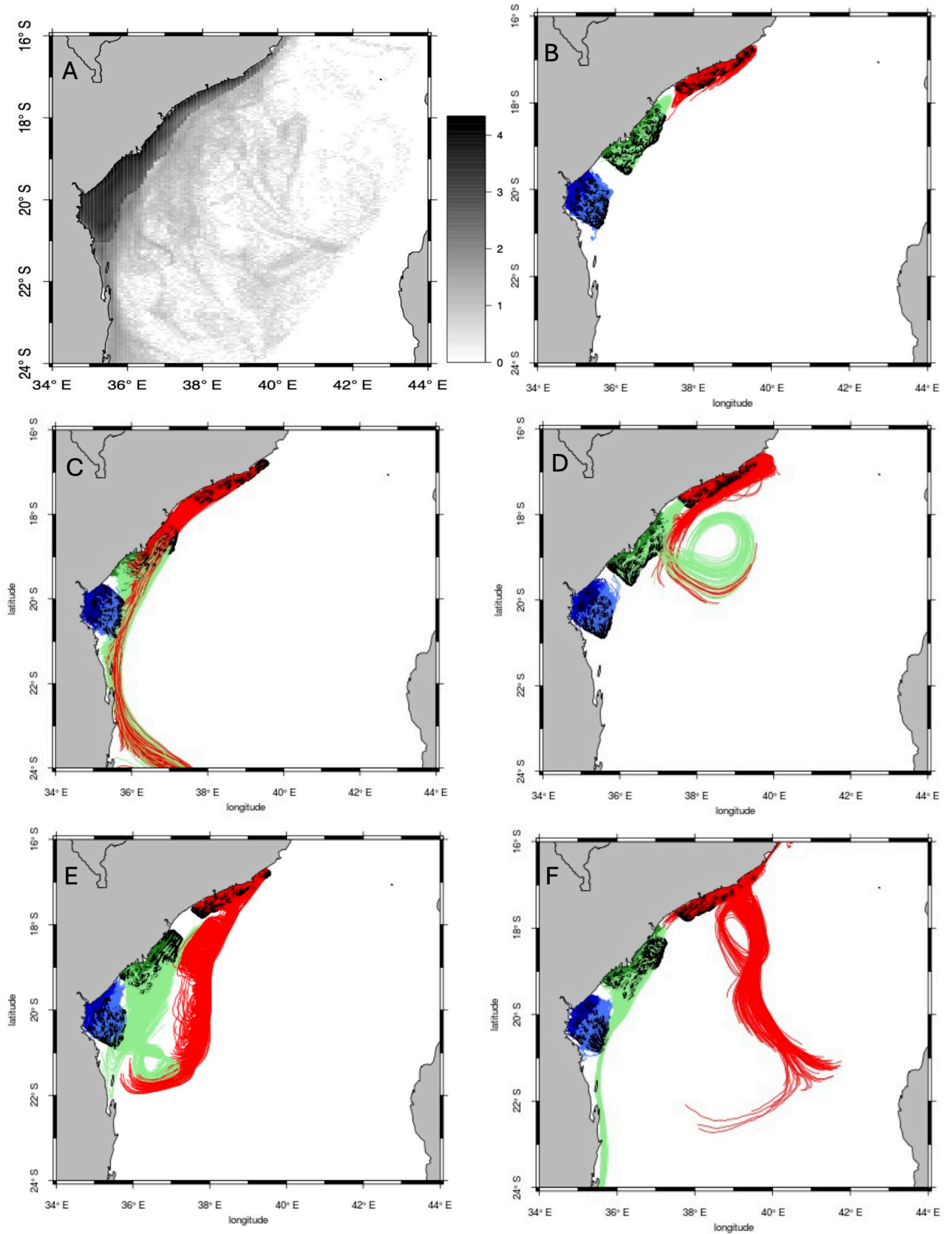
Fig 2. (A) Simulated larval density (numbers km^{-2}, logarithmic scale) at the end of the simulations from all release areas and release times (every 3 days for five model years) during the five years experiment, and (B–F) examples of trajectories followed by simulated larvae over 15 days when released (black marks) from the northern (red), central (green) and southern (blue) release areas. For green and blue, dark/light colours respectively indicate inshore/offshore release areas. Base layer used to create this map is Diva-GIS country outlines in the public domain (https://www.diva-gis.org/gdata).

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mean larval loss whether larvae were released inshore or offshore (Fig 4), but the southernmost offshore area (9) experienced slightly greater loss rates than the inshore area (5).

3.2. Mechanisms responsible for larval loss

The hydrodynamic mechanisms responsible for larval loss are illustrated by snapshots of simulated shrimp larval distributions 5, 10 and 15 days after release, superimposed on the corresponding eddy circulation. For simulations where nearly all larvae stayed on the Sofala Bank (e.g., Fig 5A), there was essentially no strong eddy activity near the Sofala Bank shelf, but there were weak eddies far away (i.e. to the south, to the north and offshore).

Conversely, for simulated larvae exiting the Bank from its southern edge or crossing the Bank offshore, strong mesoscale eddy activity was apparent close to the Bank (e.g., Fig 5B–5E). For example, larvae exited to the south when there was a large anticyclonic eddy propagating southwards with a strong current over the entire 15-day period (Fig 5B). An example of larvae transported offshore is shown in Fig 5C where, five days after release, two patches of larvae were transported offshore in the core of two cyclonic features, one relatively large patch in the north ($\sim$ 18oS) and the other, smaller patch on the central ($\sim$ 20oS) Sofala Bank. On day 10, the cyclonic eddy to the north had moved southwards towards the eddy in the central region,
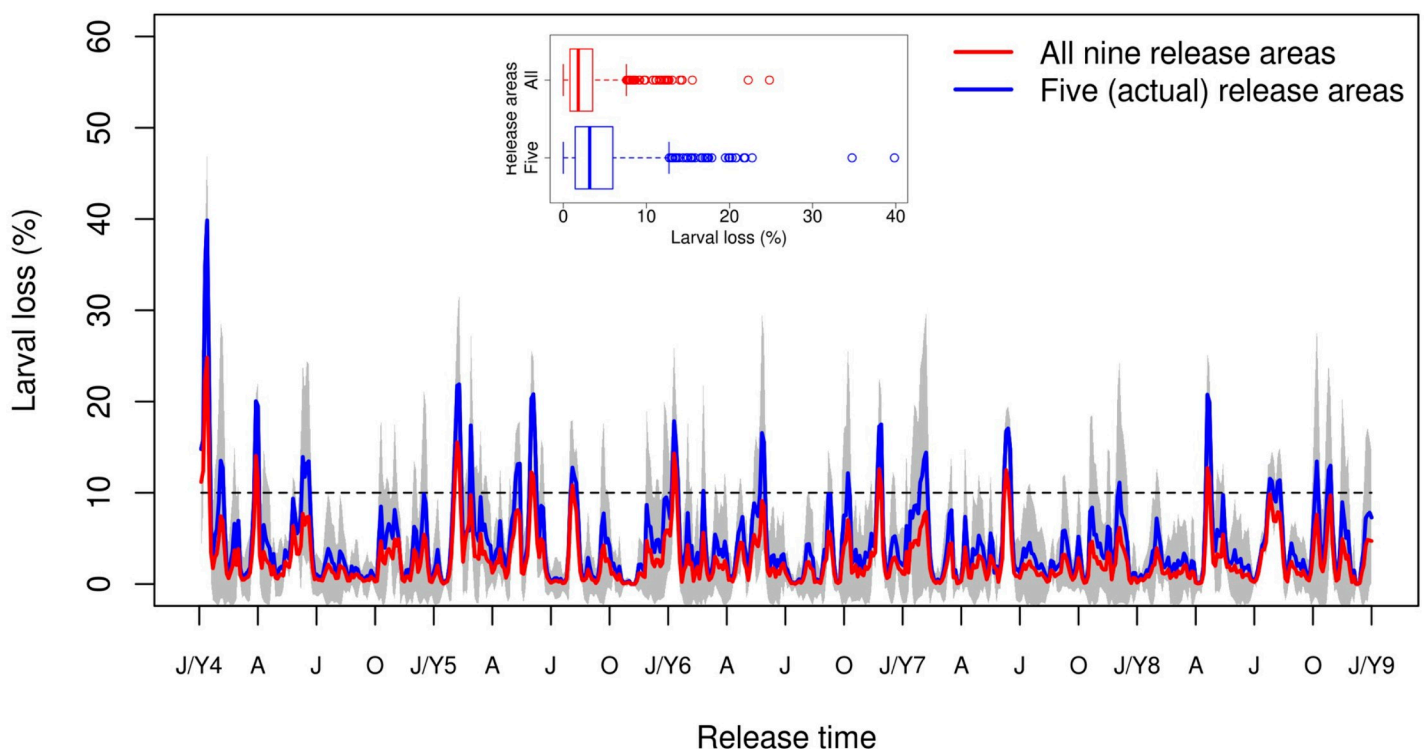
Fig 3. Time series and boxplot of mean percentage of larvae lost during the five years of simulation when larvae were released from (red) all nine release areas and (blue) the five release areas (1, 3, 5, 7 and 9 in Fig 1) corresponding to the major spawning zones for shrimp on the Sofala Bank. Grey shading represents ± s.e. for the five release areas. The horizontal dashed line indicates the 10% threshold. Letters on the X axis refer to January, April, July and, October for model years 4, 5, 6, 7, &8.

