



# Composition and diversity of larval fish in the Indian Ocean using morphological and molecular methods

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## Abstract

Although vital in fisheries management, no comprehensive studies on ichthyoplankton have been conducted in Sri Lankan waters in the north central Indian Ocean hitherto. Hence, this study is the first detailed account of diversity and species composition of larval fish based on samples collected during the southwest monsoon in 2018. In total, 80 species belonging to 69 families were identified using morphological and molecular methods targeting the COI gene. The larval fish diversity varied significantly between regions: east (North East, Central East, and South East) and west (North West, South West, and South). In their larval stages, mesopelagic families were associated with the offshore waters whereas demersal and pelagic families were related with shelf regions in the South, South East, and Central East. The larvae of pelagic families are likely dispersed by the South Monsoon Current from the west to the east regions, while demersal fish seem to be confined to the same area as conspecific adults. The most abundant larval species observed were *Selar crumenophthalmus*, *Cubiceps pauciradiatus*, and *Dipterygonotus balteatus*. High abundances of several commercially important larval tuna species were found in the South East, Central East, and South regions indicating that these waters could be important nursery grounds. Furthermore, *Callionymus simplicicornis* was recorded for the first time in the Indian Ocean, and seven additional species were found new to Sri Lankan waters. The results from this study also highlight the importance of using combined morphological and molecular methods and the need for strengthening fish nucleotide databases in poorly studied areas of the Indian Ocean.

**Keywords** Ichthyoplankton · Species assemblages · COI gene · Spawning · Sri Lankan waters

## Introduction

Ichthyoplankton studies not only provide valuable information on the species richness and spawning activity of fishes but also identify nursery areas for larval fish (Ayala et al. 2016; Ahern et al. 2018). Traditionally, ichthyoplankton samples have been identified based on their meristic, morphometric, and pigmentary characteristics (Rodriguez et al. 2017).

However, in some cases, the use of available descriptive information to identify ichthyoplankton to species level has led to misidentification (Fox et al. 2005). The recent applications of molecular techniques have to a large degree solved this issue and significantly improved knowledge on ichthyoplankton diversity around the globe. In fact, in the recent years, higher larval diversity has been reported in several studies using molecular methods in temperate and tropical marine ecosystems. In the oligotrophic areas of Sargasso Sea, 154 species from 50 families were discovered combining morphological and molecular methods (Ayala et al. 2016). In the southeastern Gulf of California, 47 novel species were found after analyzing ichthyoplankton samples using molecular techniques (Ahern et al. 2018). Likewise, in the central Red Sea, 62 new larval fish families were discovered using a combination of morphological and DNA barcoding approaches (Isari et al. 2017).

In tropical Indian Ocean regions, only few larval identification studies have been described, mostly based on morphological features. Hence, these areas could benefit enormously

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of the advantages of molecular methods to identify ichthyoplankton, combined with morphology (Leis 2015). As DNA barcode-based studies rely on the information provided in databases, expansion of these by submission of DNA sequences is invaluable. Indeed, a study using DNA barcoding found an underestimation of species diversity from both sides of the Indian Ocean (Zemlak et al. 2009). This has been also observed in other studies where 115 adult fish species, including members of the commercially important families Scombridae, Carangidae, Lutjanidae, and Clupeidae, were targeted using molecular methods (Lakra et al. 2011). Taxonomic studies combining morphological and molecular methods on larval and adult fish from the Indian Ocean are scarce (Zemlak et al. 2009; Lakra et al. 2011; Collet et al. 2017). In addition, knowledge concerning the diversity of larval fish in Sri Lankan waters is almost lacking. The adult diversity, however, is known to some extent, mainly based on morphological studies. Recent work exhibited high species diversity in the waters around Sri Lanka and adjacent areas (Joshi et al. 2016; Krakstad et al. 2018). During the same survey as this study, Krakstad et al. (2018) recorded more than 400 species and 100 families of adult fish. Bottom trawl catches from their study showed the South East region to have the highest diversity as compared to the other regions. They further revealed that demersal fish families, Leiognathidae, Diodontidae, Acanthuridae, and Carangidae, dominated in the inner shelf area, whereas in the outer shelf areas, Lutjanidae, Lethrinidae, Carangidae, and Serranidae were abundant.

In the Indian Ocean, monsoon winds play an important role generating currents, waves, variations in sea surface temperature, and other abiotic factors which influence fish behavior, seasonality, distribution, and abundance (Subarna 2018). This can be especially observed during southwest monsoon period, where a distinct pattern in physical properties and productivity characteristics clearly distinguish the eastern and western regions (de Vos et al. 2014; Krakstad et al. 2018). The sea surface temperature (SST) distribution demarcates the survey area into two main distinct zones, a warmer east and a cooler west (Krakstad et al. 2018). Their investigations showed that salinity contrasted the SST with east areas having comparatively lower values (influence from river inflow from the Bay of Bengal) than waters west of Sri Lanka. Furthermore, the east coast is less productive than the west (Yapa 2000; Krakstad et al. 2018).

