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Fish larvae distribution among different habitats in coastal East Africa

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Fish larvae abundances, diversity and trophic position across shallow seagrass, coral reef and open water habitats were examined to characterize their distribution in coastal East Africa. Larvae were identified to family and analysed for abundance differences between sites and habitats, trophic level using stable-isotope analysis and parental spawning mode. Abundances differed greatly between sites with the highest numbers of larvae occurring in the open-water and seagrass habitats. Larval fish diversity was high across habitats with 51 families identified with small differences between sites and among habitats. Notably, larvae of abundant large herbivorous fishes present in reef and seagrass habitats were almost completely absent at all sampling locations. In the seagrass, demersal spawned larvae were more abundant compared with the reef and open-water habitats. Stable-isotope analysis revealed that fish larvae have a varied diet, occupying trophic level two to three and utilizing planktonic prey. This study offers new insights into distributional aspects of fish larvae along the East African coast where such information is sparse.

KEYWORDS

coral reef, fish larvae, seagrass, spawning mode, trophic position, western Indian Ocean

1 | INTRODUCTION

Fish larval dispersal and spatial patterns of abundance are a crucial factor influencing recruitment and management of fish stocks (Hjort, 1914; Huwer *et al*., 2016). Although the larval dispersal and early life history of economically important species in the northern hemisphere, and to some extent also in equatorial regions, are well studied (Leis *et al*., 2013), little is known about the early life history of marine coastal fishes of relatively limited commercial importance from the tropical regions (Levin, 2006). Seagrass beds close to coral reefs have increased abundance of fish species that utilize them as nursery habitats and for feeding migration (Berkström *et al*., 2013). The early life history of most teleosts in tropical coral reef and seagrass habitats is, regardless of adult life history, characterized by a pelagic larval stage, during which their main dispersal takes place (Cowen *et al*., 2000; Leis, 2010). In the past 20 years, the understanding of the dispersal of marine coastal fish populations has changed from seen as completely open to recruitment, to taking into account the complexity of self-recruitment and source–sink relationships (Caley *et al*., 1996; Crochelet *et al*., 2013). As larval distribution is largely dependent on currents, the flows around spawning grounds are what dictate dispersal or retention (Bakun, 2006; Wolanski & Kingsford, 2014). However, pelagic larvae do not simply drift with the currents (Paris & Cowen, 2004; Sponaugle *et al*., 2002) and Leis (2006) argues that although the pre-flexion stage of larvae should be considered planktonic with regard to the relative swimming abilities, the post-flexion stage should be viewed as nektonic, as this stage is more capable of prey capture, predator evasion and swimming against currents. This effectively means that the major dispersal of tropical marine coastal fish larvae primarily takes place during the pelagic larval stage (Hamner & Largier, 2012; Leis, 2006).

In addition, the pre-flexion stage larvae are not passive particles, but rather use their ability to migrate vertically in order to either stay in an area or distribute themselves horizontally (Brogan, 1994; Sponaugle *et al*., 2002). Several studies have pointed out that even at the very early stages, larvae migrate vertically following the general

plankton migrations in a trade-off between finding food and hiding from predators (Fortier & Harris, 1989; Leis *et al*., 2006). This migratory pattern is common in many studies from pelagic locations (Irisson *et al*., 2010), but for fish larvae residing on shallow reefs and in seagrass beds, the habitat structure might reduce the spatial scale at which they can migrate and in contrast to off-shore larvae, this in turn might affect how and where they find food, what organisms are available as food and also the possibility to hide from predators. In addition, flow-regimes might differ substantially between seagrass and reef (Björk *et al*., 2008), which, in turn, might affect larval composition of these different habitats based on the development state at hatching and swimming capabilities. Given that tropical and temperate regions differ in seasonal and daily temperature and light regimes, reproductive strategies in the northern hemisphere are not applicable for species residing in tropical habitats (Johannes, 1978). Most research on larval dispersal in the tropics has been carried out in the Caribbean Sea and the Great Barrier Reef, Australia, but there does not seem to be a consensus on to how to predict distances of dispersal, as species with similar modes of spawning and length of pelagic larval phase differ depending on local hydrodynamic conditions (Almany *et al*., 2017).

During the pelagic larval phase, starvation and predation are major limiting factors affecting larval survival, generally resulting in large cohorts of pre-flexion larvae but very reduced assemblages of post-flexion larvae (Miller *et al*., 1988; Sampey *et al*., 2007). Despite the common nature of the pelagic larval phase, larvae differ substantially in their state of development and dispersal during this time. This is a result of two distinct modes of reproduction that have evolved, namely demersal and pelagic spawning. The demersal mode is generally characterized by attaching larger and fewer eggs to a substratum and guarding them until hatching, whereas pelagic spawners shed their gametes into the open-water column, offer no parental care and generally have smaller but more numerous eggs with a substantially shorter (< 48 h) incubation period (Wittenrich, 2007). A crucial result of these two spawning modes is that demersal spawned larvae hatch at an advanced developed state, with functional eyes, developed mouthparts and swimming capabilities and that the hatching occurs in a relatively controlled environment (Wittenrich, 2007).

From a trophic point of view, fish larvae in the marine food web are generally seen as consumers of different stages of herbivorous copepods and at the same time, food for zooplanktivorous predators (Pepin & Dower, 2007). However, studies on the trophic role of fish larvae are scarce and examining gut contents can be difficult. As gape size for many marine teleost larvae generally correlates with an increase in body length (Krebs & Turingan, 2003), ontogenetic diet shifts also occur for an array of species (Llopiz, 2013; Llopiz & Cowen, 2009a). In a study by Østergaard *et al*. (2005), the authors describe a clear correlation between ontogenetic increase in gape size and prey size found in the guts of larvae of four different families of reef-associated fish. As many fish larvae have rapid gut evacuation or might suffer from regurgitation during capture (Fortier & Harris, 1989; Llopiz & Cowen, 2009b), the use of other means of trophic positioning than gut content analysis, such as stable-isotope analysis (SIA), might give useful insights into the trophic role of fish larvae and how they relate to other zooplankton groups.