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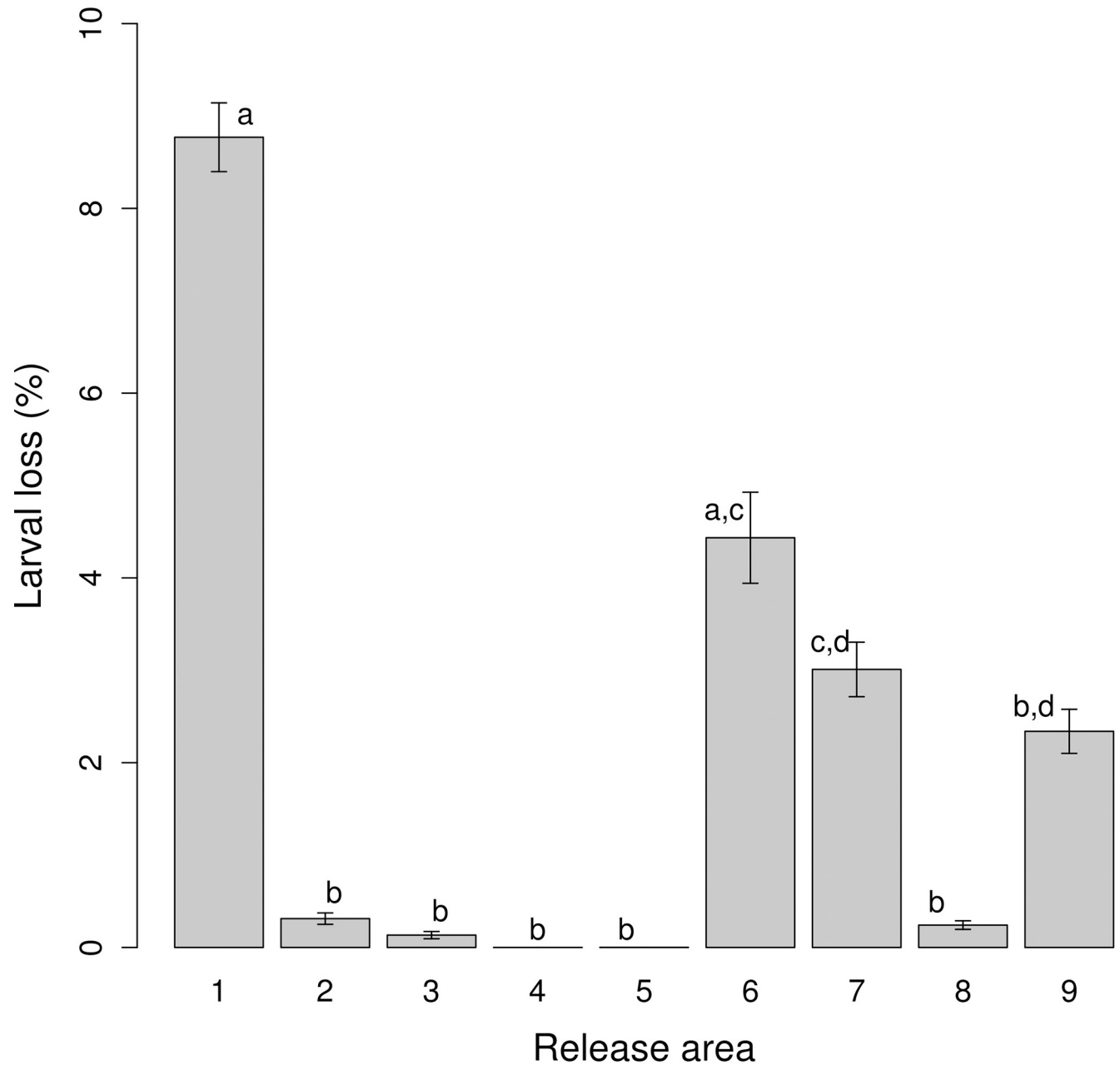
Fig 4. Mean± s.e loss rates (%) from the nine release areas on the Sofala Bank: 1 –northern, 2 –north-central inshore, 3 –central inshore, 4 –south-central inshore, 5 –southern inshore, 6 –north-central offshore, 7 –central offshore, 8 –south-central offshore, 9 –southern offshore, as depicted in Fig 1. Letters (a to d) on the top of the bars represent groups with similar loss rates identified from the Tukey post-hoc tests.

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and both had entrained larvae with them. On day 15 the two cyclonic features almost merged, and the two patches of larvae also joined (Fig 5C). In Fig 5D, initially only a few larvae from the northern release area were advected offshore by a very small and weak cyclonic eddy centred at ∼ 17oS, while a developing anticyclone/cyclone dipole feature, with anticyclone to the north and immediately to the south of the larvae offshore, was already apparent. On day 10 this dipole eddy had developed and began driving larvae offshore. On day 15, more larvae were transported offshore by the anticyclonic eddy whereas others were transported back near
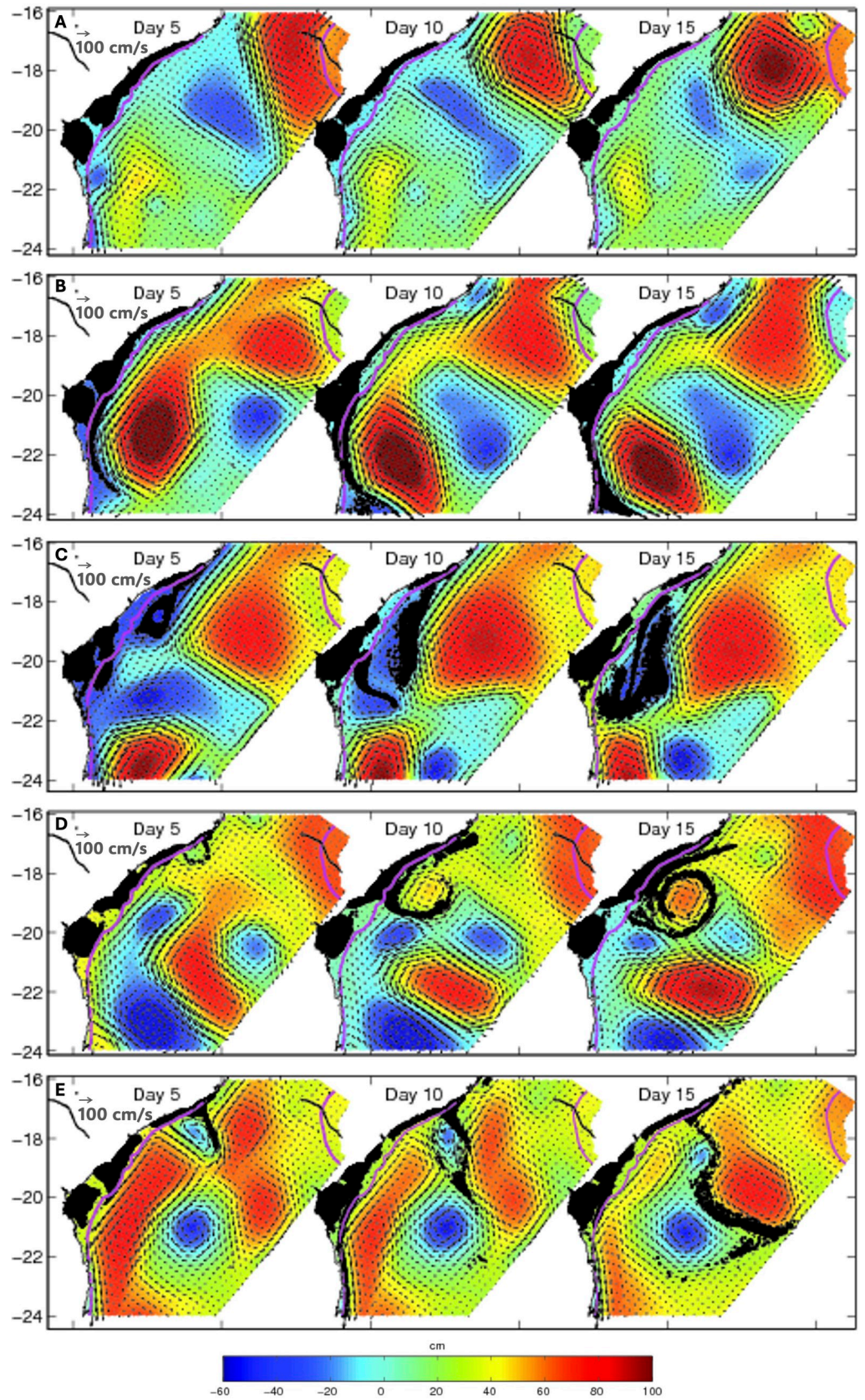
Fig 5. Snapshots of simulated shrimp larval distributions (black dots) 5, 10 and 15 days after their release, superimposed on the corresponding ROMS–derived surface current velocity (arrows, in cm s^{-1}) and sea surface height (SSH in cm, colours). The purple line indicates the 50 m isobath. Base layer used to create this map is Diva-GIS country outlines in the public domain (https://www.diva-gis.org/gdata).

