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The 'suitcase hypothesis': Can entrainment of meroplankton by eddies provide a pathway for gene flow between Madagascar and KwaZulu-Natal, South Africa?

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Similarities in the marine fauna found off the coasts of southern Madagascar and KwaZulu-Natal Province (KZN), South Africa, led to the development of the 'suitcase project,' with the aim of establishing whether eddies that form off southern Madagascar may package and transport biological material across the Mozambique Channel, facilitating connectivity and gene flow. Meroplankton (larval stages of fishes and benthic invertebrates) were collected on the Madagascan shelf and along a transect through a cyclonic eddy in the Mozambique Channel. The samples were analysed using microscopy and DNA barcoding, seeking to identify species known to be common to both the southeast coast of Madagascar and the east coast of South Africa and thereby to reveal potential indicators of connectivity between these regions. The greatest zooplankton biovolume in the upper 200 m occurred on the shelf, followed by in the western part of the eddy and in the region outside the eddy to the west, and was lowest in the region outside the eddy to the east. The meroplankton were dominated by taxa of coastal origin and these were also most abundant on the shelf and in the western part of the eddy, with the lowest abundances in the region outside the eddy to the east. The findings show greater zooplankton biovolumes and larval abundances and the presence of reef-associated larval assemblages on the Madagascan shelf and along the transect through the cyclonic eddy, providing support for the suitcase hypothesis that planktonic organisms are entrained within eddies as they propagate south-westwards of the Madagascan shelf.

Keywords: biovolume, connectivity, DNA barcoding, fish larvae, invertebrate larvae, larval dispersal, mesoscale eddies, Mozambique Channel, phylogenetic analysis

Supplementary material: Supplementary Information available online at http://dx.doi.org/10.2989/1814232X.2017.1399292 tabulates the fish CO1 sequences obtained in this study combined with sequences downloaded from BOLD and GenBank to produce a neighbour-joining tree (Appendix S1), and the sequence divergences calculated using the Kimura 2-parameter model (Appendices S2 and S3).

Introduction

Mesoscale eddies are found in all oceans (Rhines 2001) but are particularly prominent at the ends of western boundary currents (WBC). The Agulhas Current (AC) is the largest WBC in the global ocean (Bryden et al. 2005), and it is the only WBC with frequent mesoscale activity in its source region, generated by two zones of high mesoscale variability: the Mozambique Channel (MC) (Schouten et al. 2002) and the South East Madagascar Current (SEMC) (Siedler et al. 2009). Mesoscale eddies are features of ocean circulation, with horizontal spatial scales of 10–1 000 km and timescales of 1–3 years, which may entrain planktonic organisms, influencing their distribution and acting as vectors of transport (Rodríguez et al. 1999; Mackas and Galbraith 2002; Batten and Crawford 2005; Holliday et al. 2011). Through the clockwise rotation of cyclonic eddies in the southern hemisphere, a vertical upwelling flow is caused in their interiors, which in turn causes a divergence (outward flow) of surface waters; hence, subsurface nitrate-rich water is pushed upwards into the euphotic zone (Bakun 2006), resulting in increased primary production in the cores of cyclonic eddies (Yentsch and Phinney 1985; Falkowski et al. 1991; McGillicuddy and Robinson 1997; McGillicuddy et al. 1998). In anticyclonic eddies, the opposite occurs: anticlockwise rotation and convergence cause surface waters to be pushed downwards (downwelling) (Bakun 2006). Eddies may also entrain productive water of coastal origin and, as a consequence, they may function as nursery grounds for organisms like fish larvae (Rodríguez et al. 1999; Govoni et al. 2010).

A number of recent studies conducted on mesoscale eddies in the MC (e.g. Barlow et al. 2014; Halo et al. 2014a; Hancke

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et al. 2014; Huggett 2014; Lamont et al. 2014; Lebourges-Dhaussy et al. 2014; Marsac et al. 2014; Ménard et al. 2014; Potier et al. 2014; Ternon et al. 2014a) demonstrated the origins and importance of eddies in the largely oligotrophic system of the MC, where they provide mechanisms by which the physical energy of the ocean system can be converted to trophic energy to support biological processes and food webs (Bakun 2006; Godø et al. 2012). The MC eddies could also help to explain the interesting biological observation of the disjunct distribution of subtropical invertebrate and fish species found off the coasts of both KwaZulu-Natal (KZN), South Africa, and southeast Madagascar. The biota on the southeast coast of South Africa comprises species of both subtropical and tropical origin (Teske et al. 2011). This coastline is profoundly influenced by the warm, southward-flowing AC, which could explain the presence of tropical biota in this region (Teske et al. 2011). The disjunct distribution of certain subtropical species on the coasts of both KZN and Madagascar is less easily explained. These species include several fishes of the family Sparidae (ST Fennessy, Oceanographic Research Institute [ORI], pers. comm.), as well as various non-endemic invertebrates, including the mussel *Perna perna* (Berry 1978), shallow-water spiny lobster *Panulirus homarus* (Charbonnier and Crosnier 1961), deep-water spiny lobster *P. delagoae* (Gopal et al. 2006), ghost crab *Ocypode madagascariensis* (Jackson et al. 1991), the estuarine crabs *Scylla serrata* and *Varuna litterata* (Petrocci and Lipton 1994), and the corals *Acropora austera* and *Platygyra daedalea* (M Schleyer, ORI, unpublished data). Additionally, southern Madagascan gammaridean amphipods (Ledoyer 1982) have striking similarities to coastal and marine amphipods found in northern KZN (CF Mackay, ORI, unpublished data).

There are no distinct westward- or eastward-flowing ocean currents linking South Africa and Madagascar which could possibly explain this similarity in fauna and the distributions of these species. Several studies on mesoscale turbulence from the southern Madagascan region (Lutjeharms et al. 1981; Gründlingh 1995; Biastoch and Krauss 1999; Chapman et al. 2003; Schouten et al. 2003; Quartly and Srokosz 2004; Quartly et al. 2006; Siedler et al. 2009) suggest that westward-propagating eddies could provide oceanic connectivity between the southeast coast of Madagascar and the east coast of South Africa. The similarity of fauna on both the Madagascan and KZN coasts gave rise to the 'suitcase' concept (Marsac et al. 2014) that eddies may be able to entrain invertebrate and fish larvae from the southern Madagascan shelf and transport them westwards across the MC to the east coast of South Africa.

The aim of this study was to investigate the 'suitcase hypothesis,' whereby (invertebrate and fish) larvae may be entrained by mesoscale eddies and transported across the MC. Physical and biological parameters were sampled on the southern Madagascan shelf and along a transect through a cyclonic eddy in the Mozambique Basin. The abundance and taxonomic composition of meroplankton on the southern Madagascan shelf were compared to those along the eddy transect. We used DNA barcoding to identify larvae of possible species for which adults are found on the KZN coast and southeast coast of Madagascar.

Materials and methods

Sampling was conducted during a 24-day cruise, in July 2013, on the RS *Algoa*, as part of the African Coelacanth Ecosystem Programme (ACEP). The RS *Algoa* sailed from Durban, South Africa, to undertake a study of a cyclonic eddy that had originated off the southern tip of Madagascar and to collect comparative samples from the Madagascan coast. The eddy was first detected on 16 June 2013, as an enclosed, coherent eddy in the southeastern Mozambique Channel and was a month old when it was sampled during this cruise, according to a mesoscale eddy-tracking algorithm as used by Halo et al. (2014b). Sampling was conducted at 20 stations on the Madagascan shelf, and at 25 stations along a transect through the eddy (Figure 1). A detailed description of satellite-derived sea surface height, geostrophic velocity and chlorophyll concentration in the study area is presented in Barlow et al. (2017: Figures 1 and 2), who note that four stations along the transect were located outside of the eddy to the east (stations 30–33) and two stations were located outside the eddy to the west (stations 53 and 54).

Environmental parameters

Hydrographic sampling was conducted in the upper 1 000 m using a SBE 911plus Sea-Bird CTD-F (conductivity, temperature, depth-fluorescence) fitted with a 12-bottle (5 l) Niskin Rosette system. Vertical fluorescence profiles were converted to chlorophyll-*a* (Chl-*a*) equivalents (mg m^{-3}) by scaling to the Chl-*a* concentrations measured by high-performance liquid chromatography (HPLC) (Barlow et al. 2017). Contour maps of sea surface temperature (°C) and Chl-*a* (mg m^{-3}) on the Madagascan shelf, as well as vertical profiles through the cyclonic eddy, and the horizontal distribution of zooplankton biovolume (ml m^{-3}) were visualised using Surfer (Golden Software 2011).