For the western Indian Ocean (WIO), fish larvae distribution and species composition among habitats is, largely, understudied (Nordlund *et al*. 2014). In this region, coastal fish production supports livelihoods and is an essential source of animal protein. Fisheries have increased *c*. fivefold in this region since the 1960s and today most of the coastal fish stocks of the region are considered to be fully exploited (Laipson & Pandya, 2009). Given that seagrass beds and coral reefs experience increasing human pressure, it is important to understand the function of these habitats for fish recruitment and larval distribution to implement proper management actions.

To improve the understanding of distribution patterns of tropical fish larvae and their role in shallow reef and seagrass habitats, spatial differences in abundance of fish larvae in the upper water column (0–10 m) were investigated in the WIO region. Specifically, we examined how larval abundance, diversity, trophic position and spawning mode vary among sites and habitat types of seagrass beds, coral reefs and open water. This study offers necessary baseline data for future research along the East African coast.

2 | MATERIALS AND METHODS

2.1 | Field sampling

Sampling was aimed at pre-flexion fish larvae in nine different sites along the East African coast, including Zanzibar (Tanzania), the Tanzanian mainland and Mozambique, with sub-surface plankton net tows in 2013 and as close to the seagrass canopy as possible in 2014. The focus on pre-flexion stage larvae was chosen due to the young larvae's limited swimming ability, thus investigating, among other things, if parental spawning mode influenced larval location. The sampling in 2013 took place from late October to early December and included two sites on the west coast of Zanzibar: Changu Island and Fumba; two sites outside Kunduchi on the Tanzanian mainland: Mbudya and Mbudya Open; and two sites on the west coast of Inhaca Island in Mozambique: Barreira Vermelha and Ponta Puduine (Figure 1). Three different habitats, reef, seagrass and open water, were sampled at each site except for Changu Island where no open-water tows were carried out. All tows on each site, except in Fumba, were carried out for three consecutive days during daylight (typically ranging from 09.00 hours to 15.00 hours). Fumba was only sampled for 1 day in 2013, starting at the time of the lowest tide in daytime. The reef and seagrass habitats were sampled by means of sub-surface tows, ranging from right below the surface down to approximately 2 m, depending on waves, depth and bottom structure. The open-water tows were oblique facing away from the reef wall, starting at approximately 8–10 m depth and finishing at the surface. The reef tows were carried out for 15 min, 5–20 m from the reef crest on the side facing open sea (away from nearest shore). The seagrass tows were carried out for 15 min over a seagrass bed dominated by *Thalassodendron ciliatum* and close to the sampled reef. The open-water tows were carried out for 5 min as and close to the sampled reef as possible, where the depth was great enough and the risk of getting the net stuck on anything solid could be avoided. All tows were replicated twice and kept separate, resulting in six replicates per habitat for each site (except Fumba, as mentioned above). Sampling was conducted with a conical ichthyoplankton net measuring 1500 mm in length and 500 mm in width at the opening. The cod end was equipped with a

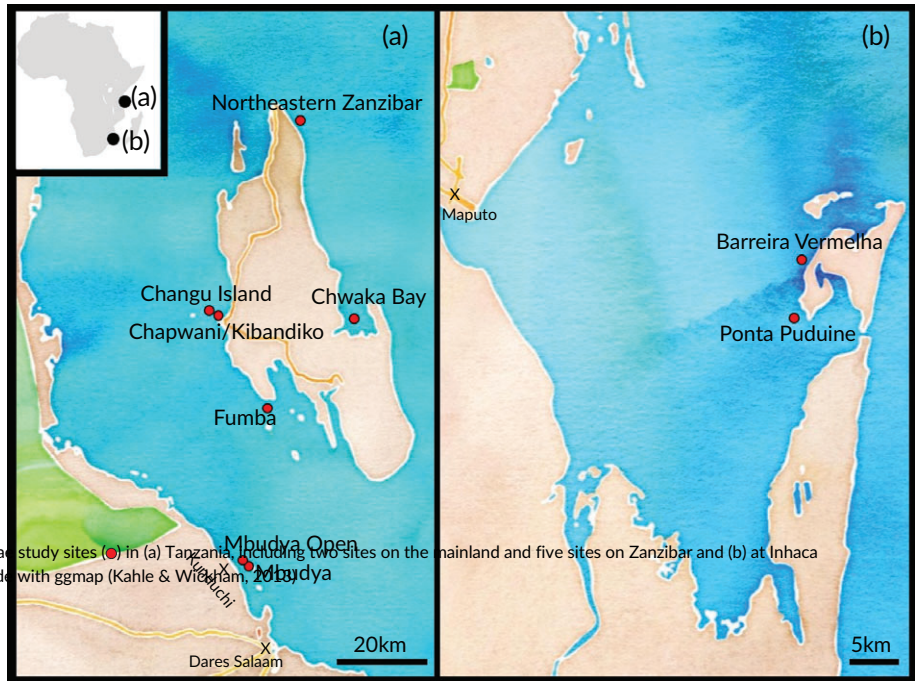

FIGURE 1 Location of fish larvae study sites (●) in (a) Tanzania, including two sites on the mainland and five sites on Zanzibar and (b) at Inhaca Island in Mozambique. Map made with ggmap (Kahle & Wickham, 2013)

300 μm mesh as the largest mesh size in the net. The net was towed 15 m behind small boats at a speed of 5 ± 1 km h^{-1} for the reef and seagrass habitats and 2 ± 1 km h^{-1} for the open-water tows. At Ponta Puduine, there was no reef structure *per se*, but rather scattered corals which only allowed towing above, as opposed to next to the reef structure. All sampling of the different habitats within each site was conducted within 1 km distance of each other. All samples were fixed in a 2% formalin and seawater solution immediately after sampling. Before shipping to Sweden, all samples were transferred to a 5% formalin solution for long-term storage.