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the shelf while circling. In Fig 5E, on day five some larvae from the northern area were advected offshore, also by an anticyclone/cyclone eddy dipole centred at ∼ 17oS. At day 10, a few larvae trapped in the cyclonic eddy were transported back to the continental shelf while most others were transported further offshore by a second larger cyclonic eddy. On day 15, many larvae were entrained into dipole current frontal eddies as they meandered through the Mozambique Channel, reaching the eastern limit of our model domain near Madagascar, whereas a small number of larvae entrained into the cyclonic eddy were transported further south.

To consolidate these illustrative results, we assessed the role of dominant mesoscale eddy circulation patterns identified by self-organizing maps, using cross-correlations. Firstly, four generic eddy activity patterns were identified (Fig 6): an anticyclonic/cyclonic eddy pair dipole with the anticyclone to the north (pattern 1, 33% of occurrences); a cyclonic/anticyclonic eddy dipole with the cyclone to the north (pattern 2, 28% of occurrences); a well-developed and strong large anticyclonic eddy offshore (pattern 3, 14% of occurrences); and a young or decaying small anticyclonic eddy, with weak currents, surrounded by weak cyclonic eddies to both north and south (pattern 4, 25% of occurrences). More information on the use of SOM can be found in [31]. The cross-correlation analyses between time series of simulated larval loss and each of the four identified patterns of eddy fields showed that simulated larval loss was not significantly correlated with patterns 1 and 4. There was a negative correlation with pattern 2, but it was only significant from 7 to 15 days after release (time lag), and a positive correlation with pattern 3, which was only significant from 5 to 9 days after release (Fig 7).

3.2.1 Dispersal distance. The total distances travelled by all simulated larvae show a bimodal distribution with a first, larger mode at ∼ 100 km and a second, minor peak at ∼ 650 km (Fig 8). The distribution is skewed to the right, with a long tail extending up to 1600 km (Fig 8). For linear displacement, defined as the straight-line distance from the origin to the final location of the simulated larvae, there also was a bimodal distribution, but shorter by ∼ 50 km at each mode (S1 Fig) and the skewed tail to the right also was shorter, extending only to ~900 km.

3.3. Effect of cool temperature on larval mortality

There were differences in simulated larval mortality among the six low temperature thresholds used (ANOVA: $F_{5,714}$ = 50.02; P < 0.001). Simulated larval mortality was significantly higher for simulations using the highest lethal temperature values (24 and 25oC) and different from all other values (Tukey's ANOVA; P < 0.001). For 24 and 25oC there was a strong seasonality in larval mortality, as could be expected, with global mortality during winter (mid-July to mid-September, e.g., with 24oC; Fig 9). There were also periods of increased larval mortality in late summer (February) and autumn (May to June). The result for 23oC, although not significantly different from that for 22°C (Tukey's ANOVA; P = 0.132), was markedly different from other temperatures. The massive winter larval mortality observed for 24 and 25oC appeared for a shorter period for 23oC, limited to a winter peak in September. There were no significant differences in simulated larval mortality for lethal temperature thresholds of 20, 21 and 22oC, which differed from temperatures of 23, 24 and 25oC, with the massive mortality no longer apparent. Both 20 and 21oC yielded the lowest larval mortality. In these cases, there was no
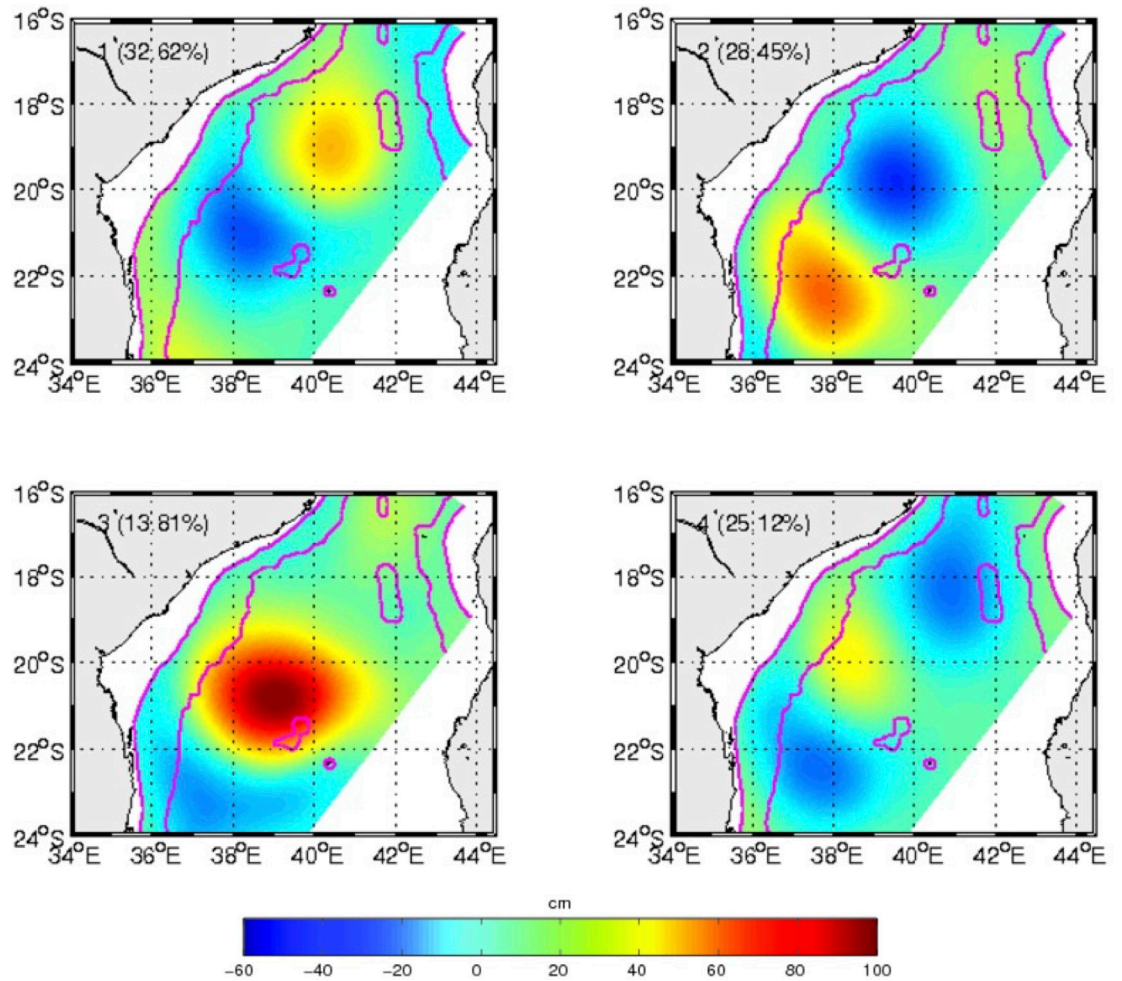
Fig 6. 2x2 self-organizing maps (SOMs) for sea surface height anomalies (SSHA in cm) derived from ROMS years 4–8. In the top left corner of each panel the numbers 1–4 indicate the SOM pattern and its frequency of occurrence is reported in %. Blue colours (negative SSHA) indicate cyclonic eddies whereas red colours (positive SSHA) are for anticyclonic eddies. The purple lines indicate the 200 and 2000 m isobaths. Base layer used to create this map is Diva-GIS country outlines in the public domain (https://www.diva-gis.org/gdata).

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clear seasonality but pulses of elevated mortality of ~40% at different short periods (e.g., with 20oC; Fig 9): late summer (February), autumn (May and June) and winter (August).