Zooplankton sampling

Two types of nets were used to collect plankton samples. A Hydro-Bios bongo frame fitted with 300- and 500-µm mesh nets was used to sample meroplankton (which could include the larvae of bivalves, echinoderms, decapods and fishes) in the upper 200 m, or down to 5 m above the bottom at shallower depths (<200 m). Bongo nets were towed obliquely through the water column, at 2 knots, to maximise the volume of water filtered. A neuston net fitted with 900-µm mesh was towed at the surface for 15–20 minutes, at 2 knots, to collect neustonic plankton. Due to time constraints following a period of bad weather, only two bongo hauls were made on the Madagascan shelf: one to the east (station 20) and one to the west (station 26) (Figure 1). Samples were preserved in ethanol (99%) for later extraction of meroplankton.

Biovolume and microscope analysis

In the laboratory, bongo net (500-µm mesh) and neuston net samples from all stations were poured into a measuring cylinder, settled overnight, and then the volume was recorded. Biovolume (ml m^{-3}) was calculated by dividing the settled volume (ml) by the volume of seawater filtered through the net (m^3).

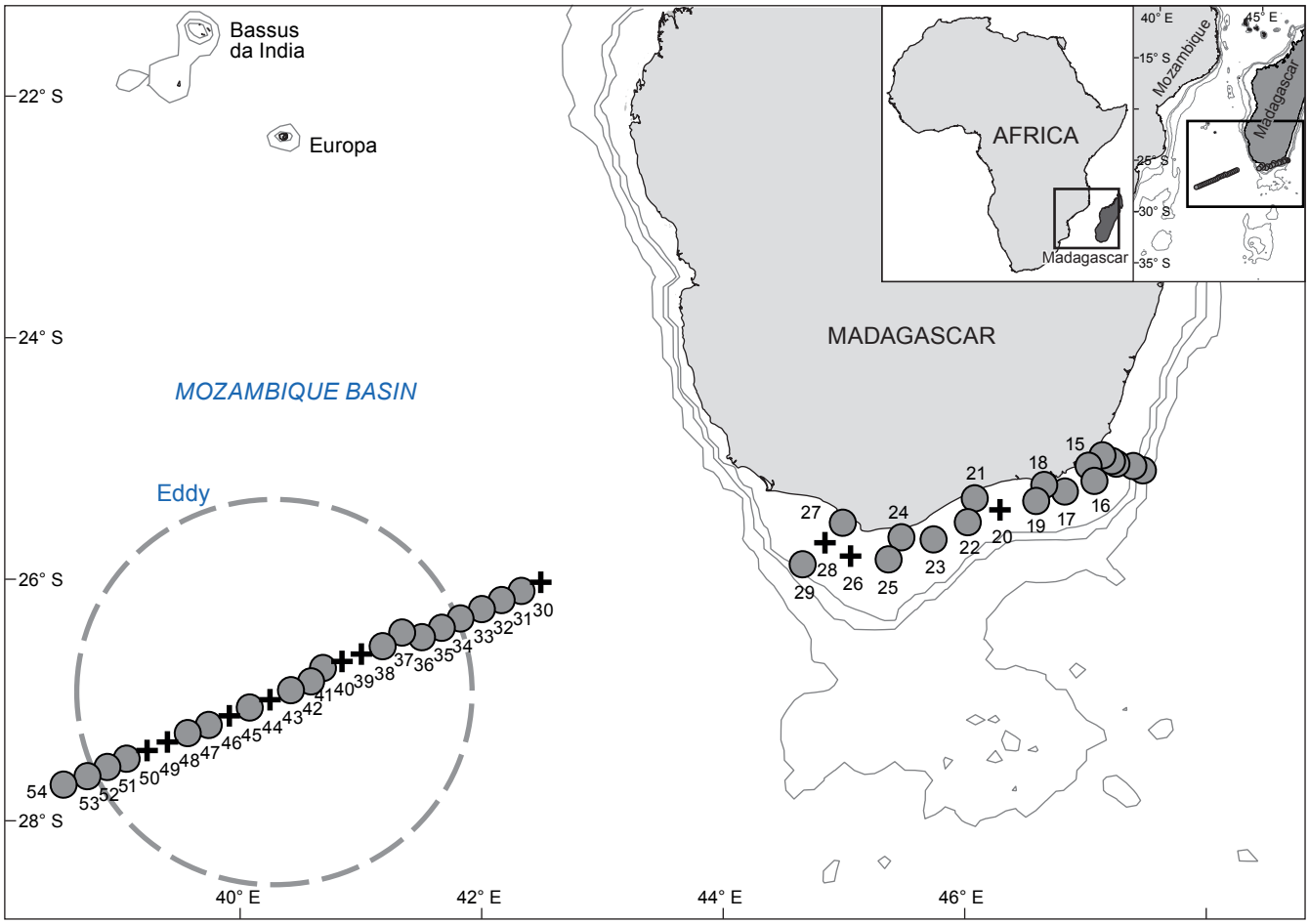

Figure 1: Sampling stations on the Madagascan shelf and along a transect through a cyclonic eddy in the Mozambique Basin (upper left) during July 2013. Stations where meroplankton were selected for microscope analysis and DNA barcoding are indicated by a cross

Representative stations from the Madagascan shelf (stations 20, 26, 28), the cyclonic eddy (stations 39, 40, 44, 46, 49 and 50) and the region outside the eddy (station 30) were selected for microscope analysis of both the 500-µm bongo net and neuston net samples (Figure 1). The whole sample was sorted under a stereomicroscope to select the meroplankton, which were placed into vials for DNA barcoding. Meroplankton were identified to the lowest possible taxonomic level, under a stereomicroscope, using relevant guides, such as those of Gurney (1942), Brownell (1979), Conway et al. (2003) and Richards (2005). In particular, larvae of potential key indicator adult species were sought (i.e. those known to occur on both the southeast coast of Madagascar and the east coast of South Africa). The extracted larvae were used for DNA barcoding to confirm microscopic identification. For this study, we focused on only the decapod and fish larvae because of their greater abundances across all samples.

The Pearson (1896) product-moment correlation was used to test for relationships between zooplankton biovolume and environmental parameters when variance was homogenous among the samples and the data were normally distributed. Otherwise, a Spearman's rank correlation (Kendall 1948) was calculated. Environmental parameters considered were near-surface temperature (at 7 m), temperature at 100 m and at the depth of maximum fluorescence, as well as near-surface fluorescence (at 7 m) and maximum fluorescence. To compare the zooplankton biovolume on the Madagascan shelf with that both within the eddy and in the regions outside the eddy for both the neuston and bongo 500-µm nets, a one-way analysis of variance (ANOVA) was used, followed by Tukey HSD *post hoc* tests (Winer et al. 1971) when variance was homogenous among the samples (Levene's [1960] test) and the data were normally distributed; otherwise a Kruskal–Wallis test (Siegel and Castellan 1988) was performed. Statistical analyses were conducted using STATISTICA 7.0.

DNA barcoding

A standardised gene region, a fragment of the mitochondrial cytochrome c oxidase subunit I (CO1) gene, was used to identify meroplankton to the lowest possible taxonomic level. Total DNA was extracted from decapod and bivalve larvae, using the GeneJet Genomic DNA Purification Kit (Thermo Scientific), according to the specifications of the manufacturer. DNA was extracted from fish larvae using the 'salting out' method (Sunnucks and Hales 1996).