Sampling in 2014 took place in early November to mid-December and was restricted to seagrass beds in Zanzibar, with two sites on the west coast: between the islands Chapwani and Kibandiko and Fumba; and two sites on the east coast: Chwaka Bay and north-eastern Zanzibar (Figure 1). Sampling was conducted in the same manner regarding net size, boats and speed as in 2013, but with seven tows per site over seagrass beds dominated by *T. ciliatum* as close to the canopy as possible, ranging between 0.75 and 6 m depth. Additionally, the ichthyoplankton net was fitted with a flow meter.

2.2 | Abundance, habitat preference, diversity and spawning modes

The total catch of fish larvae from all samples constituted the basis for abundance calculations and identification. Using Leis and Carson-Ewart (2004) and FAO species identification sheets (Fischer & Bianchi, 1984), larvae were identified to family and categorized according to one of the following developmental stages: yolk-sac stage, pre-flexion, flexion, post-flexion, or settlement stage larvae/juvenile. Yolk-sac stage larvae were kept separate, although Leis and Carson-Ewart (2004) classify them as pre-flexion, and any settlement-stage larvae were grouped together with juveniles. The family Syngnathidae does not have a larval stage and was classified as juveniles. Spawning modes for all identified families were defined as pelagic (broadcast spawners) or demersal in accordance with Leis and Carson-Ewart (2004), Choat (2012), Luiz *et al.* (2013) and FishBase (Froese & Pauly, 2014). Substratum spawners, mouth brooders and the syngnathids with brood pouches of different morphologies (Wilson *et al.*, 2001) were all grouped together as demersal spawners, providing some form of parental care whether it is guarding, brooding or simply deciding where the eggs are supposed to hatch. Prior to analysis of spawning modes, the monodactylids, isonids and schindleriids were removed due to the species-specific spawning modes of the first and the lacking knowledge about the biology and spawning modes of the latter ones (Fischer & Bianchi, 1984; Leis & Carson-Ewart, 2004). The geographic distribution of all identified families included in the sampled locations was verified using FishBase (Froese & Pauly, 2014), Mwaluma *et al.* (2014) and OBIS (2016).

2.3 | Trophic level: stable-isotope analysis

Fish larvae and zooplankton from the reef habitats were used for SIA from five sites (Mbudya, Mbudya Open, Fumba, 2013, Barreira Vermelha and Ponta Puduine), which represented species composition found on other sites and habitats. To cover the range of at least two trophic levels and different carbon sources, we selected five zooplankton groups, based on similar size and taxonomy (small copepods, < 1 mm; large copepods, 2.5–3 mm; planktonic shrimps, 3–4 mm; chaetognaths, 5–15 mm; and crab larvae, 1–3 mm), which included plankton prey smaller than the smallest fish larvae found and seven benthic plant taxa (*Gracilaria* sp., *Halimeda* sp., *Hypnea* sp., *Padina* sp., *Ulva* sp., *Thalassia* sp., *Zostera* sp.). The dry mass of each replicate for SIA was for the different groups; zooplankton > 0.5 mg, benthic plants > 4.0 mg and fish larvae > 0.1 mg. The small copepods selected for analysis were abundant in the digestive tract of the chaetognaths

(P. Hedberg, January 2014, personal observation) and were chosen, therefore, as herbivore baseline (trophic-level two) and the carnivorous chaetognaths as trophic-level three. Only adult copepods were selected and algae and seagrasses were identified to genus using Oliveira *et al.* (2005). For Barreira Vermelha and Fumba 2013, all $\delta^{15}N$ values of taxa other than the small copepods were raised by 0.33‰ and 0.64‰, respectively, as these are the factors by which the small copepods differed from their mean. All $\delta^{15}N$ values for Mbudya, Mbudya Open and Ponta Puduine were lowered by 0.22‰, 0.35‰ and 0.39‰, respectively. To compare trophic levels between sites, taxa were standardized using the average small copepod $\delta^{15}N$ value of 5.92‰. To correct for any effect of formalin to isotopic $\delta^{13}C$ signatures, an average depletion of 1.65‰ as suggested by Sarakinos *et al.* (2002) was considered.

For SIA of fish larvae, specimens were selected and classified into size groups by upper jaw length (L_{UJ}) as an indicator of mouth size (Salas-Berrios *et al.*, 2013). Larvae were divided into four groups: yolk-sac stage larvae with no visible mouth, small, medium and large mouth. Mouth size did not necessarily correspond to developmental stage. As larvae were quite few (n = 190) and mass was a major concern for SIA, a general measure of spread did not work for classification. Instead, large was considered anything that was twice the size of small with small being <0.2 mm and large >0.4 mm and anything in between as medium. L_{UJ} was measured with Jenoptik ProgRes Capture Pro 2.8.8 software, from the tip of the snout to the posterior end of the maxilla. In preparation for SIA, all specimens were soaked for approximately 6 h in deionized water, pooled within site and group, placed in tin capsules and dried at 60°C for 24 h. All samples were sent to the University of California Davis, USA, where stable isotopes of carbon and nitrogen ($\delta^{13}C$ and $\delta^{15}N$) were measured. Trophic isotope fractionation, *i.e.*, the difference between two trophic levels, was calculated as the difference in mean $\delta^{15}N$ value for chaetognaths (trophic-level three) and for small copepods (trophic-level two). All sites were merged to represent the trophic level of each taxa and different fish larvae groups.

2.4 | Data analysis

Abundance calculations and analyses between sites and among habitats were based on total catch and spawning mode specific analysis and diversity was based on identified larvae. As sites and habitats were sampled differently and no flowmeter was fitted to the ichthyoplankton net in 2013, the flow for all 2013 samples was standardized using the mean flow per minute of the 2014 samples: $1{,}00{,}000n(t\bar{f})^{-1}$ = larvae 100 m^{-3}, where n is the number of larvae, t is time sampled and $\bar{f}$ is mean flow per minute based on the 2014 samples. All samples in 2014 were analysed with each tow's actual flow: $1{,}00{,}000\ nV^{-1}$ = larvae 100 m^{-3}, where n is number of larvae and V is the volume (litres) filtered.