4. Discussion

Most penaeid shrimps, including the two species (*P. indicus* and *M. monoceros*) considered here, have well-known life histories. Adults spawn in marine waters [47], the eggs then hatch and larvae drift shoreward at the sea surface into estuarine brackish water where juveniles grow to sub-adults and return to the marine environment [2–4]. Here, we used a coupled bio-physical modeling approach to demonstrate that environmental events can disrupt this life cycle at spatial and temporal scales. At times, larvae can be passively transported away from coastal areas favourable to their recruitment. Many larvae potentially can exit the Sofala Bank at its southern edge or offshore, with subsequent impacts on recruitment, and hence on fisheries targeting shrimps. We also revealed the key but complex role in larval loss and mortality played by eddies traveling along the Mozambique Channel.
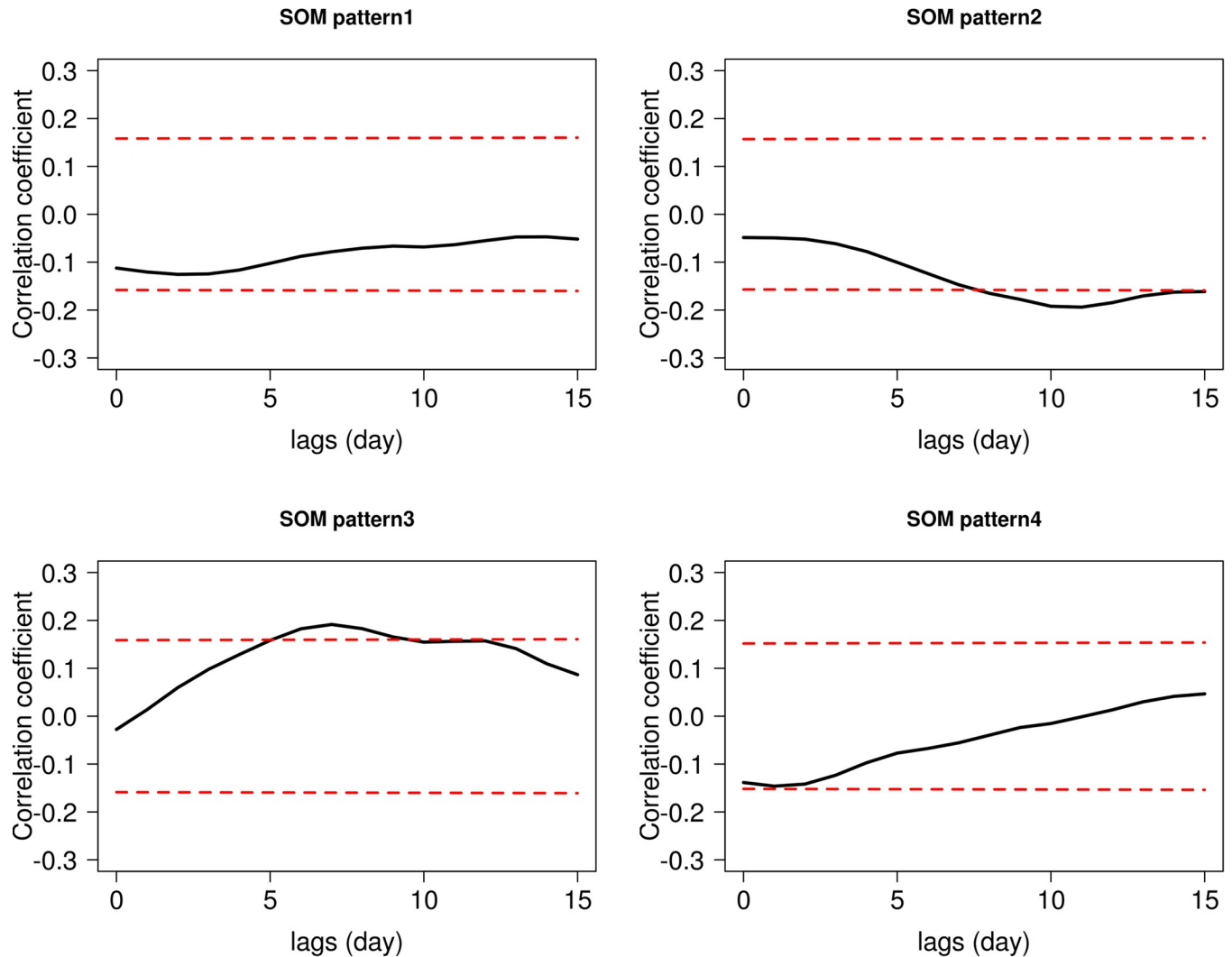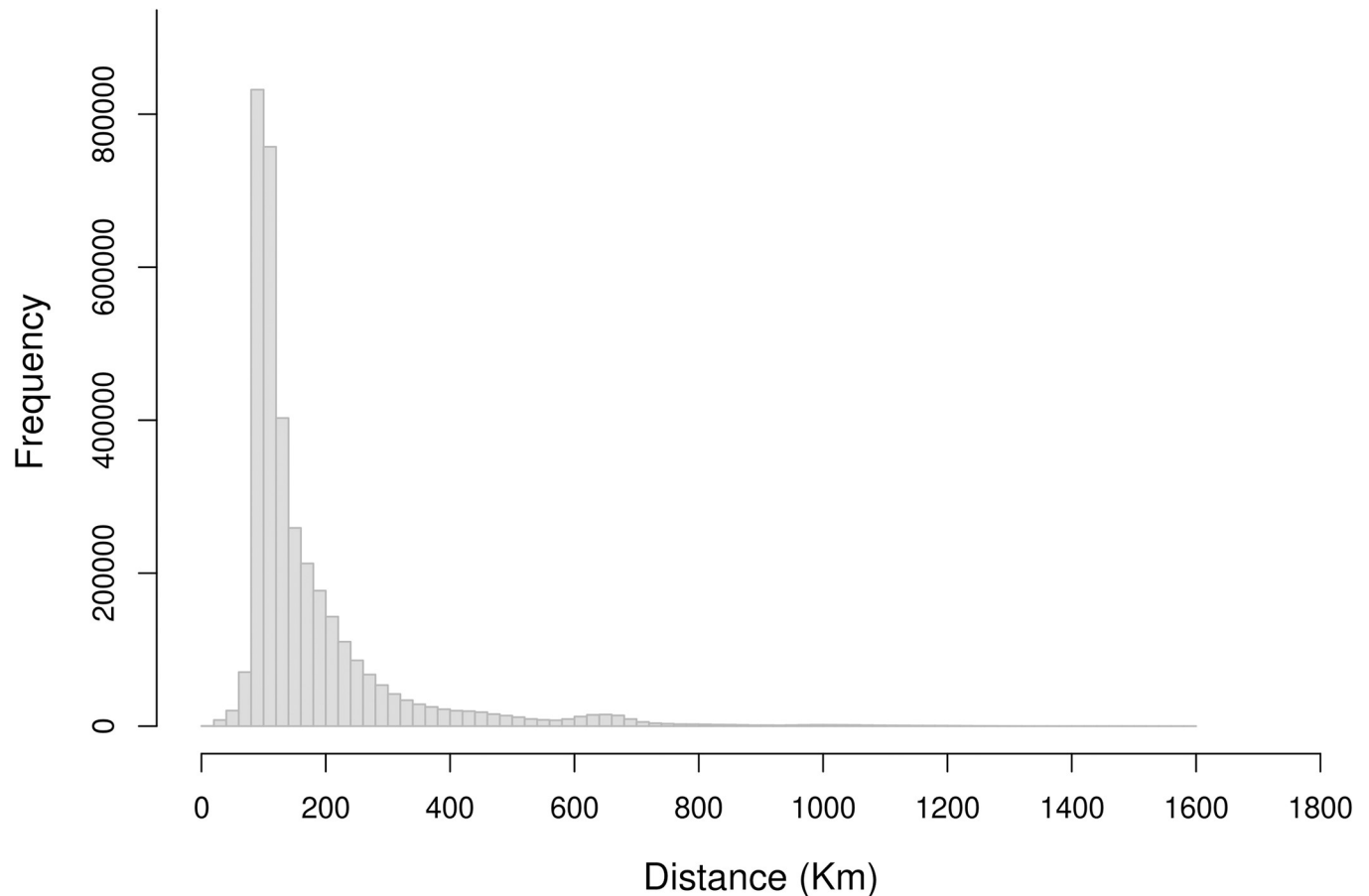
Fig 7. Cross-correlations between time series of simulated larval loss (Fig 3) and Euclidian distances to each of the 4 self-organizing map (SOM) patterns (Fig 6) identified as characterizing the dominant mesoscale eddy circulation over the study area. Dashed red lines indicate the 95% confidence level corrected for autocorrelation following [54].

4.1. Loss of shrimp larvae governed by turbulent eddy activity

We demonstrated that simulated larvae removed from the Bank had highly variable trajectories, characterized by curvilinear parts and loops, clearly revealing the influence of offshore mesoscale eddy activity. The observed differences between the total distance travelled along trajectories and the linear distance from the release to the final location confirmed that the movements were not straight-line [55], corroborating eddy-induced larval transport. The predominantly southward propagation nature of the Mozambique Channel eddy field [23, 24] explains the higher density of lost larvae found in the southern and central part of our domain than in the northern part. Other studies have reported the influence of eddies on larval dispersal for fish, including anchovy in the Kuroshio Current system [56], reef fish in the Hawaiian Ridge [35, 57], sardine in the California Current system [38, 58], and an assemblage of several fish families in the Gulf of California [37] and the East Australian Current System [36]. Eddies could either enhance fish larval local retention or promote transport to distant sites

Fig 8. Distribution of the total distance (km) travelled by simulated larvae.

[35, 38, 59]. We found significant cross-correlations between simulated larval loss and certain eddy patterns. The presence of large and strong anticyclonic eddies off the shelf significantly increased shrimp larval loss. On average, 4−6 such eddies occur per year in the Mozambique Channel [22–24], which is consistent with the number of occurrences of increased larval loss events obtained in our simulations. This suggests that these events are due to eddies. Large anticyclonic eddies interact with the shelf, generating strong southward coastal currents [31] and entraining coastal larvae.