The fragment of interest was replicated by polymerase chain reaction (PCR) using the universal primers LCO1

1490 (at a final concentration of 0.2 µM) and HCO1 2198 (0.2 µM) (Folmer et al. 1994). These primers were successful with the prawn larvae, but failed to amplify shrimp and crab larvae. In these cases, degenerate primers were used: dgLCO1490 (0.2 µM) and dgHCO2198 (0.2 µM) (Meyer 2003). The primers Fish F1 (1 µM) and Fish R1 (1 µM) (Ward et al. 2005) were used initially for the fish larvae, but when visualising PCR success on 1% agarose gels, double bands were observed, indicating non-specific amplification. A switch was made to primers VR1-T1 (1 µM) and VF2-T1 (1 µM) (Ivanova et al. 2007), which worked successfully for most fish larvae. For those that failed, the amplification was repeated using the degenerate (Meyer 2003) primers. For larvae that failed to work with the above-mentioned primers (such as the phyllosoma and some fish larvae), the mitochondrial 16S ribosomal RNA gene was amplified using primers 16Sar (0.2 µM) and 16Sbr (0.2 µM) (Palumbi 1996). The PCR reactions included 1 × buffer, 3 mM $MgCl_2$, 1 mM of each dNTP, primers at the above concentrations, 0.5 U *Taq*-polymerase (Southern Cross Biotechnology, Cape Town, South Africa) and 3 µl of extracted DNA, made up to the final volume (25 µl) with ultrapure water. PCR reactions were performed in an Applied Biosystems Veriti 96-well Thermal Cycler. The thermocycling profile included an initial denaturing step of 2 min at 95 °C, followed by 35 cycles of 30 s at 95 °C, 40 s at 48 °C and 1 min at 72 °C, followed by 10 min at 72 °C. The shrimp and crab larvae failed to be amplified initially with this thermocycling process, and, using optimisation, the suitable annealing temperature was determined to be 46 °C for the larvae of both groups. PCR products were visualised after electrophoresis in a 1% agarose gel, stained with ethidium bromide under UV light, and then purified using Exonuclease I – Shrimp Alkaline Phosphatase (ExoSAP; Thermo Fisher Scientific) (Werle et al. 1994). Purified products were then sequenced using Sanger/BigDye 3.1 (Applied Biosystems) fluorescently labelled terminator chemistry. Cycle-sequencing products, purified using an EDTA/NaOAc/EtOH protocol, were sequenced using an ABI-Hitachi 3500 genetic analyser. Due to time constraints and quality concerns over some of the initial sequencing, certain samples were sequenced by a commercial sequencing facility (Macrogen, Seoul, South Korea).

Sequences were edited and trimmed using Chromas Lite 2.1 software (Technelysium Pty Ltd., South Brisbane, Queensland, Australia) and then submitted for identification to the Barcode of Life Data Systems (BOLD: http://www.boldsystems.org). BLAST (Altschul et al. 1990) searches on GenBank (http://www.ncbi.nlm.nih.gov) were used to assign identities to unknown samples that could not be matched using BOLD. CO1 DNA sequences of fish larvae generated in this study were aligned using ClustalX2.1 (Larkin et al. 2007). Sequence divergences were calculated using the Kimura 2-parameter (K2P) distance model (Kimura 1980), in order to facilitate comparison to other barcoding studies. Neighbour-joining (NJ) trees (Saitou and Nei 1987) were constructed, based on K2P distances, in MEGA 6 (Tamura et al. 2013) to provide a graphic representation of the divergence patterns and distance relationships. The analysis of genetic distances was complemented by downloading related sequences from BOLD and GenBank for comparison with unknown sequences. To test the reliability and robustness of the relationships depicted in the tree, it was bootstrapped using 1 000 replicates (Felsenstein 1985).

Results

Environmental conditions

Cool near-surface water temperatures (<22 °C) were recorded inshore on the south-west and south-east shelf of Madagascar, with warmer water of the SEMC (23–24 °C) recorded farther offshore off the southeast coast (Figure 2a). Near-surface Chl-*a* concentrations on the Madagascan shelf were highest at station 26 on the south-west shelf (1.08 mg m^{-3}) and station 12 on the south-east shelf (1.06 mg m^{-3}) (Figure 2b).

Vertical sections of temperature along the eddy transect indicated weak doming of the isotherms, with slightly cooler water (22–22.5 °C) in the upper 100 m associated with the eddy (Figure 3a). Chl-*a* concentrations within the eddy were highest at stations 42–47 (Figure 3b). The CTD profiles indicated rather homogenous features, with no clear distinctions, and thus could not indicate the eddy core.

Zooplankton biovolume

Mean neuston biovolume on the Madagascan shelf (0.08 ml m^{-3}) was not significantly higher than that within the eddy (0.06 ml m^{-3}) or in the regions outside the eddy (0.05 ml m^{-3}) (ANOVA; F (2, 36), $p > 0.05$; Table 1). However, in samples made with the bongo net (500-µm mesh), mean zooplankton biovolume in the upper 200 m was significantly higher on the Madagascan shelf (0.63 ml m^{-3}) than within the eddy (0.18 ml m^{-3}) and outside the eddy (0.11 ml m^{-3}) (ANOVA; F (2, 24), $p < 0.05$; Table 1). Areas of highest neuston biovolume on the Madagascan shelf were associated with relatively cool water (<22 °C), and with high Chl-*a* concentrations to the west (1.08 mg m^{-3}), but not on the eastern shelf (Figure 2c). In the eddy, there were no clear patterns, and the highest neuston and bongo net biovolumes were associated with intermediate Chl-*a* concentrations (Figure 3c). A significant relationship was found between neuston biovolume and fluorescence at 7 m (Spearman rank $r = 0.42$, $p < 0.05$), but no significant relationships were found between zooplankton biovolume and any other environmental parameters, for either the neuston or the bongo net samples.

Meroplankton abundance and composition

Total abundances of invertebrate larvae collected with the neuston net were fairly low on the Madagascan shelf and outside the eddy, with the highest recorded along the eddy transect (18.82 ind. 100 m^{-3}; Table 2). Crab larvae were the most abundant group on the shelf, while prawn larvae dominated within the eddy. Phyllosoma larvae were found on the Madagascan shelf in low numbers but were not found within the eddy. Total invertebrate larval abundances collected with the bongo net were 10-times higher on the shelf as compared with in the neuston-net catches, but were of a similar magnitude within and outside the eddy (Table 2). Highest abundances were recorded on the Madagascan shelf (51.39 ind. 100 m^{-3}), followed by within