All analyses were conducted in R (R Core Team, 2012). The effects of site, habitat and spawning mode on fish larvae abundance were analysed using linear mixed effects models with the package lme4 in R (Bates *et al.*, 2012). All three models were tested individually with an ANOVA and a Tukey HSD test in the package multcomp in R (Hothorn *et al.*, 2008). The effect of site was analysed with habitat as random factor, the effect of habitat was analysed with site as random factor and the effect of spawning mode was analysed for each habitat with site as random factor. Simpson's diversity index was calculated using the diversity function in the package vegan in R (Oksanen *et al.*, 2013).

3 | RESULTS

3.1 | Abundance, habitat preference and diversity

A total of 2279 fish larvae in various developmental stages were caught across the nine different sites. Out of these, 1834 individuals spanning across 51 families were identified, leaving 445 individuals unidentified (see Table 1 for the most dominant families). The unidentified larvae consisted mostly of yolk-sac and pre-flexion larvae; most of the latter were too damaged to allow identification. The pre-flexion stage was represented in 46 families. Most families occurred in all three habitats without preference. Apogonids, blennids and gobiids occurred in very high numbers throughout all habitats and in both years. Pinguipedids were caught only at Fumba in 2013 and leiognathids only at Inhaca Island (*i.e.*, at Barreira Vermelha and Ponta Puduine). Schindleriids were only caught in the post-flexion stage and all scarids caught in 2014 were either post-flexion or juvenile stage individuals.

Fish larvae abundance varied substantially among sites (Figure 2a). The mean larvae abundance 100 m^{-3} ranged from 2.5 100 m^{-3} (Changu Island) to 92.6 100 m^{-3} (Fumba 2014), and in general, there was a significant separation among sites. (ANOVA, $F_{9,118}$ = 10.637, P < 0.05, all interactions not shown). Fumba on Zanzibar reached very high abundances in both years, indicating that this site has a high fish larval productivity. The number of families found at each site differed substantially (Figure 3a), but were not necessarily coupled with abundances. The open-water habitats had the highest mean larvae abundance (35.1 100 m^{-3}) among habitats in 2013 (ANOVA, $F_{2,90}$ = 7.531, P < 0.05), whereas the mean abundances in the reef and seagrass habitats were 13.8 and 18.5 100 m^{-3}, respectively, and not significantly different from each other (P > 0.05) (Figure 2b). No major diversity differences could be detected among habitats were 2013, whereas the seagrass habitat in 2014 showed clearly lower Simpson's diversity index compared to all habitats in 2013 (Figure 3b).

3.2 | Spawning modes

A comparison of larvae with regard to spawning modes showed a distinct separation in the seagrass habitats, where the demersally spawned larvae were more common than pelagically spawned larvae, both in 2013 (ANOVA, $F_{1,32}$ = 4.077, P < 0.05) and in 2014 (ANOVA, $F_{1,28}$ = 8.867, P < 0.01), making up 64.3% and 89.4% in 2013 and 2014, respectively, of the total catch in the seagrass habitats (Figure 4). For the two other habitats, both spawning modes were present, although they did not differ from each other (Reef: ANOVA, $F_{1,32}$ = 0.052, P > 0.05, Open water: ANOVA, $F_{1,22}$ = 1.014, P > 0.05). *Spratelloides* Bleeker 1851 is the only genus within the clupeid family in tropical waters that spawn demersal eggs (Leis & Carson-Ewart, 2004). As larvae were identified to family level,

TABLE 1 Dominant families (≥ 0.5% of total catch) of fish larvae caught in different East African coastal habitats with numbers (*n*) from actual catch across all habitats and both years

	Habitat				Larval developmental stage				Total	
Family	Open (*n*)	Reef (*n*)	SG13 (*n*)	SG14 (*n*)	Preflexion (*n*)	Flexion (*n*)	Postflexion (*n*)	Juvenile (*n*)	(*n*)	% Of all families Σn[a]
Apogonidae[b] (cardinalfishes)	39	27	98	76	239	1	–	–	240	10.5
Blennidae[b] (blennies)	14	20	20	56	102	–	5	3	110	4.8
Callionymidae[cg] (dragonets)	3	4	4	3	7	1	6	–	14	0.6
Carangidae[c] (jacks)	3	8	4	1	12	1	1	2	16	0.7
Clupeidae[c] (sprats, sardines & herrings)	21	22	19	29	91	–	–	–	91	3.9
Engraulidae[c] (anchovies)	2	1	4	5	12	–	–	–	12	0.5
Gobiidae[b] (gobies)	61	53	79	466	640	1	12	6	659	28.9
Labridae[c] (wrasses)	2	1	5	11	8	–	6	5	19	0.8
Leiognathidae[b,d] (ponyfishes)	11	11	47	–	68	1	–	–	69	3.0
Microdesmidae[b] (dartfishes)	1	1	22	2	25	1	–	–	26	1.1
Monacanthidae[b] (filefishes)	2	5	5	1	10	–	–	3	13	0.6
Mullidae[c] (goatfishes)	1	12	12	–	23	1	1	–	25	1.1
Pinguipedidae[c,e] (sandperches)	17	30	10	–	57	–	–	–	57	2.5
Pomacentridae[b] (damselfishes)	8	15	23	34	78	–	2	–	80	3.5
Scaridae[c,f] (parrotfishes)	1	–	–	30	1	–	20	10	31	1.4
Schindleriidae[g] (infantfishes)	–	–	–	12	–	–	12	–	12	0.5
Sciaenidae[c] (drums)	3	2	8	–	11	2	–	–	13	0.6
Sillaginidae[c] (smelt–whitings)	17	16	16	–	45	2	2	–	49	2.2
Sparidae[c] (porgies)	3	7	2	–	9	–	3	–	12	0.5
Syngnathidae[b] (pipefishes)	3	23	18	13	–	–	–	57	57	2.5
Tetraodontidae[b] (puffers)	2	4	7	4	17	–	–	–	17	0.7
Tripterygiidae[b] (triplefin blennies)	1	11	32	16	60	–	–	–	60	2.6

Open, Open water; SG13, seagrass beds sampled in 2013; SG14, seagrass beds sampled in 2014.
[a] Σn, Grand total of all larvae caught (2279).
[b] Classified as demersal spawners.
[c] Classified as pelagic spawners.
[d] Only caught Barreira Vermelha and Ponta Puduine around Inhaca Island in 2013.
[e] Only caught Fumba in 2013.
[f] All individuals caught in 2014 (SG14) are either postflexion or juvenile stage.
[g] All individuals caught are postflexion stage.

the possibility that they constituted a major portion of the clupeids could not be ruled out. We ran the analysis with them as either pelagic or demersal spawners and this did not change the outcome (data not shown). Only one species in the family Siganidae is known to spawn pelagic eggs (Choat, 2012). This was also considered during the analysis in the same manner as mentioned for the clupeids, but this did not change the outcome (data not shown).