In the present paper, the larval fish species diversity and composition in the Indian Ocean were mapped for the first time using both molecular and traditional (based on morphological and meristic features) approaches in parallel. We hypothesized that (i) the abiotic (temperature, salinity, and oxygen) and biotic (Chlorophyll *a*, zooplankton) differences in the east and west regions play an important role in shaping overall diversity and abundance patterns of larval fish and (ii)

shallow and off shelf waters are important in structuring demersal, pelagic, and mesopelagic larval fish families. The east region is a combination of polygons North East (NE), Central East (CE), and South East (SE), while the west region is the remaining survey area consisting of strata North West (NW), South West (SW), and South (S) (Fig. 1 and Krakstad et al. 2018).

## Materials and methods

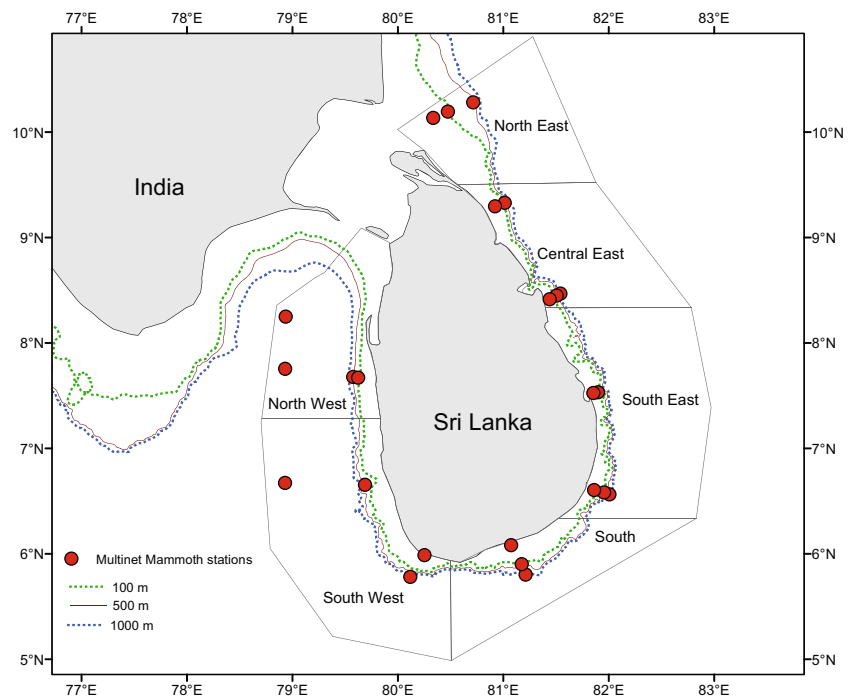
### Study site and sample collection

The ecosystem survey on the R/V Dr. Fridtjof Nansen in Sri Lankan waters (located between latitudes 5° 24' and 10° 23' N and longitudes 78° 55' and 82° 25' E) was conducted from 24 June to 16 July 2018. The time frame overlapped with the southwest monsoon period (de Vos et al. 2014). The geographic area investigated was subdivided into six polygons as NE (18,071 km<sup>2</sup>), CE (18,896 km<sup>2</sup>), SE (28,780 km<sup>2</sup>), S (16,231 km<sup>2</sup>), SW (33,746 km<sup>2</sup>), and NW (18,397 km<sup>2</sup>) (Fig. 1). These polygons were predefined for management purposes based on previous oceanographical studies (Krakstad et al. 2018). There is a relatively narrow continental shelf and a steep slope in most regions off Sri Lanka with 500 m depth contour delineating the shelf and deep waters.

A shipboard conductivity, temperature, and depth profiler (Sea Bird 911 CTD), with an oxygen sensor and a fluorometer attached to a 12-bottle rosette system, was used to measure vertical distributions of temperature, salinity, and oxygen in the waters around Sri Lanka (Krakstad et al. 2018). Zooplankton was collected using a WP2 ring net with a diameter of 0.56 m and equipped with a 180 µm mesh size. After retrieval, the WP2 net sample collected at the cod end bucket was transferred into a Motoda splitter for dividing into equal halves. One-half was preserved in 4% formaldehyde for species composition analyses at the laboratory. The other half was used for obtaining size fraction information on zooplankton biomass (Krakstad et al. 2018). The total biomass (g m<sup>-2</sup> dry weight, at 0–30 m) corresponding to larval fish stations was used in this study (Fig. 1).