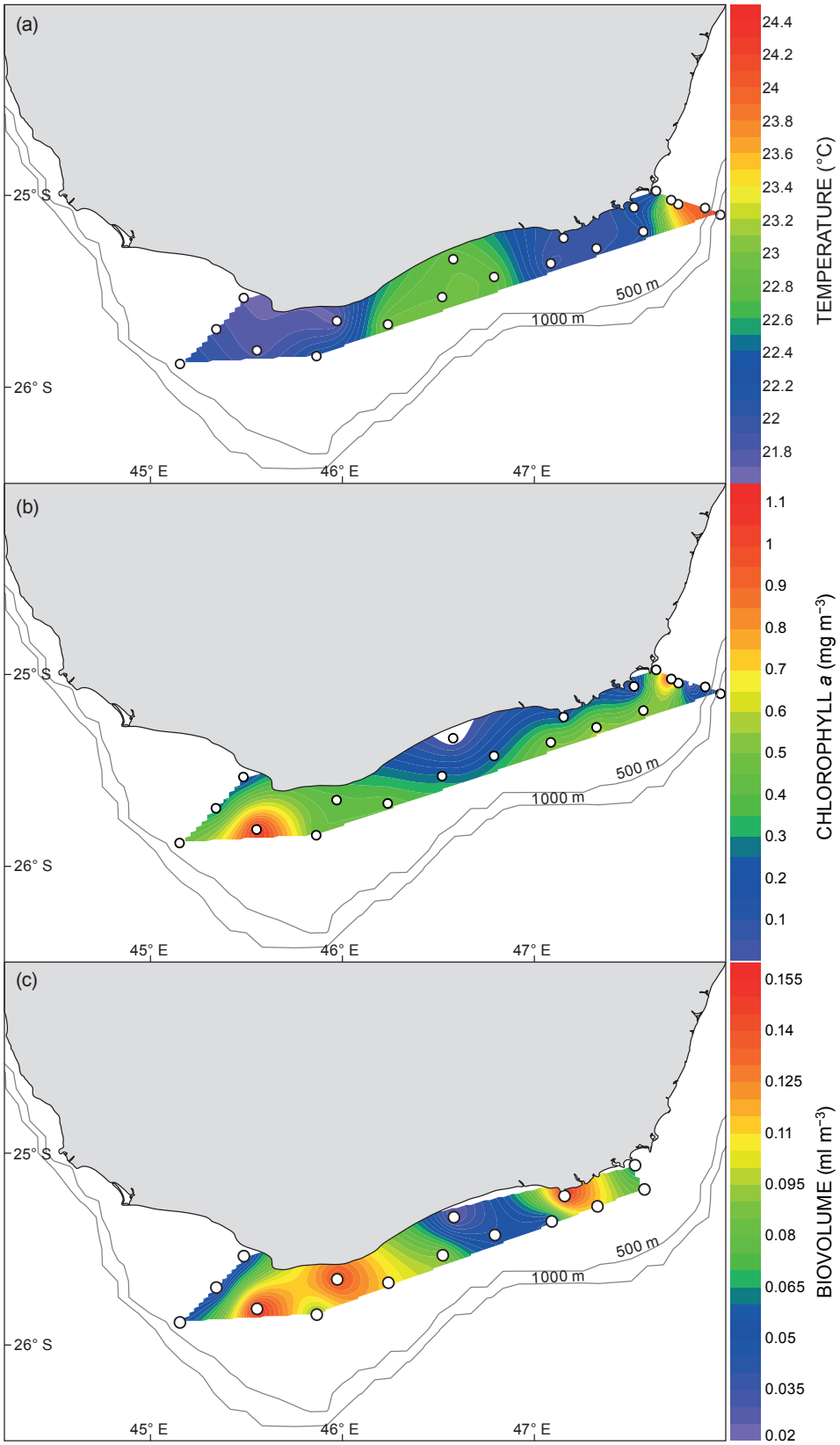

Figure 2: (a) Near-surface (7 m) temperature (°C), (b) near-surface (7 m) chlorophyll-*a* concentration (mg m^{-3}), and (c) neuston net biovolume (ml m^{-3}) on the southern Madagascan shelf

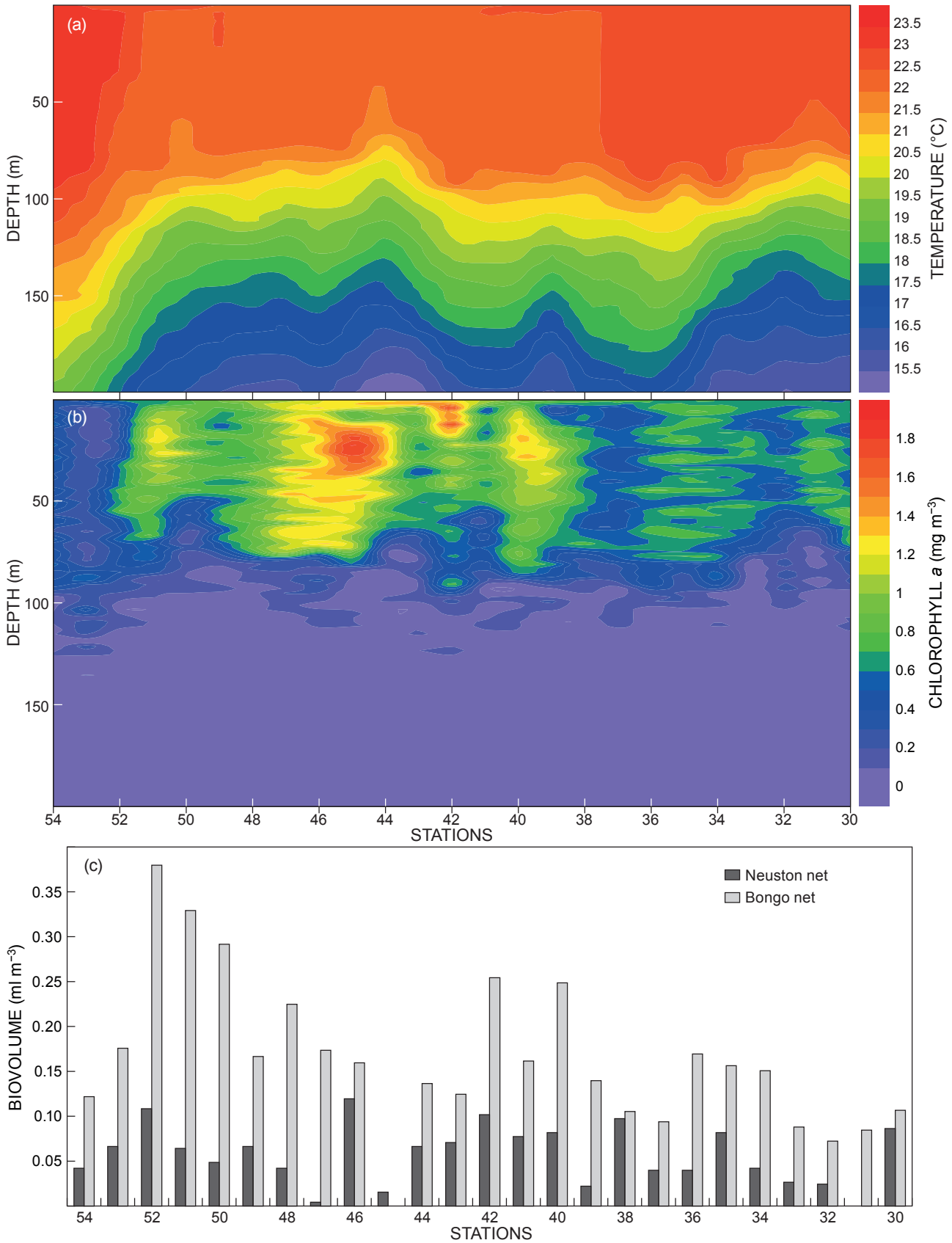

Figure 3: (a) Thermal structure from the surface to 200 m depth, (b) chlorophyll-*a* concentrations (mg m^{-3}) along the eddy transect to 200 m depth, and (c) zooplankton biovolume (ml m^{-3}) collected with the neuston and bongo nets (500-µm mesh) along the eddy transect

Table 1: Mean (± standard deviation) of settled zooplankton biovolume collected with the neuston and bongo nets on the Madagascan shelf, outside of the eddy and within the eddy (July 2013)

Location	Neuston biovolume (ml m^{-3})	*n*	Bongo biovolume (ml m^{-3})	*n*
Madagascan shelf	0.08 ± 0.04	15	0.63 ± 0.08	2
Outside eddy	0.05 ± 0.03	5	0.11 ± 0.04	6
Eddy	0.06 ± 0.03	21	0.18 ± 0.09	21

Table 2: Mean (ind. 100 m^{-3}) and relative abundances (% of total) of invertebrate larvae of various taxonomic groups collected with the neuston and bongo nets on the Madagascan shelf, outside the eddy, and along the eddy transect

Larval group	Madagascan shelf	%	Outside eddy	%	Eddy	%
			Neuston-net samples			
Prawns	0.94	17.39	3.29	50.00	9.88	52.5
Shrimps	0.24	4.35	1.41	21.43	1.18	6.25
Crabs	3.06	56.52	1.88	28.57	7.76	41.25
Phyllosoma	1.18	21.74	–	–	–	–
Total	5.41	100	6.59	100	18.82	100
			Bongo-net samples			
Prawns	12.04	23.42	1.07	33.33	10.41	61.70
Shrimps	26.39	51.35	1.42	44.44	3.77	22.34
Crabs	12.04	23.42	0.36	11.11	2.15	12.77
Phyllosoma	0.93	1.80	–	–	0.36	2.13
Bivalves	–	–	0.36	11.11	0.18	1.06
Total	51.39	100	3.20	100	16.88	100

the eddy (16.88 ind. 100 m^{-3}). Shrimp larvae dominated the invertebrate meroplankton on the shelf and outside the eddy, whereas prawn larvae dominated within the eddy. Phyllosoma larvae were found in low abundances on the Madagascan shelf and within the eddy, particularly towards the west. Bivalve larvae were present in low numbers within and outside the eddy.

Low larval fish abundances were also recorded with the neuston net on the Madagascan shelf, with the highest abundance outside of the eddy (7.29 ind. 100 m^{-3}; Table 3). The dominant families of fish larvae collected on the Madagascan shelf (especially on the eastern shelf) with the neuston net were Mullidae and Sphyraenidae, together comprising >60% of total larval fish abundance. Outside the eddy, Centropomidae comprised 74.2% of total larval fish abundance, and within the eddy Mullidae comprised 30% of total larval fish abundance. Total larval fish abundances collected with the bongo net (Table 3) were highest on the Madagascan shelf (58.33 ind. 100 m^{-3}), followed by within the eddy (11.13 ind. 100 m^{-3}). Dominant fish families included Carangidae, Lutjanidae and Myctophidae, on both the Madagascan shelf and within the eddy. Collectively, Carangidae, Lutjanidae and Myctophidae comprised 80% of total larval fish abundance on the Madagascan shelf, with Carangidae comprising 70.6% of total larval fish abundance.