3.3 | Trophic level

The SIA showed that Barreira Vermelha and Fumba 2013 had lower $\delta^{15}N$ values (5.59‰ and 5.28‰, respectively) than Mbudya, Mbudya Open and Ponta Puduine (6.14‰, 6.27‰ and 6.31‰, respectively) based on the trophic position of small copepods (trophic-level; two Figure 5). The trophic isotope fractionation was 2.51 based on chaetognaths (8.43‰) and the small copepod group (5.92‰). The adjusted $\delta^{15}N$ value for fish larvae ranged from trophic-level two to four. There are, however, a few uncertainties with the estimated trophic-level four, since the calculated level four is at 10.94‰ (using the trophic-enrichment factor of 2.51) and the yolk-sac stage larvae at site Fumba 2013 are at 10.07‰ and the medium larvae at site Mbudya Open are at 11.26‰. Yolk-sac stage larvae were the only larvae that were consistently at trophic-level three or higher. The $\delta^{13}C$ values of the zooplankters and fish larvae ranged from −17.02‰ to −23.08‰.

4 | DISCUSSION

This study demonstrates distribution patterns and diversity of fish larvae in tropical habitats and shows substantial differences in fish larvae abundance among different habitats and among sites. The overall highest abundance of larvae was reached in the open-water habitats in 2013 and was as high in the seagrass in 2014. The seagrass beds had high dominance of demersally spawned larvae in 2013 and 2014, whereas there were no differences between pelagically and demersally spawned larvae in the reef and open-water habitats in 2013. The

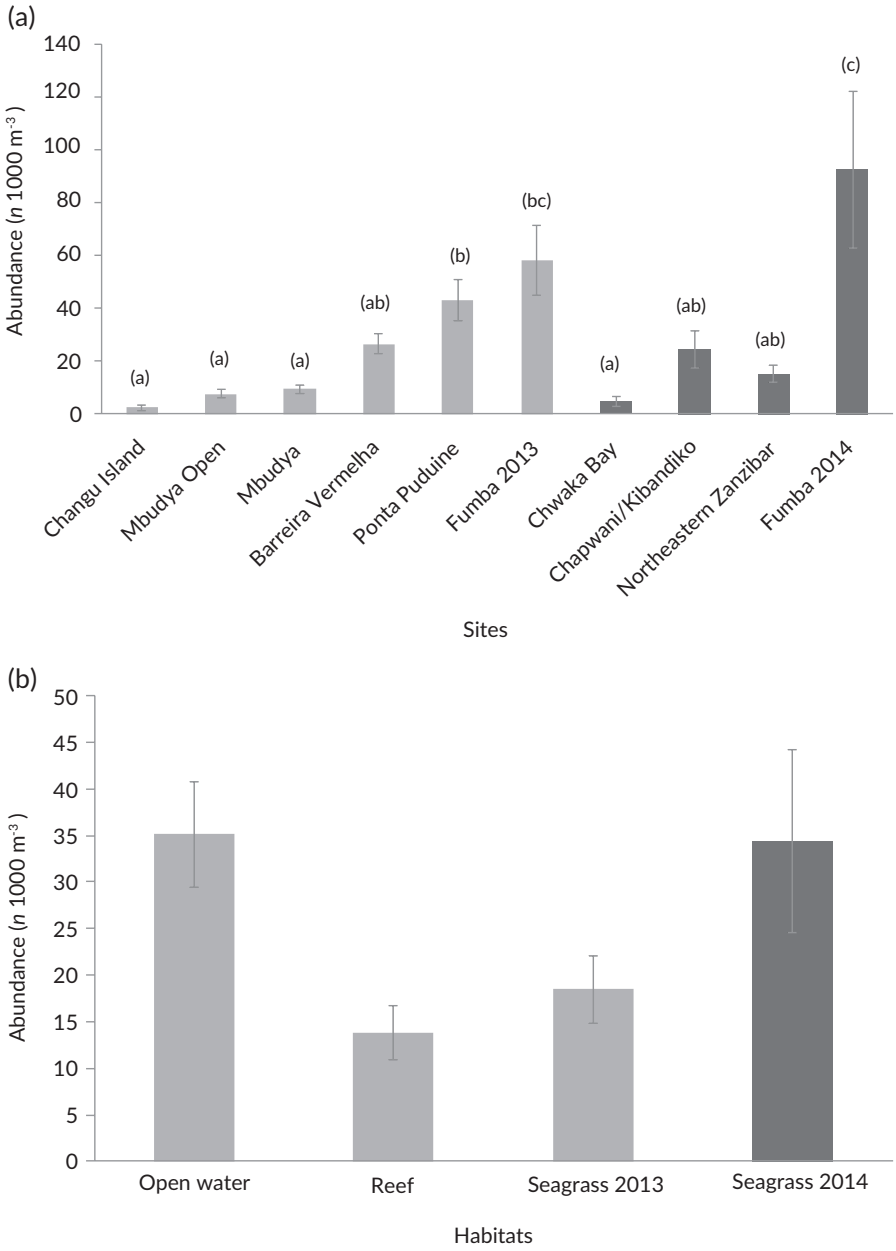

FIGURE 2 Mean (± SE) fish larval abundances across different (a) sites and (b) habitats 2013 and 2014. Different lowercase letters show significant differences between columns ($P < 0.05$). (▫) 2013, and (▪) 2014

high number of families observed across all habitats is an indication of the high diversity of fish larvae in this tropical region.