When anticyclonic eddies were small and weak (< 20 cm; Fig 5), the tendency to push larvae off the Bank was still observed, although it lacked statistical significance. Such small features suggest developing or decaying eddies with weak associated currents [31], not strong enough to push away a significant number of coastal larvae. When superimposing the distribution of simulated larvae on the corresponding eddy and current fields, we saw that a weak eddy could only entrain a limited number of larvae, whereas this number increased with the eddy's development and strength. Therefore, not only the presence of anticyclonic eddies, but also their size, age, strength, and proximity to the shelf [31] played a role in entraining larvae away from the Bank. Coastal processes such as river plumes [60] and tides [61] influencing the inner shelf circulation are unlikely to drive offshore larval loss as much as offshore eddies [31]. The role of rivers and tides on settlement of shrimp larvae near the coast is further addressed in another study [62].
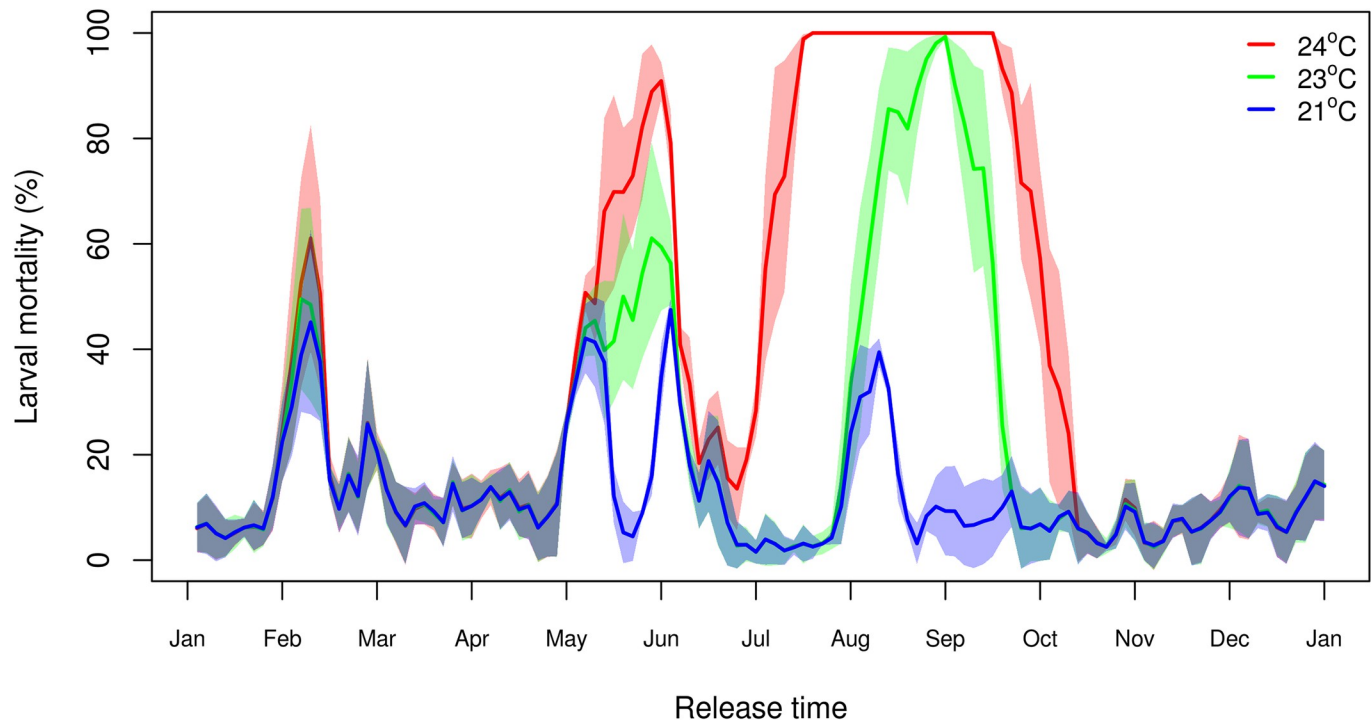
Fig 9. Mean percentage of simulated larval mortality when using different low lethal temperatures for model year 5. Shading indicates mean ± s.e.

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Eddy dipoles with the anticyclone to the south significantly prevented larvae from exiting the Bank, promoting larval shelf retention. This type of eddy pair dipole generates a strong convergent current towards the coast [31], which can act as a barrier preventing the simulated larvae from exiting the Bank. In contrast, eddy dipoles with the anticyclone to the north generated coastal current convergence, resulting in a strong offshore current between the eddies [30, 31, 63], which advected coastal upwelled water offshore [32]. Here, although not statistically significant, simulated larvae exiting the bank were positively correlated with the presence of these dipoles. We found no preferred locations or pathways for simulated larvae advected offshore, as the eddies and dipoles are not always in the same place, which could explain the lack of significant correlation in this case. Moreover, the anticyclone in pattern 1 (Fig 8) was too weak to transport significant numbers of larvae offshore.

Simulated larvae transported offshore or southwards off the Sofala Bank mostly originated from the northern and central areas. These areas are characterized by a narrow continental shelf, and thus are closely and directly exposed to the impact of eddy activity [24]. Conversely, most larvae originating from the southern area, where the continental shelf is wider and semi-enclosed, like in Beira Bay, were not advected offshore nor to the south. This happens because this region is protected and also further away from the exposure and impact of the eddy activity. These results confirm that larval retention is low in regions exposed to high-energy circulation and comparatively high in protected regions [64–66]. Moreover, for the northern and central regions, simulated larvae had significantly more chance of being transported offshore when originating from offshore than inshore spawning areas, corroborating that larval transport is greater when more exposed to the energetic offshore eddy activity. This result is consistent with a lower stock size of *M. monoceros* than *P. indicus* over the Sofala Bank (e.g., [17]) because *M. monoceros* spawns more offshore [47], and thus is more vulnerable to the eddies' influence. However, although the southern area is wider, we found no difference in larval

transport for larvae originating inshore or offshore, because both spawning areas are protected from the energetic ocean circulation. In this study, we found no significant differences in larval loss for simulated larvae originating from the actual spawning areas [47] or the non-spawning areas. It has been hypothesised that species naturally spawn in areas that offer favourable conditions for successful larval transport [67]. This suggests that spawning location is not the main factor determining coastal retention/loss, but possibly interactions between the ocean circulation at mesoscales, and favourable habitat, play important roles.

Although there was connectivity from the northern to the central region of the Sofala Bank, in the direction of the net flow, we identified that the shrimp stock in the southern region is somehow isolated off Beira Bay. Indeed, simulated larvae originating from the northern and central areas that were entrained into the eddies and transported southward along the shelf-break eddy corridor bypassed Beira, i.e. did not connect to the inner shelf stock there (Fig 2). Connectivity between populations, or stocks, of marine organisms is important for the maintenance of these structures, and their resilience to recover from natural and anthropogenic threats [65, 68], including climate change. Over the last two decades, the annual catches of the two shrimp species of the Sofala Bank have shown a dramatic decline, with recent depletion in stock size after a critical very low catch (~2000 tons) in 2011/2012 (e.g., [14, 15]). Moreover, shrimp catches are historically low off Beira compared to other regions on the Sofala Bank and, for this reason, the shrimp stock off Beira is reserved for the semi-industrial but not industrial fleets [14]. Owing to our finding that the shrimp stock off Beira is possibly largely isolated from the others of the Bank, hence relying on local supply of larvae, it can be anticipated that this stock is highly vulnerable to the effect of potential threats and its recovery would be difficult.

4.2 Possible connectivity with other shrimp stocks in the region

A recent review reported that the Mozambique Channel eddy activity could aid connectivity among distant populations in the southwestern Indian Ocean region [9]. We further highlighted eddy-induced connectivity for shallow-water shrimp species from the Sofala Bank. We showed cross-channel connectivity from the coast of Mozambique to the western coast of Madagascar, consistent with previous biophysical model studies for mangrove propagules [69], soft coral [70], reef species [71] and fish larvae [72]. While those studies investigated species with long pelagic larval duration, here we considered species with a comparatively short duration of 15 days, similar to previous estimates observing cross-channel transport of oceanographic surface drifters between the Mozambique and Madagascar shelves in 19 days [73]. We showed that coastal shrimp larvae could be transported across the Channel by strong and fast frontal currents between eddies [30], which is similar to European eel larval transport from the east to the west in the North Atlantic Ocean [74].

Simulated larvae entrained into the eddy-induced strong current to the south of the model domain reached the southernmost limit (24˚S) in 5–10 days. This limit is at Inhambane Bay where there is suitable habitat for settlement, implying that larvae from the Sofala Bank stock could connect with the shrimp stock in Inhambane Bay. Post-larval and juvenile stages of the two shrimp species occur in Inhambane Bay, but no spawning has been identified nearby to support this population [15]. Our results suggest that juvenile shrimp in Inhambane Bay could originate from the Sofala Bank, being transported southwards by the "eddy corridor" [21, 24].

Since some of our simulated larvae travelled long distances rapidly, up to 1600 km in their 15-day dispersal phase, associated with eddy edges or filaments, we hypothesise that connectivity to more distant shrimp stocks, such as at Maputo Bay ($\sim$ 800 km from the Sofala Bank) and the Natal Bight in South Africa ($\sim$ 1250 km), is possible. These sites are, however, outside

our current model domain so this long-distance connectivity should be confirmed using a larger domain. Several biophysical modelling studies reported similar long-distance southward transport of early life stages by the Mozambique Channel eddies for other species, e.g., spiny lobster [75], coral [76, 77], sea turtle [78] and tuna [79]. Further work combining a larger model domain with genetic and morphological studies is needed to be fully conclusive on connectivity among distant shrimp stocks in the region.