DNA barcoding identifications

Traditional microscope identifications were difficult due to a lack of available reference material, and most of the decapod larvae were identified only to a high taxonomic level. However, with DNA barcoding analysis, more-detailed identifications were possible. Due to time and budget constraints, randomly selected, representative specimens from each sampling area were used for DNA barcoding, and the results include only the presence of taxa and not their abundances. A total of 51 barcodes were obtained for both invertebrate and fish larvae. Most sequences were identified to the generic level only, given the lack of reference data. For this study, divergence thresholds, which were first proposed by Hebert et al. (2004), were used to identify unknown sequences. Past barcoding studies of marine fish (Ward et al. 2005) and decapods (da Silva et al. 2011) established ranges of sequence divergence that characterise individuals belonging to the same species. Hebert et al. (2003) further demonstrated that a wide gap exists between divergence values obtained in intraspecific and interspecific comparisons among congeners. These divergences increase with increasing taxonomic level (i.e. at the generic, familial or ordinal level). For this study, sequence divergences were used for species identification, and to assess generic placement and family membership based on using these divergence thresholds.

For decapod larvae, two sequences were identified to species level: the shrimp *Rhynchocinetes durbanesis* and the squat lobster *Allogalathea elegans* (Table 4). A further 18 sequences were identified to genus level; these included decapod larvae of crabs (genera *Ashtoret, Calappa*, *Ebalia, Pilumnus, Portunus, Pseudoliomera* and *Xaiva*), prawns (*Bentheogennema, Marsupenaeus, Metapenaeopsis* and *Solenocera*), and shrimp (*Acanthephyra, Eualus,*

Table 3: Mean (ind. 100 m^{-3}) and relative abundances (% of total) of fish larvae of various families collected with the neuston and bongo nets on the Madagascan shelf, outside the eddy, and along the eddy transect

Group	Madagascan shelf	%	Outside eddy	%	Eddy	%
			Neuston-net samples			
Bothidae	–	–	0.24	3.23	0.47	10.00
Bregmacerotidae	–	–	–	–	0.24	5.00
Centropomidae	–	–	5.41	74.19	0.24	5.00
Clupeidae	0.24	6.25	0.24	3.23	0.47	10.00
Exocoetidae	0.24	6.25	–	–	–	–
Mullidae	0.94	25.00	–	–	1.41	30.00
Myctophidae	–	–	1.18	16.13	–	–
Scombridae	0.24	6.25	–	–	0.24	5.00
Scorpaenidae	–	–	–	–	0.24	5.00
Serranidae	0.24	6.25	–	–	0.47	10.00
Sphyraenidae	1.41	37.50	–	–	0.24	5.00
Synodontidae	–	–	0.24	3.23	–	–
Unidentified fish larvae	0.47	12.50	–	–	0.71	15.00
Total	3.76	100	7.29	100	4.70	100
			Bongo-net samples			
Apogonidae	1.39	2.38	–	–	0.54	4.48
Blennidae	0.93	1.59	–	–	–	–
Bregmacerotidae	–	–	–	–	0.36	3.23
Carangidae	41.20	70.63	–	–	0.90	8.06
Carapidae	–	–	–	–	0.18	1.61
Centropomidae	–	–	1.07	21.43	–	–
Clupeidae	2.78	4.76	–	–	–	–
Exocoetidae	–	–	–	–	0.18	1.61
Gonostomatidae	0.46	0.79	–	–	0.54	4.84
Labridae	0.46	0.79	0.36	7.14	0.18	1.61
Lutjanidae	3.24	5.56	–	–	1.26	11.29
Mullidae	–	–	–	–	0.72	6.42
Myctophidae	2.31	3.97	2.85	57.14	5.03	45.16
Nomeidae	–	–	0.36	7.14	–	–
Scombridae	1.39	2.38	–	–	0.36	3.23
Serranidae	0.46	0.79	–	–	0.54	4.84
Sphyraenidae	0.93	1.59	–	–	0.18	1.61
Synodontidae	0.46	0.79	–	–	0.18	1.61
Trichuridae	0.46	0.79	0.36	7.14	–	–
Unidentified fish larvae	1.85	3.17	–	–	–	–
Total	58.33	100	4.98	100	11.13	100

Periclimenes and *Plesionika*) (Table 4). These invertebrate larvae were found on the Madagascan shelf and along the eddy transect.

Fish larvae identified to species level included *Decapterus macrosoma*, *Parupeneus fraserorum*, *Pseudanthias squamipinnis* and *Sarda orientalis* (Table 5). There were two possible candidate species identified for genera *Gonostoma, Oplegnathus, Priacanthus* and *Scomber*, which may reflect misidentification of these species in the BOLD reference database. In this case, identification was made to genus level (Table 5). Larvae that were identified to genus level included the genera *Bregmaceros*, *Callionymus*, *Chromis*, *Epinephelus*, *Gonostoma, Halichoeres*, *Lotella*, *Nealotus*, *Ostorhinchus*, *Oplegnathus*, *Polysteganus, Priacanthus*, *Pseudanthias*, *Pyramodon*, *Scomber*, *Symbolophorus, Taaningichthys* and *Vinciguerria*. Fish larvae identified to family level included representatives of the Ammodytidae, Bothidae, Gonostomatidae, Myctophidae and Notosudidae.

In cases of failed amplification with CO1, a 16S rDNA fragment was amplified instead. Two unknown phyllosoma larvae and one fish larva were identified using 16S rDNA. These included phyllosoma larvae of the genera *Scyllarus* and *Panulirus* (Table 4), and a fish larva of the genus *Paralabrax* (Table 5).

Phylogenetic analysis

Sequences obtained in this study were combined with sequences downloaded from BOLD and GenBank (Supplementary Appendix S1, available online) to produce a neighbour-joining (NJ) tree (Figure 4). The NJ tree was used to display a graphic representation of the divergence patterns and distance relationships between sequences. Due to a lack of reference data and available sequences for the invertebrate larvae, the NJ tree was produced using only larval fish sequences. Tight clusters and short branch lengths among unknown larvae and downloaded data for representative species indicate very small genetic distances and, together with high bootstrap support, confirm highly accurate species identifications for these larvae. Sequence divergences, calculated using the K2P model,

Table 4: Unknown invertebrate larvae identified through DNA barcoding. Bold font indicates sequences identified to species level

Unknown specimen no.	Family	Genus	Species	Gene	BOLD % similarity	GenBank % similarity
C1	Portunidae	*Xaiva*		CO1	98.2	–
C2	Portunidae	*Portunus*		CO1	86.29	–
C3	Leucosiidae	*Ebalia*		CO1	86.29	–
C7	Matutidae	*Ashtoret*		CO1	87.71	–
C8	Xanthidae	*Pseudoliomera*		CO1	99.81	–
C9	Pilumnidae	*Pilumnus*		CO1	84.67	–
C13	Calappidae	*Calappa*		CO1	100	–
P1.2	Penaeidae	*Metapenaeopsis*		CO1	89.05	–
P1.4	Benthesicymidae	*Bentheogennema*		CO1	86.18	–
P3	Solenoceridae	*Solenocera*		CO1	89.38	–
P5	Penaeidae	*Marsupenaeus*		CO1	89.27	–
S1	Acanthephyridae	*Acanthephyra*		CO1	98.89	–
S2	Palaemonidae	*Periclimenes*		CO1	100	–
S3	Hippolytidae	*Eualus*		CO1	86.62	–
S4	**Rhynchocinetidae**	***Rhynchocinetes***	***durbanensis***	**CO1**	100	
S5	Pandalidae	*Plesionika*		CO1	84.26	–
C11	**Galatheidae**	***Allogalathea***	***elegans***	**CO1**	100	–
Ph1	Scyllaridae	*Chelarctus*		CO1	82.36	–
Ph2	Scyllaridae	*Scyllarus*		16S	–	81
Ph3	Palinuridae	*Panulirus*		16S	–	99

are presented in Supplementary Appendices S2 and S3. K2P distances among specimens in each of these clusters varied from 0 to 0.2%. These clusters represent *Decapterus macrosoma, Parupeneus fraserorum, Pseudanthias squamipinnis* and *Sarda orientalis*. Those unknown fish larvae which had two possible candidate species identifications (*Gonostoma elongatum, Oplegnathus robinsoni, Priacanthus* aff. *arenatus* and *Scomber colias*) also showed tight clusters with downloaded fish-species data and fell within the 2% divergence threshold characterising conspecifics. Certain unknown fish larvae also showed tight clusters with *Callionymus marleyi*, *Epinephelus rivulatus*, *Halichoeres zeylonicus* and *Pseudanthias connelli*, but had higher genetic distances (from 3 to 8%), falling beyond the 2% threshold characterising congeneric species.