4.1 | Differences in fish larvae abundance and spawning modes across sites and habitats

Factors influencing fish larvae abundances at the particular sites of the current study are probably flow regimes and the general condition of the reefs and seagrass beds, as well as seasonality in spawning, connectivity and fishing pressure. Many of these factors have neither been studied nor published to any greater extent in conjunction with larval investigations for the areas in question. Notably, Fumba, which had a very high abundance of larvae in both years, is located in the shallow and partially protected conservation area of Menay Bay, Zanzibar (Tyler *et al.*, 2011). As no published data are available on localized flow in the area, there is little room for speculation regarding this. However, tides are not only following a north–south flow regime (Torell *et al.* 2007), but are heavily influenced by reefs, islands and sandbanks in the area. Whether this gives rise to the so called 'sticky-water effect' (Andutta *et al.*, 2012), where larvae are retained for longer periods of time than otherwise expected remains unknown, but certainly warrants further investigation of this particular area.

As the open-water tows had high abundances of larvae, there might be reasons to assume that fish larvae are increasingly abundant in the deeper strata. This pattern has been shown by studies sampling in deeper offshore waters (Irisson *et al.*, 2010; Paris & Cowen, 2004), but is also confirmed for shallow habitat sampling by Leis (1986). The reasons for this could be predator avoidance as larvae are harder to spot at less illuminated depths, to avoid advection as deeper flows might be moderate compared to surface currents and to avoid harmful

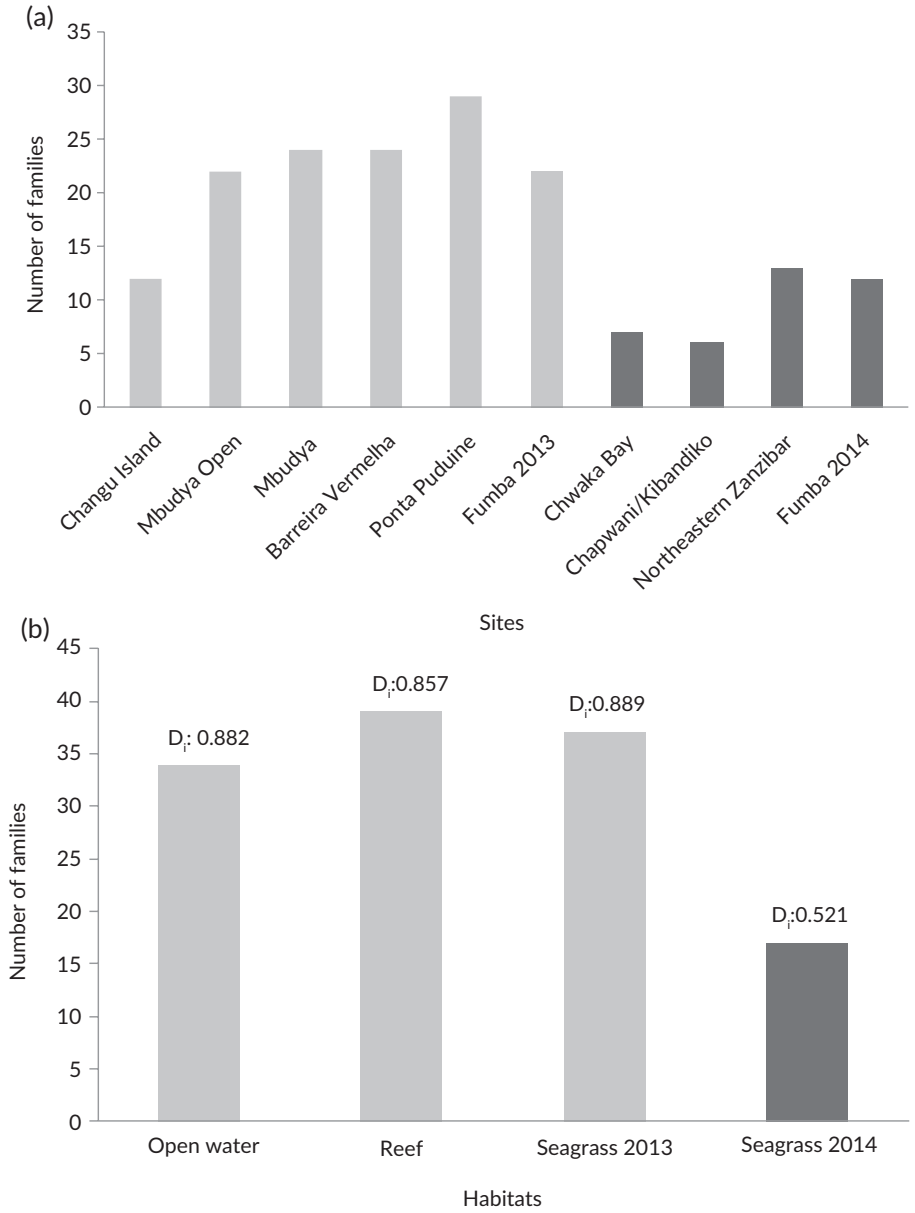

FIGURE 3 Total number of fish larvae families across different (a) sites and (b) habitats 2013 and 2014. Simpson's diversity index (1 – *D*) is given above each habitat. (▨) 2013, and (■) 2014

UV radiation (Irisson *et al*., 2010; Paris & Cowen, 2004). Typically, when sampling for fish larvae with tow nets, sampling is conducted either further offshore from large boats with advanced equipment and at much greater depths (25–200 m) than in the current study (Leis, 1993; Llopiz & Cowen, 2009b; Østergaard *et al*., 2005). As all sites in general were part of very shallow larger areas (< 15 m depth), the use of advanced deeper-water equipment was not feasible. As stated by Nordlund *et al*. (2014), however, the entire WIO coastal zone is understudied whereby near-shore sampling, as described by Leis (1986) and Mwaluma *et al*. (2010), could provide baseline data.