4.3 Shrimp larval mortality driven by low temperature and cool-eddies

Penaeid shrimps occur and develop naturally in warm tropical and subtropical waters. Being ectothermic (cold-blooded organisms that do not regulate or do not maintain constant body temperatures), cold water directly affects their cellular processes, physiological metabolism, protein structures, and mortality [41]. Thus, cool temperature is among the most important stressors affecting penaeid shrimps, as demonstrated for *Litopenaeus vannamei* in aquaculture [42, 43]. It has been proposed that shrimp larvae become intolerant or lethargic at temperatures below their optimum of 25oC [39, 40], with mortality occurring below 23oC [43]. Here, we tested the effects of simulated shrimp larvae dying when exposed to temperatures below different thresholds and found only episodic events of mortality for lethal temperatures between 20 and 23˚C. However, simulated larval mortality increased significantly for lethal temperatures of 24˚ and 25oC, particularly over an extended winter period. This finding is consistent with lower shrimp recruitment and stock observed after winters on the Sofala Bank, especially for *P. indicus* [14].

We showed that simulated larval mortality caused by cool water temperature could also occur during summer and autumn, i.e., during seasons when the water is generally warm (Fig 9). Interestingly, these mortality events coincided with the presence of cold cyclonic eddies (e.g., the eddy event demonstrated in Figs 2E and 5C, and larval loss in Fig 3 and ultimately larval mortality in Fig 9, all observed in February year 5), suggesting that there is an influence of eddies on shrimp early life stages for both dispersal and mortality. Cyclonic mesoscale eddies are highly productive [80, 81], and have associated predators foraging on planktonic organisms [82, 83], which could further increase shrimp larval mortality. This result contrasts with other studies suggesting that eddies, particularly the cold and nutrient-rich cyclones, provide favourable feeding conditions for fish larvae, enhancing development, growth, and survival [56, 58, 59]. We found that eddy-induced larval mortality from cool temperatures had a larger impact (>40%) than larvae lost from the Sofala Bank (~ 20%). This could be partly explained by larval mortality being quantified for both the Sofala Bank inner and outer shelf, whereas larval loss applied only to eddy circulation linked to the outer shelf. A semi-permanent coastal cyclonic eddy with upwelled cold water has been observed over the shelf [32, 84], and increased numbers of larvae within this eddy (Figs 2 and 5) would be exposed to low temperature mortality. These two shrimp species spawn all year round on the Sofala Bank, with periods of increased spawning activity that determine the main recruitment into the fishery, especially for *P. indicus* [14, 15]. If cold cyclonic eddies coincide with periods of maximum spawning, there could be severe implications for the fisheries, for food security of coastal communities, and for sustained economy activities.

The five-year model simulation consistently resulted in eddy-induced larval loss every year (Figs 2–7), and there have been previous observations of intermittent cool-water events, especially in summer [32, 84]. Thus, although our low temperature simulations were limited to one year (Fig 9), they showed a strong larval mortality pattern for all six lethal temperature thresholds in winter and during the events of cold-core cyclonic eddies; these results should be applicable to other years. Further studies combining in situ experiments and physiological models

along with larval dispersal models, e.g., Ichthyop-DEB (Dynamic Energy Budget [85]), are needed to test the results of the present study showing effects of simulated low temperatures on shrimp larvae.

5. Conclusions

Turbulent and highly energetic mesoscale eddy activity can transport coastal shrimp larvae downstream or offshore, removing them from favourable estuarine nursery grounds and increasing the risk of mortality. Although eddy transport can promote connectivity with other distant populations, it can have negative effects locally for offspring entering a fishery, resulting in poor recruitment. Mesoscale eddies not only influenced larval advection but also impacted larval survival through temperature effects of cold eddies. Under current business-as-usual scenarios, the impacts of climate change are projected to increasingly enhance eddy activity. This will exacerbate eddy-induced larval loss and mortality, potentially reducing fish catches, negatively affecting food security and well-being for more than 2/3 of the country's population, and impacting the blue economy income. This can be even more dramatic and recovery more difficult when the eddies coincide with increased spawning periods, which are important for maintaining sustainable stocks. Policy makers and fisheries managers should consider eddy-induced larval transport away from favourable coastal ecosystems and temperature mortality in the light of increasing climate change impacts.

Supporting information

S1 Fig. Distributions of the linear distances (km) travelled by simulated larvae from their origins to their final locations.
(TIF)

Author Contributions

Conceptualization: Bernardino S. Malauene, Christophe Lett, Francis Marsac, Pierrick Penven, Silvia Abdula, Coleen L. Moloney, Michael J. Roberts.

Data curation: Silvia Abdula.

Formal analysis: Bernardino S. Malauene, Christophe Lett, Pierrick Penven, Coleen L. Moloney.

Funding acquisition: Francis Marsac, Michael J. Roberts.

Investigation: Bernardino S. Malauene, Christophe Lett, Francis Marsac, Pierrick Penven, Silvia Abdula, Coleen L. Moloney, Michael J. Roberts.

Methodology: Bernardino S. Malauene, Christophe Lett, Coleen L. Moloney.

Project administration: Bernardino S. Malauene.

Software: Christophe Lett, Pierrick Penven.

Supervision: Christophe Lett, Francis Marsac, Pierrick Penven, Coleen L. Moloney, Michael J. Roberts.

Visualization: Bernardino S. Malauene, Coleen L. Moloney.

Writing – original draft: Bernardino S. Malauene.

Writing – review & editing: Bernardino S. Malauene, Christophe Lett, Francis Marsac, Pierrick Penven, Silvia Abdula, Coleen L. Moloney, Michael J. Roberts.

References

1. Anger K., The biology of decapod crustacean larvae. Vol. 14. 2001: AA Balkema Publishers Lisse.

2. Jones A.C., Dimitriou D.E., Ewald J.J., and Tweedy J.H., Distribution of Early Developmental Stages of Pink Shrimp,Penaeus Duorarum, in Florida Waters. Bulletin of Marine Science, 1970. 20(3): p. 634–661.

3. Rothlisberg P.C., Church J.A., and Forbes A.M.G., Modelling the advection of vertically migrating shrimp larvae. Journal of Marine Research, 1983. 41: p. 511–538.

4. Dall W., Hill B.J., Rothlisberg P.C., and Staples D.J., The Biology of the Penaeidae (Advances in Marine Biology, Vol. 27). 1990: Elsevier Academic Press, London. 489.

5. Laxminarayana A., Backyard Hatchery Technology For The White Prawn Penaeus Indicus. 1995.

6. Kumlu M., Eroldogan O.T., Aktas M., and Sag̃lamtimur B., Larval growth, survival and development of Metapenaeus monoceros (Fabricius) cultured in different salinities. Aquaculture Research, 2001. 32 (2): p. 81–86.

7. Pineda J., Hare J.A., and Sponaugle S., Recent Progress in Understanding Larval Dispersal: New Directions and Digressions. Integrative and Comparative Biology. Oceanography, 2007. 20(3): p. 22–39.

8. Dubois M., Rossi V., Ser-Giacomi E., Arnaud-Haond S., López C., and Hernández-García E., Linking basin-scale connectivity, oceanography and population dynamics for the conservation and management of marine ecosystems. Global Ecology and Biogeography, 2016. 25(5): p. 503–515.

9. Lett C., Malauene B.S., Hoareau T.B., Kaplan D.M., and Porri F., Corridors and barriers to marine connectivity around southern Africa. Marine Ecology Progress Series, 2024. 731: p. 105–127.

10. Hidalgo M., Rossi V., Monroy P., Ser-Giacomi E., Hernández-García E., Guijarro B., et al., Accounting for ocean connectivity and hydroclimate in fish recruitment fluctuations within transboundary metapopulations. Ecological Applications, 2019. 29(5): p. e01913. https://doi.org/10.1002/eap.1913 PMID: 31144784

11. Quinzán M., Castro J., Massutí E., Rueda L., and Hidalgo M., Disentangling the influence of fishing, demography, and environment on population dynamics of Iberian Peninsula waters fish stocks. ICES Journal of Marine Science, 2020. 77(1): p. 1–11.

12. Jackson C.,J., P.C. Rothlisberg, and Pendrey R.C., Role of larval distribution and abundance in overall life-history dynamics: a study of the prawn Penaeus semisulcatus in Albatross Bay, Gulf of Carpentaria, Australia. Marine Ecology Progress Series, 2001. 213: p. 241–252.

13. Ivanov B.G. and Hassan A.M., Penaeid Shrimps (Decapoda, Penaeidae) Collected off East Africa by the Fishing Vessel "Van Gogh", 1. Solenocera ramadani sp. nov., and Commercial Species of the Genera Penaeus and Metapenaeus. Crustaceana, 1976. 30(3): p. 241–251.