Some of the unknown larvae were clearly associated with representatives of some species and a particular genus in neat clusters, but with slightly longer branch lengths and, hence, larger genetic distances. This might suggest that the unknown larvae are congeneric but belonging to a different species. These genetic distances between unknown larvae and downloaded data for species (*Callionymus marleyi*, *Chromis chrysura*, *Lotella* sp., *Nealotus tripes*, *Polysteganus baissaci*, *Pyramodon* sp., *Scopelosaurus lepidus*, *Symbolophorus rufinus*, *Taaningichthys minimus* and *Vinciguerria nimbaria*) were between 1 and 10%.

Sequences separated by rather longer branches and K2P distances varying from 10 to 20% indicated that unknown larvae belonged to a different genus, but to the same families as *Ammodytoides* sp., *Arnoglossus polyspilus*, *Cyclothone microdon* and *Diogenichthys laternatus*, for which data were downloaded.

Using the K2P distances and NJ tree, DNA barcoding proved to be 100% successful at identifying unknown sequences to the family level, 55% at the genus level, and 23% at the species level. Failure of DNA barcoding was mainly due to amplification failure because of poor-quality DNA extracted from some of the bivalve larvae and some phyllosoma larvae.

Discussion

Zooplankton biovolume on the Madagascan shelf

In this study, highest mean zooplankton biovolume (0.63 ml m^{-3}) was recorded on the Madagascan shelf with the bongo net (500 µm), three times that found in the eddy, although only two shelf stations were sampled. Mean zooplankton biovolume collected with the neuston net was much lower (0.05–0.08 ml m^{-3}) and did not differ significantly between volumes found on the Madagascan shelf and in the eddy. Zooplankton production is generally higher in coastal waters as compared with in the open ocean (Nair 2001), as is also the case for the south-west Indian Ocean (SWIO). For example, Huggett (2014) recorded a high mean mesozooplankton (>200 µm) biovolume (1.9 ml m^{-3}) near the coast, south of Nacala, Mozambique, during a cruise in 2010. Sampling of macrozooplankton during fisheries surveys (1977–1978) off the Mozambique coast yielded mean biovolumes of 0.8–1.4 ml m^{-3}, with higher values of 1.8–4.6 ml m^{-3} on the Sofala Bank (Saetre and de Paula e Silva 1979; Huggett and Kyewalyanga 2017: Table A5.3). Leal et al. (2009) measured neuston biovolumes of 0.05–1.15 ml m^{-3} on the Sofala Bank, up to two-times higher than in this study. The Sofala Bank is a productive shelf region influenced by tidal currents and great hydrological variability, owing to discharges from the Zambezi Delta, as well as mesoscale oceanographic features of the MC (Lutjeharms 2006; Ternon et al. 2014b). A survey in the western MC (February–March 1980) revealed higher zooplankton biomass inshore as compared with offshore further south in the channel (18° S), where high zooplankton biomass was associated with

Table 5: Unknown fish larvae identified through DNA barcoding. Bold font indicates sequences identified to species level

Unknown specimen no.	Family	Genus	Species	Gene	BOLD % similarity	GenBank % similarity
F2	Oplegnathidae	*Oplegnathus*	*peaolopesi/robinsoni*	CO1	100	–
F4	Bothidae			CO1	–	89
F5	**Mullidae**	***Parupeneus***	***fraserorum***	**CO1**	100	–
F8	Notosudidae			CO1	96.45	–
F11	**Carangidae**	***Decapterus***	***macrosoma***	**CO1**	100	–
F12	Priacanthidae	*Priacanthus*	aff. *arenatus/arenatus/ hamrur*	CO1	99.11	–
F13	Serranidae	*Epinephelus*		CO1	99.65	–
F14	Bregmacerotidae	*Bregmaceros*		CO1	98.2	–
F16	Scombridae	*Scomber*	*colias/japonicus*	CO1	100	–
F17	Myctophidae	*Symbolophorus*		CO1	99.03	–
F18	Myctophidae			CO1	90.41	–
F19	Gempylidae	*Nealotus*		CO1	–	91
F20	Labridae	*Halichoeres*		CO1	99.41	–
F21	Carapidae	*Pyramodon*		CO1	98.92	–
F22	Apogonidae	*Ostorhinchus*		CO1	–	82
F24	Pomacentridae	*Chromis*		CO1	92.88	94
F25	Serranidae	*Pseudanthias*		CO1	99.52	–
F26	Callionymidae	*Callionymus*		CO1	99.36	–
F27	Moridae	*Lotella*		CO1	91.59 cf. *tosaensis*	94*rhacina*
F28	**Carangidae**	***Decapterus***	***macrosoma***	**CO1**	100	–
F29	**Mullidae**	***Parupeneus***	***fraserorum***	**CO1**	100	–
F30	**Scombridae**	***Sarda***	***orientalis***	**CO1**	100	–
F32	**Serranidae**	***Pseudanthias***	***squamipinnis***	**CO1**	100	–
F33	Serranidae	*Paralabrax*		16S	–	98
F34	Myctophidae	*Taaningichthys*		CO1	98.28	–
F35	Phosichthyidae	*Vinciguerria*		CO1	98.21	–
F36	Gonostomatidae			CO1	99.38	–
F37	Ammodytidae			CO1	93.24	–
F38	Sparidae	*Polysteganus*		CO1	93.43	91*coeruleopunctatus*
F39	Gonostomatidae	*Gonostoma*	*elongatum/denudatum*	CO1	100	–
F40	**Mullidae**	***Parupeneus***	***fraserorum***	**CO1**	100	–

the southern edge of a strong cyclonic eddy located south of Angoche (Nehring et al. 1987). Malauene et al. (2014) found that elevated Chl-*a* concentrations at Angoche are largely driven by north-easterly monsoon winds, but also through cyclonic/anticyclonic eddies interacting with the shelf. In the present study, elevated sea-surface Chl-*a* and low sea-surface temperature on the southern Madagascan shelf were associated with elevated zooplankton biovolume. These oceanographic conditions have been observed previously along the southern coast of Madagascar, where hydrographic data and satellite and sea-surface-temperature imagery showed elevated Chl-*a* and cooler water, indicating upwelling on the southeast coast of Madagascar (Di Marco et al. 2000; Machu et al. 2002). Similar conditions were also noted in a more recent study on the southern coast of Madagascar (26° S), where Pripp et al. (2014) found elevated Chl-*a* and primary production on the south coast in response to upwelling, as revealed by high sea-surface salinity and low sea-surface temperature.

Zooplankton biovolume in the eddy

In this study, highest mean zooplankton biovolumes were recorded in the western part of the eddy transect, followed by in the region outside the eddy to the west, and lower zooplankton biovolumes were found in the region outside the eddy to the east. It is expected that a high zooplankton biovolume would be found within cyclonic eddy cores, as the cores are highly productive due to upwelling in their interiors (Bakun 2006). For example, in oligotrophic systems, Huggett (2014) found higher mesozooplankton biovolume (0.3 ml m^{-3}) in cyclonic eddies than in anti-cyclonic eddies in the MC. Landry et al. (2008) recorded mesozooplankton biomass in a cyclonic eddy to be 80% greater than in the surrounding waters at the Hawaiian Islands. In the western Bay of Bengal, mesozooplankton biomass was five-times greater (and density 18-times greater) in cold-core eddies (Fernandes and Ramaiah 2009). In the Gulf of Mexico, acoustic backscatter intensity reflected from epipelagic zooplankton communities revealed elevated zooplankton and micronekton in cold-core eddies as compared with in warm-core eddies.

In this study, Chl-*a* concentrations along the eddy transect showed patterns contrasting to those of zooplankton biovolume. The highest Chl-*a* concentrations were recorded from stations 43–48, whereas zooplankton biovolume was highest to the west of the eddy, at stations 50–52.