The seagrass habitats had high fish larvae abundances, particularly in 2014 and there was a higher abundance of demersally spawned larvae in the seagrass habitats compared with the reefs and open-water habitat. The reason for the spawning mode dependent abundance in the seagrass habitats can probably be attributed to the calmer currents and hydrodynamics of the seagrass beds (Björk *et al*., 2008), as they were mostly located in a relatively protected zone between the reef and the shore. If the reef structure attenuates wave action and creates calmer conditions towards the shore and the seagrass bed further reduces flows and wave action (van der Heide *et al*., 2011; Parsons *et al*., 2015), conditions for retention of larvae that are capable of weak swimming already in the pre-flexion stage should be favourable. The seagrass habitats at Inhaca Island (Barreira Vermelha and Ponta Puduine) in southern Mozambique are, however, not located between the reef and the shore, but rather face open water. The findings that the demersally spawned larvae were more abundant than pelagically spawned larvae in seagrass beds, but not in the other habitats, indicate that there might be a higher retention of larvae in this habitat. If retention is higher, there might be a higher level of self-recruitment of demersally spawned

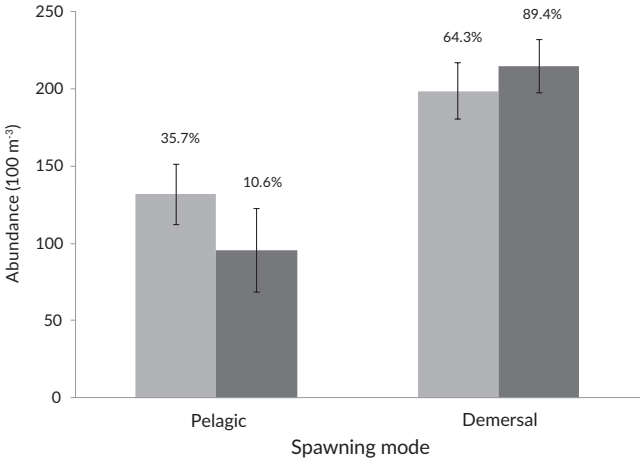

FIGURE 4 Mean (± SE) fish larval abundance for the two different spawning modes (demersal and pelagic) in the seagrass habitats 2013 and 2014. The number above each bar is the percentage contributions of each spawning mode based on total catch of fish larvae in the seagrass habitat. (▫) 2013, and (▪) 2014

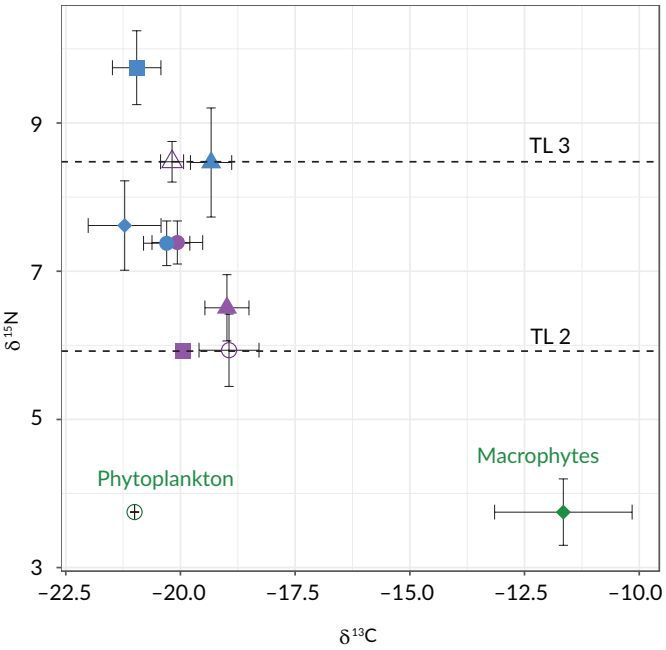

FIGURE 5 Mean (± SE) stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope ratios across all reef sites merged for taxa and type of fish larvae. - - - TL - - -, Trophic level. A mean value for marine phytoplankton from Burkhardt *et al*. (1999) is included as reference (○) Phytoplankton, (◆) Macrophyte, (■) CopS, (●) CopL, (▲) Shrimp, (○) Cheatognaths, (△) Yolk-sac larvae, (■) Small mouth, (●) Medium mouth, and (▲) Large mouth (◆)

larvae in the seagrass habitat. As larvae were identified to family level, it remains unknown if they belong to species primarily found in seagrass beds or in other shallow-water habitats as well. Even if the larvae were not spawned in the seagrass habitat, advection to or actively seeking this habitat could be a way of retaining their position close to the natal habitat or to avoid further advection. This is a research area of small-scale self-recruitment currently lacking in the literature that should be further investigated.

4.2 | Comparison between larval and adult life stages

The present study found no differences in fish larvae diversity among habitats. However, the larval community composition differed substantially from the adult composition in both the reef and seagrass habitats (in Changu Island, Mbudya, Mbudya Open and Barreira Vermelha). An observational study on adult fish communities conducted at the same time as our fish larval surveys in 2013 showed that the five families dominating adult fish biomass on the reef were Acanthuridae, Chaetodontidae, Labride, Pomacentridae and Scaridae and in the seagrass beds Acanthuridae, Labridae, Lethrinidae, Scaridae and Siganidae (Skoglund, 2014), which were also very abundant in terms of numbers (P. Hedberg, October to December 2013, personal observation). All these families are almost completely absent from the larval tows of 2013, but post-flexion and juvenile scarids (but no pre-flexion individuals) were caught in the seagrass habitat in 2014. The adult fish composition, which was observed by visual census line-transects (Skoglund, 2014), however, most likely underrepresents small, cryptic and nocturnal species. The most abundant coastal fish larvae found here belonged to the families Apogonidae, Blennindae and Gobiidae, which have largely small, cryptic and often nocturnal (Apogonidae) fishes, explaining part of the discrepancy between adult and juvenile fish families.