14. Palha de Sousa, L., S. Abdula, B. Palha de Sousa, and J. Penn, Assessment of the shallow water shrimp fishery of Sofala Bank, Mozambique 2014 (O camarao do Banco de Sofala 2014). 2015, Maputo, Mozambique: Investigational Report No33. Instituto Nacional de Investigação Pesqueira (In Portuguese). pp. 66.

15. Abdula, S., N. Dias, A. Inacio, and E. Morais, A pescaria de Camarão no Banco de Sofala 2018. 2019, Maputo, Mozambique Instituto Nacional de Investigação Pesqueira (In Portuguese). pp. 84.

16. Mafuca, J.M., R.J. Mutombene, O. Filipe, S. Abdula, B.S. Malauene, A.J.R. Quick, et al., Planning for climate change resilience—collation, update and review of Mozambique's marine fisheries data and management. (Forthcoming in this issue—Under publication).

17. Palha de Sousa L., Brito A., Abdula S., Penn J., and Howell D., O Camarao do Banco de Sofala 2008. 2008, Maputo: Unpublished report Instituto Nacional de Investigação Pesqueira. pp. 65.

18. Lipangue A., Malauene B.S., and Roberts M.J., Assessment of coastal communities' vulnerability to climate change induced marine food (in)security in Mozambique. (Forthcoming in this issue—Under publication). PLOS Climate.

19. Diop H., Keithly W.R. Jr, Kazmierczak R.F. Jr, and Shaw R.F., Predicting the abundance of white shrimp (Litopenaeus setiferus) from environmental parameters and previous life stages. Fisheries Research, 2007. 86(1): p. 31–41.

20. Ehrhardt N.M. and Legault C.M., Pink shrimp,Farfantepenaeus duorarum,recruitment variability as an indicator of Florida Bay dynamics. Estuaries, 1999. 22(2): p. 471–483.

21. Sætre R. and da Silva A.J., The circulation of the Mozambique Channel. Deep-Sea Research I, 1984. 31: p. 485–508.

22. de Ruijter W.P.M., Ridderinkhof H., Lutjeharms J.R.E., Schouten M.W., and Veth C., Observations of the flow in the Mozambique Channel. Geophysical Research Letters, 2002. 29(10): p. 1502–1504.

23. Schouten M.W., de Ruijter W.P.M., van Leeuwen P.J., and Ridderinkhof H., Eddies and variability in the Mozambique Channel. Deep-Sea Research II, 2003. 50: p. 1987–2003.

24. Halo I., Backeberg B., Penven P., Ansorge I., Reason C., and Ullgren J.E., Eddy properties in the Mozambique Channel: A comparison between observations and two numerical ocean circulation models. Deep Sea Research Part II: Topical Studies in Oceanography, 2014. 100(0): p. 38–53.

25. Penven P., Halo I., Pous S., and Marie L., Cyclogeostrophic balance in the Mozambique Channel. Journal of Geophysical Research: Oceans, 2014. 119(2): p. 1054–1067.

26. Backeberg B.C., Penven P., and Rouault M., Impact of intensified Indian Ocean winds on mesoscale variability in the Agulhas system. Nature Climate Change, 2012. 2(8): p. 608–612.

27. Vianello, P., B.S. Malauene, and M.J. Roberts, Long-term change in sea surface temperature, ocean productivity and eddies patterns on the Mozambique shelf and channel. (Forthcoming in this issue— Under publication). PLOS Climate.

28. Beech N., Rackow T., Semmler T., Danilov S., Wang Q., and Jung T., Long-term evolution of ocean eddy activity in a warming world. Nature Climate Change, 2022. 12(10): p. 910–917.

29. Li J., Roughan M., and Kerry C., Drivers of ocean warming in the western boundary currents of the Southern Hemisphere. Nature Climate Change, 2022. 12(10): p. 901–909.

30. Roberts M.J., Ternon J.-F., and Morris T., Interaction of dipole eddies with the western continental slope of the Mozambique Channel. Deep Sea Research Part II: Topical Studies in Oceanography, 2014. 100(0): p. 54–67.

31. Malauene B.S., Moloney C.L., Lett C., Roberts M.J., Marsac F., and Penven P., Impact of offshore eddies on shelf circulation and river plumes of the Sofala Bank, Mozambique Channel. Journal of Marine Systems, 2018. 185: p. 1–12.

32. Malauene B.S., Shillington F.A., Roberts M.J., and Moloney C.L., Cool, elevated chlorophyll-a waters off northern Mozambique. Deep Sea Research Part II: Topical Studies in Oceanography, 2014. 100(0): p. 68–78.

33. Jose Y.S., Aumont O., Machu E., Penven P., Moloney C.L., and Maury O., Influence of mesoscale eddies on biological production in the Mozambique Channel: Several contrasted examples from a coupled ocean-biogeochemistry model. Deep Sea Research Part II: Topical Studies in Oceanography, 2014. 100(0): p. 79–93.

34. Adams D.K. and Flierl G.R., Modeled interactions of mesoscale eddies with the East Pacific Rise: Implications for larval dispersal. Deep Sea Research Part I: Oceanographic Research Papers, 2010. 57 (10): p. 1163–1176.

35. Vaz A.C., Richards K.J., Jia Y., and Paris C.B., Mesoscale flow variability and its impact on connectivity for the island of Hawai'i. Geophysical Research Letters, 2013. 40(2): p. 332–337.

36. Garcia V., Schilling H.T., Cruz D.O., Hawes S.M., Everett J.D., Roughan M., et al., Entrainment and development of larval fish assemblages in two contrasting cold core eddies of the East Australian Current system. Marine Ecology Progress Series, 2022. 685: p. 1–18.

37. Sánchez-Velasco L., Lavín M.F., Jiménez-Rosenberg S.P.A., Godínez V.M., Santamaría-del-Angel E., and Hernández-Becerril D.U., Three-dimensional distribution of fish larvae in a cyclonic eddy in the Gulf of California during the summer. Deep Sea Research Part I: Oceanographic Research Papers, 2013. 75: p. 39–51.

38. Nieto K., McClatchie S., Weber E.D., and Lennert-Cody C.E., Effect of mesoscale eddies and streamers on sardine spawning habitat and recruitment success off Southern and central California. Journal of Geophysical Research: Oceans, 2014. 119(9): p. 6330–6339.

39. Wyban J., Walsh W.A., and Godin D.M., Temperature effects on growth, feeding rate and feed conversion of the Pacific white shrimp (Penaeus vannamei). Aquaculture, 1995. 138(1–4): p. 267–279.

40. López-Martínez J., Rábago-Quiroz C., Nevárez-Martínez M.O., García-Juárez A.R., Rivera-Parra G., and Chávez-Villalba J., Growth, reproduction, and size at first maturity of blue shrimp, Litopenaeus stylirostris (Stimpson, 1874) along the east coast of the Gulf of California, Mexico. Fisheries Research, 2005. 71(1): p. 93–102.

41. Yang J., Zhang Z., Lin G., Li M., Zhang Y., and Mai K., Organic copper promoted copper accumulation and transport, enhanced low temperature tolerance and physiological health of white shrimp (Litopenaeus vannamei Boone, 1931). Fish & Shellfish Immunology, 2023. 132: p. 108459. https://doi.org/10.1016/j.fsi.2022.108459 PMID: 36455776

42. Lu H., Chen W., Liu F., Huang M., Peng K., Zhao J., et al., A genetic linkage map of the Pacific white shrimp (Litopenaeus vannamei): QTL mapping for low-temperature tolerance and growth-related traits and identification of the candidate genes. Aquaculture, 2023. 562: p. 738834.

43. Wang Z., Qu Y., Zhuo X., Li J., Zou J., and Fan L., Investigating the physiological responses of Pacific white shrimp Litopenaeus vannamei to acute cold-stress. PeerJ, 2019. 7: p. e7381. https://doi.org/10.7717/peerj.7381 PMID: 31372323

44. Lett C., Verley P., Mullon C., Parada C., Brochier T., Penven P., et al., A Langrangian tool for modelling ichthyoplankton dynamics. Enviromental Modelling & Software, 2008. 23: p. 1210–1214.

45. Swearer S.E., Treml E.A., and Shima J.S., A review of biophysical models of marine larval dispersal. Oceanography and Marine Biology, 2019.

46. Shchepetkin A.F. and McWilliams J.C., The regional ocean modeling system (ROMS): A split-explicit, free-surface, topography-following-coordinate oceanic model. Ocean Modell., 2005. 9: p. 347–404.

47. Malauene B.S., Lett C., Marsac F., Roberts M.J., Brito A., Abdula S., et al., Spawning areas of two shallow-water penaeid shrimps (Penaeus indicus and Metapenaeus monoceros) on the Sofala Bank, Mozambique. Estuarine, Coastal and Shelf Science, 2021. 253: p. 107268.

48. Malauene B.S., Lett C., Marsac F., Penven P., C.l. Moloney, and Roberts M.j, Processed outputs and R codes from a dispersal model to investigate the influence of offshore eddies on larval transport loss and cool-water mortality of two commercial shrimp species on the Sofala Bank, Mozambique Channel. 2024, SEANOE.