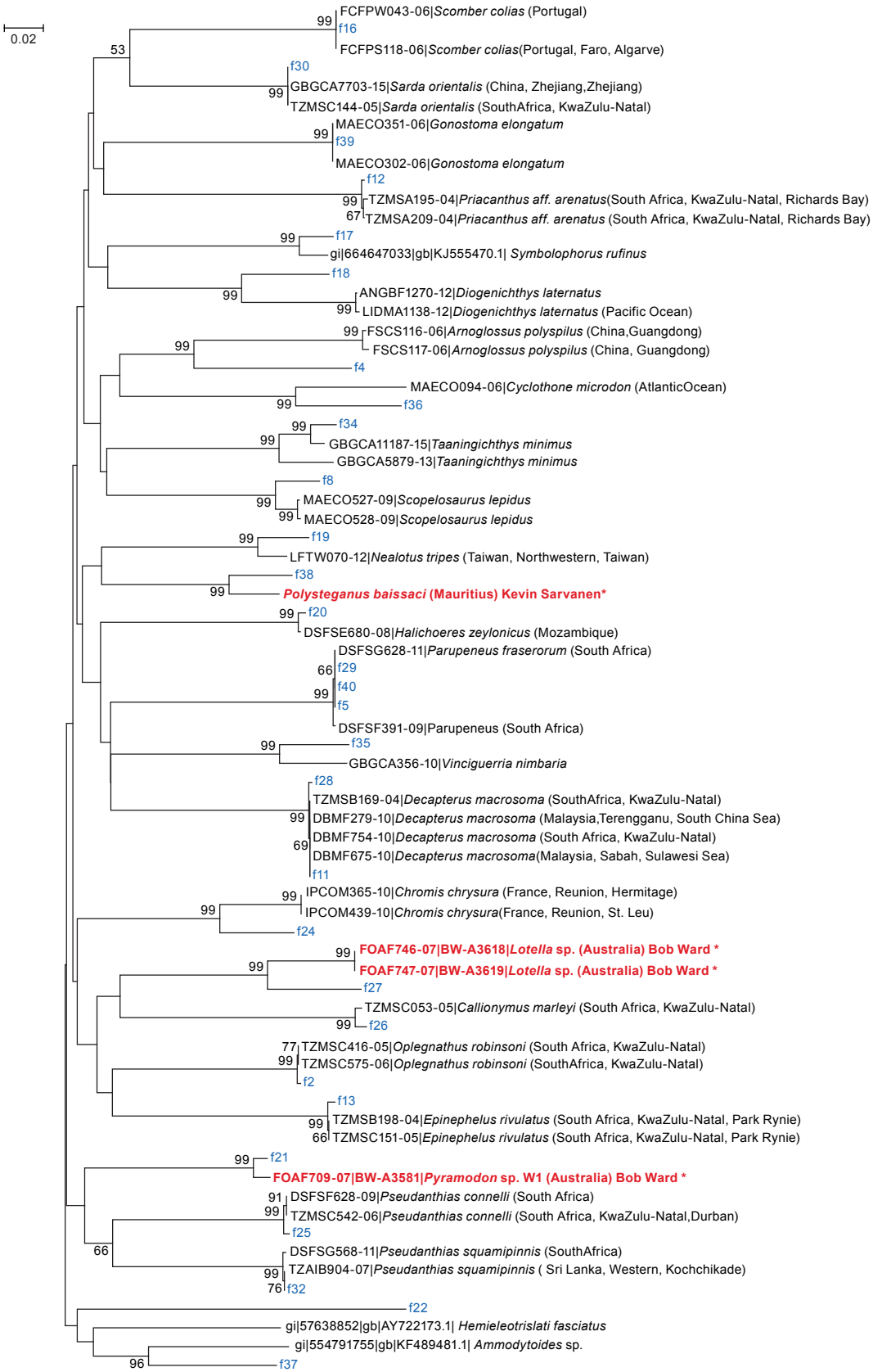

Figure 4: Neighbour-joining tree of CO1 sequences to display a graphic representation of the divergence patterns and distance relationships between sequences. Red sample names represent unpublished data, black sample names are extracted from BOLD or GenBank, and blue sample names represent unknown data. Numbers at nodes represent bootstrap values

Studies conducted in the Sargasso Sea documented similar observations to this study, with higher zooplankton biomass recorded in a cyclonic eddy's periphery than in the core (Goldthwait and Steinberg 2008). Hernández-León et al. (2001) also found elevated biomass in an eddy periphery as compared with in its core, in the vicinity of the Canary Islands. In both of the above studies, the eddies were mature and it was suggested that higher zooplankton biovolume or biomass found at eddy peripheries could be due to an outward drift of zooplankton towards the eddy periphery during the eddy's decay (Bakun 2006). In this study, however, the cyclonic eddy was sampled when it was about one month old, and the lack of strong doming in the thermal profile indicated that the eddy was not fully 'spun up.' Furthermore, studies on micronekton and top predators in the MC also found higher abundances at the eddy peripheries (Weimerskirch et al. 2004; Sabarros et al. 2009; Tew-Kai and Marsac 2009; Sánchez-Velasco et al. 2013). These studies suggested that eddies tend to advect coastal waters at their periphery when they propagate along the coast, and thereby distribute nutrient-rich waters into the open ocean.

Meroplankton distribution and species composition

Invertebrate larvae

In this study, larvae of prawns, shrimps and crabs prevailed on the Madagascan shelf, as well as in the eddy. Phyllosoma larvae were also present, but in lower numbers and mainly on the Madagascan shelf, with only one found along the eddy transect. Prawn larvae were dominated by two families, Penaeidae and Benthesicymidae. Penaeidae are normally found in shallow waters along the continental shelf and occur in large quantities (Chan 1998), whereas Benthesicymidae are either deep, benthic dwellers or members of the meso- and bathypelagic fauna (Vazquez-Bader et al. 2004).

Shrimp larvae were dominated by the family Palaemonidae, genus *Periclimenes.* This genus is known to associate with anemones and is found in warmer waters throughout the world, with the greatest diversity on tropical reefs (Bruce 2004). One larval shrimp identified to species level was the rhynchocinetid shrimp *Rhynchocinetes durbanensis*; this species, initially known only from South Africa (Gordon 1936), is widely distributed in the Indo-West Pacific and is associated with coral or rocky reefs in shallow waters (Gordon 1936).

Dominant crab larvae included representatives of the family Portunidae and were found on both the Madagascan shelf and along the eddy transect. Portunids are commonly found in tropical and subtropical estuarine and nearshore habitats (Shields 1992).

The phyllosoma larvae identified represented two families, Palinuridae (spiny lobsters) and Scyllaridae (slipper lobsters). Spiny lobsters are inhabitants of reef and rocky shores in tropical to temperate seas (Diaz et al. 2002); the genus *Panulirus* is characteristic of shallow tropical waters and has a wide geographic distribution (Ptacek et al. 2001). Scyllaridae are also widespread in shallow tropical to temperate waters, but are more abundant in tropical waters and have been recorded deeper than 300 m (Baisre 1994). The phyllosoma larvae identified in this study fall under the subfamily Scyllarinae, which consists of small-sized slipper lobsters found in tropical lagoons, on continental shelves and slopes, and on deep-sea ridges and seamounts (Booth et al. 2005).

Lastly, a squat lobster larva was also identified to species level. *Allogalathea elegans,* widely distributed in the Indo-West Pacific and sighted off northern Mozambique and Madagascar (Baba et al. 2008), is a shallow-water species, but is sometimes found down to 146 m, and is associated with crinoids (Cabezas et al. 2011).

Fish larvae

Dominant fish larvae identified in this study belonged to coastal/reef, benthic, epipelagic and mesopelagic families. Coastal/reef fish families included the Centropomidae, Mullidae and Serranidae; epipelagic fish families included the Sphyraenidae and Carangidae; benthic fish families included the Bothidae and Bregmacerotidae; and mesopelagic fish families included the Myctophidae and Gonostomatidae. Carangids off eastern Australia have been described as coastal or shelf species (Keane and Neira 2008). The presence of Myctophidae is easily explained, being a diverse family of oceanic fishes that have been collected in many regions of the world and that represent a high proportion of the total larvae collected in oceanic plankton samples (Olivar and Beckley 1994). This also explains their high abundance in both nets. Myctophids also dominated eddy peripheries in the MC, with few caught in the eddy core, during a study on the influence of mesoscale features on micronekton and communities of large pelagic fishes in the MC (Potier et al. 2014). The genus *Symbolophorus* was one of the myctophids that prevailed in these fish assemblages (Potier et al. 2014) and was also present in this study.