The acanthurids, scarids and siganids, all belong to the large herbivores that are very important for the well-being of reefs and seagrass beds (Hughes *et al*., 2003) and one reason for the absence of the larval stages could be the fact that they are pelagic spawners, making their eggs and larvae more prone to being swept offshore. However, being swept offshore should mean that all pelagically spawned larvae would have the same fate and that they would not have shown up in the tows, or at least would have been very scarce. As this is not the case for many of the pelagically spawned larvae found in our study, another scenario seems more likely. Most genera of adult fishes of the above-mentioned families with pelagic spawning mode commonly spawn on the edge of the reef, either in pairs or in large aggregations and at times when eggs are likely to be dispersed offshore to avoid predation (Domeier, 2012; Molloy *et al*., 2012). This strategy makes use of eddies and gyres, returning the larvae to either their natal reef or a new one at time of settlement (Colin, 2012; Hamner *et al*., 2007) and coupled with seasonality in spawning, might be a more reasonable explanation for their absence. In either case, pre-flexion larvae of the dominating adult families are probably not found in the vicinity of reefs and seagrass beds, but further offshore. The presence of post-flexion and juvenile scarids in the seagrass tows of 2014 supports that scarids and other families spend the first time after hatching offshore, then seeking seagrass beds at time of settlement.

4.3 | Trophic level of fish larvae

The study showed that fish larvae are part of the pelagic zooplankton food web, consuming mainly other zooplankters that in turn consume carbon from pelagic primary production, as macrophytes have less negative $\delta^{13}C$ values (Michener & Kaufman, 2007).. Possible formalin induced $\delta^{13}C$ depletion was considered at an average of 1.65‰

(Sarakinos *et al*., 2002) but created no overlap between animals and macrophytes, thus formalin preservation had no influence on $\delta^{13}C$ values. While the main food for most reef-associated larval fishes are various developmental stages of copepods (Llopiz & Cowen, 2009a; Østergaard *et al*., 2005), development is vastly different for many families (Leis & Carson-Ewart, 2004) and mouth size does not necessarily correlate with developmental stage. While mouth size probably is the most crucial factor in prey selection among larvae, some larvae do not move on to larger prey as soon as they would be able to do that (Llopiz & Cowen, 2009a). The only larvae that were at trophic-level three or higher were the yolk-sac stage larvae, which is most likely the maternal $\delta^{15}N$ signal, as no prey had been ingested (Jardine *et al*., 2008). For accurate trophic positioning of fish larvae, mouth size could be used, but in combination with a division of at least family or genus level.

4.4 | Concerns regarding fish stock management

Management of marine fish stocks and fish populations should recognize the importance of fish larval dispersal since movements of adult and juvenile fishes are quite well known, but dispersal patterns of larvae and predictions regarding this are not (Palumbi, 2004). Sale *et al*. (2005) point out that there is much difficulty in predicting source–sink relationships and the dispersal or retention of larvae between areas if the hydrodynamics of an area is not known. The importance of hydrodynamics on a very fine scale is supported by Leis (1986, 2007), who argues that in constructing dispersal models, general assumptions should not be made as spawning mode, location and conditions vary among species. These factors influencing larval dispersal should be implemented in management of fish stocks as they are understudied in general, but particularly in the WIO. This warrants further research on the dispersal of fish larvae, especially in these data-poor regions.

As shown in this study, there is a difference in larval composition in seagrass beds compared with nearby reef and open water habitats regarding the spawning mode. This finding supports that seagrass beds are important habitats for fish recruitment (Duarte *et al*., 2008) and that spawning mode is of importance. Also, as pointed out by Kenworthy *et al*. (2010), the interconnectivity between reef and seagrass habitats is a key feature in preserving biodiversity and not only habitats perceived as valuable, like coral reefs, should for this reason be considered. Further, models trying to predict the spatial fate of eggs and larvae indicate that dispersal and retention is dependent on seasonal cycles of hydrodynamics as well and relatively short dispersal on the order of tens of kilometres rather than hundreds of kilometres (Cowen *et al*., 2003). The short dispersal distances suggested by Cowen *et al*. (2003) indicate that even if dispersed rather than retained, management need to consider distances of dispersal. The published literature on dispersal and retention of larvae points in both directions, which, further adds to the complexity of the topic. Some studies focusing on a few particular species have observed a clear self-recruitment pattern (Almany *et al*., 2007; D'aloia *et al*., 2013), while others see a clear dispersal pattern (Eble *et al*., 2011; Harrison *et al*., 2012). It is therefore important to approach the question of drivers behind dispersal and retention, respectively, on a case-to-case basis taking all of these factors into account. Whether the demersally spawned larvae in this study were retained at each site or originated from elsewhere is unknown, but our findings warrant further studies regarding the possible self-recruitment within seagrass beds. Understanding larval dispersal is important in management of fish stocks and the marine resources since growing human populations along the WIO rely on them for food and income (O'Donnell *et al*., 2017).

4.5 | Future directions

The WIO region is changing rapidly due to anthropogenic activities and the exact effects this will have on habitat loss, eutrophication, temperatures and planktonic productivity affecting larval distribution and survival are not clear (Munday *et al*., 2009). An understanding of how different habitats are utilized by fish larvae is vital to maintain populations. As there are very few studies on fish larval ecology in the WIO, more effort should be directed towards research on the early life history of fishes with regards to their dispersal and how this will be affected by human activities and future environmental change, particularly in the WIO, considering that this region has been the fastest warming tropical seascape in the world over the past half century (Roxy *et al*., 2014). Therefore, any general conclusions drawn there, might aid research for other tropical locations.

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Author contributions

P.H., F.F.R. and M.W. conceived and designed the sampling design. M.G. and N.S.J. chose sampling sites, provided work permits and handled logistics. P.H. and F.F.R carried out the sampling and data analysis. P.H. identified the fish larvae, P.H. and M.W. wrote the manuscript; all other authors provided inputs to the manuscript.

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