49. Peliz A., Marchesiello P., Dubert J., Marta-Almeida M., Roy C., and Queiroga H., A study of crab larvae dispersal on the Western Iberian Shelf: Physical processes. Journal of Marine Systems, 2007. 68: p. 215–236.

50. Liao I.C. and Chien Y.-H., The Pacific White Shrimp, Litopenaeus vannamei, in Asia: The World's Most Widely Cultured Alien Crustacean, in In the Wrong Place—Alien Marine Crustaceans: Distribution, Biology and Impacts, Galil B.S., Clark P.F., and Carlton J.T., Editors. 2011, Springer Netherlands: Dordrecht. p. 489–519.

51. Hijmans R.J., geosphere: Spherical Trigonometry. 2014.

52. Kohonen T., Self-Organizing Maps. 3 ed. 2001, Berlin: Springer-Verlag. 501 pp.

53. Wehrens R. and Buydens L.M.C., Self- and Super-organizing Maps in R: The kohonen Package. Journal of Statistical Software, 2007. 21(5): p. 1–19.

54. Cuif M., Kaplan D.M., Lefevre J., Faure V.M., Caillaud M., Verley P., et al., Wind-induced variability in larval retention in a coral reef system: A biophysical modelling study in the South-West Lagoon of New Caledonia. Progress in Oceanography, 2014. 122: p. 105–115.

55. Roughan M., Cetina-Heredia P., Ribbat N., and Suthers I.M., Shelf transport pathways adjacent to the East Australian current reveal sources of productivity for coastal reefs. Frontiers in Marine Science, 2022. 8: p. 789687.

56. Nakata H., Kimura S., Okazaki Y., and Kasai A., Implications of meso-scale eddies caused by frontal disturbances of the Kuroshio Current for anchovy recruitment. ICES Journal of Marine Science, 2000. 57: p. 143–152.

57. Lobel P.S. and Robinson A.R., Transport and entrapment of fish larvae by ocean mesoscale eddies and currents in Hawaiian waters. Deep Sea Research Part A. Oceanographic Research Papers, 1986. 33(4): p. 483–500.

58. Logerwell E.A. and Smith P.E., Mesoscale eddies and survival of late stage Pacific sardine (Sardinops sagax) larvae. Fisheries Oceanography, 2001. 10(1): p. 13–25.

59. Bakun A., Fronts and eddies as key structures in the habitat of marine fish larvae: opportunity, adaptive response and competitive advantage. Scientia marina, 2006. 70(S2): p. 105–122.

60. Nehama F.P.J. and Reason C.J.C., Modelling the Zambezi River plume. African Journal of Marine Science, 2015. 37(4): p. 593–604.

61. Chevane C.M., Penven P., Nehama F.P.J., and Reason C.J.C., Modelling the tides and their impacts on the vertical stratification over the Sofala Bank, Mozambique. African Journal of Marine Science, 2016. 38(4): p. 465–479.

62. Malauene, B.S.<, C.L. Moloney, S. Abdula, A. Brito, M.J. Roberts, F. Marsac, et al., Coastal settlement of two commercial shrimp larvae (Penaeus indicus and Metapenaeus monoceros) on the Sofala Bank, Mozambique (Forthcoming in this issue—Under publication). PLOS Climate.

63. Ternon J.F., Roberts M.J., Morris T., Hancke L., and Backeberg B., In situ measured current structures of the eddy field in the Mozambique Channel. Deep Sea Research Part II: Topical Studies in Oceanography, 2014. 100(0): p. 10–26.

64. Shanks A.L. and Brink L., Upwelling, downwelling, and cross-shelf transport of bivalve larvae: test of a hypothesis. Marine Ecology Progress Series, 2005. 302: p. 1–12.

65. Robins P.E., Neill S.P., Gimenez L., Jenkins S.R., and Malham S.K., Physical and biological controls on larval dispersal and connectivity in a highly energetic shelf sea. Limnology and Oceanography, 2013. 58(2): p. 505–524.

66. Porri F., Jackson J.M., Meden C.E.O.V.d., Weidberg N., and McQuaid C.D., The effect of mesoscale oceanographic features on the distribution of mussel larvae along the south coast of South Africa. Journal of Marine Systems, 2014. 132(0): p. 162–173.

67. Putman N.F., Shay T.J., and Lohmann K.J., Is the Geographic Distribution of Nesting in the Kemp's Ridley Turtle Shaped by the Migratory Needs of Offspring? Integrative and Comparative Biology, 2010. 50 (3): p. 305–314. https://doi.org/10.1093/icb/icq041 PMID: 21558205

68. Jones G.P., Almany G.R., Russ G.R., Sale P.F., Steneck R.S., Oppen M.J.H.v., et al., Larval retention and connectivity among populations of corals and reef fishes: history, advances and challenges. Coral Reefs, 2009. 28: p. 307–325.

69. Van der Stocken T. and Menemenlis D., Modelling mangrove propagule dispersal trajectories using high-resolution estimates of ocean surface winds and currents. Biotropica, 2017. 49(4): p. 472–481.

70. Schleyer M.H., Downey-Breedt N.J., and Benayahu Y., Species composition of Alcyonacea (Octocorallia) on coral reefs at Europa Island and associated connectivity across the Mozambique Channel. Marine Biodiversity, 2019. 49(5): p. 2485–2491.

71. Crochelet E., Roberts J., Lagabrielle E., Obura D., Petit M., and Chabanet P., A model-based assessment of reef larvae dispersal in the Western Indian Ocean reveals regional connectivity patterns—Potential implications for conservation policies. Regional Studies in Marine Science, 2016. 7: p. 159–167.

72. Reid K., Crochelet E., Bloomer P., and Hoareau T.B., Investigating the origin of vagrant dusky groupers, Epinephelus marginatus (Lowe, 1834), in coastal waters of Réunion Island. Molecular Phylogenetics and Evolution, 2016. 103: p. 98–103.

73. Hancke L., Roberts M.J., and Ternon J.F., Surface drifter trajectories highlight flow pathways in the Mozambique Channel. Deep Sea Research Part II: Topical Studies in Oceanography, 2014. 100(0): p. 27–37.

74. Blanke B., Bonhommeau S., Grima N., and Drillet Y., Sensitivity of advective transfer times across the North Atlantic Ocean to the temporal and spatial resolution of model velocity data: Implication for European eel larval transport. Dynamics of Atmospheres and Oceans, 2012. 55–56(0): p. 22–44.

75. Singh S.P., Groeneveld J.C., Hart-Davis M.G., Backeberg B.C., and Willows-Munro S., 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. Ecology and Evolution, 2018. 8(23): p. 12221–12237. https://doi.org/10.1002/ece3.4684 PMID: 30598813

76. Gamoyo M., Obura D., and Reason C.J.C., Estimating Connectivity Through Larval Dispersal in the Western Indian Ocean. Journal of Geophysical Research: Biogeosciences, 2019. 124(8): p. 2446–2459.

77. Vogt-Vincent N.S., Mitarai S., and Johnson H.L., High-frequency variability dominates potential connectivity between remote coral reefs. Limnology and Oceanography, 2023. 68(12): p. 2733–2748.

78. Jensen M.P., Dalleau M., Gaspar P., Lalire M., Jean C., Ciccione S., et al. Seascape Genetics and the Spatial Ecology of Juvenile Green Turtles. Genes, 2020. 11, DOI: https://doi.org/10.3390/genes11030278 PMID: 32150879

79. Nikolic N., Montes I., Lalire M., Puech A., Bodin N., Arnaud-Haond S., et al., Connectivity and population structure of albacore tuna across southeast Atlantic and southwest Indian Oceans inferred from multidisciplinary methodology. Scientific Reports, 2020. 10(1): p. 15657. https://doi.org/10.1038/s41598-020-72369-w PMID: 32973260

80. Tew-Kai E. and Marsac F., Patterns of variability of sea surface chlorophyll in Mozambique Channel: A quantitative approach. Journal of Marine Systems, 2009(77): p. 77–88.

81. Huggett J.A., Mesoscale distribution and community composition of zooplankton in the Mozambique Channel. Deep Sea Research Part II: Topical Studies in Oceanography, 2014. 100(0): p. 119–135.

82. Weimerskirch H., Le Corre M., Jaquemet S., Potier M., and Marsac F., Foraging strategy of a top predator in tropical water: great frigatebirds in the Mozambique Channel. Marine Ecology Progress Series, 2004. 275: p. 297–308.

83. Potier M., Bach P., Ménard F., and Marsac F., Influence of mesoscale features on micronekton and large pelagic fish communities in the Mozambique Channel. Deep Sea Research Part II: Topical Studies in Oceanography, 2014. 100(0): p. 184–199.

84. Nehring D., Hagen E., da Silva J.A., Schemainda R., Wolf G., Michelchen N., et al., Results of oceanological stuies in the Mozambique Channel in February-March 1980. Beitrage Zur Meereskunded, 1987. 56: p. 51–63.

85. Flores-Valiente J., Lett C., Colas F., Pecquerie L., Aguirre-Velarde A., Rioual F., et al., Influence of combined temperature and food availability on Peruvian anchovy (Engraulis ringens) early life stages in the northern Humboldt Current system: A modelling approach. Progress in Oceanography, 2023. 215: p. 103034.