Fish larvae identified to species level included the scad mackerel *Decapterus macrosoma*, the serranid *Pseudanthias squamipinnis* (sea goldie), the goatfish *Parupeneus fraserorum* and the striped bonito *Sarda orientalis. Decapterus macrosoma* is reef-associated, found at depths of 20–214 m, and is widely distributed in the tropical Indo-West Pacific (Paxton et al. 1989). *Pseudanthias squamipinnis* is widely distributed in the Indo-West Pacific and is a reef-associated fish, occurring in shallow waters down to 55 m (Randall et al. 1997). The goat fish *Parupeneus fraserorum* is a newly described mullid species from the coast of KZN, South Africa, with a depth range of 39–57 m, but has also been recorded off southeastern Madagascar at 27–87 m (Randall and King 2009). According to Randall and King (2009), *P. fraserorum* is known only from KZN and the southeastern coast of Madagascar. *Sarda orientalis* is a coastal species occurring at 1–167 m and has a wide distribution in the Indo-Pacific, from the east coast of Africa to the west coast of America in the eastern Pacific (Collete and Nauen 1983).

Other fish larvae identified in this study, but not found in high abundance, included representatives of other families of reef-associated fishes. The Priacanthidae (bigeyes) are distributed in tropical and subtropical waters of the Atlantic, Indian and Pacific oceans, and are generally associated with rock formations or coral reefs (Starnes

1988). The genus *Pseudanthias*, in subfamily Anthiinae of family Serranidae, are small colourful, coral-reef fishes mainly from the Indo-Pacific (Randall 2011). The Labridae (wrasses) inhabit tropical to temperate marine waters worldwide, and are mainly found in shallow habitats, such as on coral and rocky reefs, and in areas of sand, seagrasses and algae (Westneat and Alfaro 2005). The Apogonidae (cardinalfishes) are nocturnal, active inhabitants of tropical to warm-temperate reefs (Fraser and Allen 2010). The Pomacentridae (damselfishes) occur in all tropical oceans but mainly the Indo-Pacific (Allen 1991). Lastly, the Sparidae (seabreams and porgies) are widely distributed in tropical to temperate waters and occur in rocky and sandy nearshore areas or on offshore reefs, to 450 m deep (Heemstra and Heemstra 2004). Most of the fish larvae sampled were of shallow-water, reef-associated taxa, and thus shelf inhabitants.

Other studies have revealed the entrainment and advection of planktonic larvae by mesoscale eddies in oligotrophic waters. Graber and Limouzy-Paris (1997) found that larval fish assemblages within spin-off eddies in the Straits of Florida consisted predominantly of reef fishes, indicating that fish larvae were entrained from the shelf. In the Gulf of California, the highest larval abundance in plankton was concentrated at the offshore edge of an eddy, consisting mainly of coastal pelagic and demersal species. This suggests that the edge of the eddy 'captured' larvae close to the coast and then transported them around the eddy (Sánchez-Velasco et al. 2013). In the Leeuwin Current, larval fish assemblages collected within an eddy were different from those of the surrounding oceanic waters (Holliday et al. 2011). These eddy larval assemblages consisted mainly of oceanic mesopelagic fishes, but neritic taxa were also present. Holliday et al. (2011) confirmed that the occurrence of neritic taxa in the eddy was due to larvae being incorporated within the eddy while it developed in proximity to the shelf.

The majority of fish larvae were found on the Madagascan shelf and to the west side of the eddy in the Mozambique Basin. The occurrence of coastal/reef fish larvae on the Madagascan shelf is to be expected, but the presence of coastal/reef fish families in the open ocean is less easily explained. The presence of coastal/reef-associated fish in the eddy periphery in the Mozambique Basin suggests that fish larvae were entrained around the edges of the cyclonic eddy, which originated on the southern part of the Madagascan shelf, and were transported into the MC. Thus, the high zooplankton biovolumes, larval abundances and reef-associated larval assemblages found seaward along the eddy transect provide support for the 'suitcase hypothesis' wherein planktonic organisms are entrained within eddies as they propagate south-westwards of the Madagascan shelf.

Efficacy of DNA barcoding of plankton

DNA barcoding of meroplankton has been revealed to be an effective tool for taxonomic identification in this study, although identification could mostly be done only to genus level. This indicates the limited reference information available for invertebrate and fish species in this region. On a global scale, DNA barcoding has been successful as an identification tool for identifying basic groups of zooplankton (Webb et al. 2006; Machida et al. 2009; Bucklin et al. 2010; Heimeier et al. 2010; Cheng et al. 2014) and fish larvae (Pegg et al. 2006; Valdez-Moreno et al. 2010; Baldwin et al. 2011). DNA barcoding has also confirmed the accurate identification and discrimination within various groups of holozooplankton, for example copepods (Bucklin et al. 2003; Bucklin and Frost 2009; Blanco-Bercial et al. 2014), cnidarians (Ortman 2008; Ortman et al. 2010), euphausiids (Bucklin et al. 2007), ostracods (Angel 1969), pteropods (Jennings et al. 2010a) and chaetognaths (Jennings et al. 2010b).

This is the first published study to use DNA barcoding as a tool for identifying meroplankton in the SWIO. Taxonomic analysis of plankton using morphological identification is time-consuming and difficult, which is exacerbated when dealing with fragile and damaged organisms (Bucklin et al. 2011). This study has shown the efficacy of DNA barcoding to identify meroplankton where only broad identifications were otherwise possible using microscope analysis.

Connectivity between Madagascar and South Africa

The overall aim of this study was to determine whether eddies off southern Madagascar create a potential pathway for marine-fauna gene flow across the MC to southern Africa. The goatfish *Parupeneus fraserorum*, a newly described mullid found off the coasts of both Madagascar and KZN, was present on the Madagascan shelf and in the eddy. Invertebrate and fish larvae identified in this study were either coastal or reef-associated, and found on the Madagascan shelf and in the eddy. Based on these findings, it is suggested that cyclonic eddies do entrain planktonic larvae from the Madagascan shelf and transport them into the open ocean. It has also been observed through numerical models and altimetry data (Quartly and Srokosz 2004; Halo et al. 2014b) that cyclonic eddies off the southwestern region of Madagascar have strong vorticity and are highly energetic, living longer and travelling longer distances than eddies from the south-east region. This suggests that they are most likely to trap material in their cores and to transport them over long distances.

While it is suggested that eddies do entrain larvae from the Madagascan shelf, whether they transport larvae across the MC in a reasonable time before metamorphosis is still unknown. The core of a cyclonic eddy is clearly a favourable niche for larvae. However, the propagation speed of cyclonic eddies recorded crossing the MC from southwest Madagascar is 6–9 km day^{-1}, and hence the crossing would take 5–7 months to complete (Marsac et al. 2014). This would not be feasible for the survival of most marine organisms, especially benthic species. For example, some benthic organisms have an average pelagic larval phase of 80 days (Shulman and Bermingham 1995). The rock lobster *Panulirus homarus* has a phyllosoma stage lasting up to 6 months, making it an ideal species to survive being transported across the MC. Interestingly, the scalloped spiny lobster *P. homarus rubellus* appears to have distinct lineages on the southeast coast of mainland Africa and at Madagascar, suggesting an absence of contemporary gene flow across the MC (Reddy et al. 2014). It has also been shown that the African lineage appears to be ancestral and the source population for the Madagascar clade, which would negate the likelihood of eddies facilitating genetic

connectivity between the modern South African and Madagascan populations.

Another possible route for biota to cross the MC in a suitable timeframe for larval survival is via the regions between contra-rotating eddies (Marsac et al. 2014). Hancke et al. (2014) recorded a (westward) horizontal velocity of 52–170 km day^{-1} between contra-rotating eddies. In this case, it would take less than 50 days to cross the MC, favouring larval survival for most benthic and pelagic species.

This study confirms that cyclonic eddies that form off southern Madagascar can entrain planktonic larvae as they move offshore; however, further studies are required to determine whether planktonic larvae are able to cross the MC and reach the coast of KZN in time to settle, and thus facilitate connectivity and gene flow between the two regions, which would account for the similarities among the fauna. This will require the application of population genetics. Focused sampling and DNA barcoding of the genera collected along the KZN coast in the present study will be useful in this regard. Logistical constraints prohibited this in the current study, but such an endeavour will enable a more accurate identification of the species found in the eddy and provide an initial assessment of differentiation between the east coast of South Africa and the southeast coast of Madagascan.

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