Larval fish were collected using a Hydro-Bios Multinet Mammoth (1 m<sup>2</sup>, 300 µm, serial number 2000218) single net at different stations (Fig. 1). The net hauls were taken obliquely from ~25 to 0 m at stations with a 30 m bottom depth and ~100 to 0 m at stations with a bottom depth > 100 m using a single net. The net was gently rinsed, and the sample was collected from the cod end. Visible larval fish were removed from the total sample, photographed (Leica M80 10,450,167 stereomicroscope and a Nikon D610 DSLR camera) and transferred individually to Eppendorf tubes containing 96% ethanol. The rest of the Multinet Mammoth sample was split into two halves, using a Motoda

**Fig. 1** Locations of Hydro-Bios Multinet Mammoth stations during the survey 24 June to 16 July 2018 around Sri Lanka. The survey region is divided into 6 polygons as shown in the map: North East (NE), Central East (CE), South East (SE), South (S), South West (SW), and North West (NW). Red filled circles indicate Multinet Mammoth stations



splitter. One-half was preserved in 4% formaldehyde buffered with borax, and the other half in 96% ethanol. The half of the samples in formaldehyde were used for morphological taxonomic identification, and rest of the half samples in ethanol were used for DNA barcoding. The volume of the water filtered was obtained from the two flowmeters attached to the mouth of the Multinet Mammoth frame. Abundance ( $\text{No. m}^{-3}$ ) was calculated dividing the total number of larvae by the volume filtered.

### Morphological and molecular taxonomic methods

Individual fish larvae were sorted and identified to lowest possible taxonomic level based on the morphological characteristics (body form, the pigmentation pattern (mostly on fresh samples on board), and meristic and morphometric characteristics) using available keys by Leis and Carson-Ewart (2004) and Rodriguez et al. (2017). Total length of individual larval specimens was measured, and the development stages (preflexion, flexion, and postflexion) of majority of dominant larvae were determined. DNA was isolated using HotSHOT, a method widely used for DNA barcoding (Montero-Pau et al. 2008). Briefly, approximately 0.4 cm of the larval tissue was added into 0.2 mL tubes containing 50  $\mu\text{L}$  of the alkaline lysis buffer (NaOH 25 mM, disodium EDTA 0.2 mM, pH 8.0) and incubated for 30 min at 95 °C. Afterwards, 50  $\mu\text{L}$  of the neutralizing solution (Tris-HCl 40 mM, pH 5) were added to the mixture. Upon DNA isolation, PCR amplification targeting the mitochondrial COI gene was performed following the methods

described in Mateos-Rivera et al. (2020). We refer to Table S1 for details on PCR amplification, purification, and sequencing. The threshold value (>97%) used to assign the larval fish sequences to species was chosen following previous studies (Ahern et al. 2018; Burrows et al. 2019). Sequences were uploaded to the GenBank under different accession numbers (Table S2).

### Data analysis

#### Fish diversity

Fish family diversity and evenness were calculated for each sampling station and study region using the Shannon–Weaver diversity index (1; Shannon and Weaver 1949), where  $S$  is the total number of the species, and  $p_i$  is the relative abundance of each species (i.e., the numerical proportion of each species relative to total number of individuals in the community).

$$H' = - \sum_{i=1}^S (p_i \ln p_i) \quad (1)$$

Pielou's evenness index,  $J'$  (2; Pielou 1975) was used to study the equality of families for each station and study region, where  $H'$  is the calculated Shannon–Weaver diversity index value and  $S$  is the total number of species.

$$J' = \frac{H'}{\ln S} \quad (2)$$

## Spatial patterns in abiotic and biotic variables

A nonparametric Kruskal–Wallis test was performed to compare the medians of temperature, salinity, and oxygen. In addition, a principal component analysis (PCA) (Legendre and Legendre 2012) was used to explore how polygons were related to the biotic (chlorophyll *a*, zooplankton biomass, larval fish abundance of demersal, pelagic, mesopelagic, and bathypelagic categories based on habitat criteria defined by associated references in Table 1) and abiotic (temperature, salinity, oxygen, and bottom depth) variables. The PCA was performed with the software “R” v. 3.5.1 (R Core Team 2018) and applying the function “prcomp”. As the variables were on different scales, PCA analysis was run on the correlation matrix, which is equivalent to standardizing the variables to mean zero and standard deviation one.

## Results

### Temperature, salinity, and oxygen

A distinct pattern in Sri Lankan waters was observed when comparing temperature, salinity, and oxygen conditions (Fig. 2). In the east region the water was warmer (~29 vs. 27 °C) and slightly less saline (~34 vs. 35) compared to west (Fig. 2a, b). The south region seems to be a transition zone, with somewhat lower temperatures (26.5 °C) than both east and west and moderate salinity values (34.5). Oxygen levels were more or less constant in the upper layers (~4.5 ml L<sup>-1</sup>) in the east while it was lower and more variable (3.4–4.4 ml L<sup>-1</sup>) in the west (Fig. 2c). This regional difference between east (NE, CE, and SE polygons) and west (S, SW, and NW) regions is supported by the Kruskal–Wallis test, where the median of temperature, salinity, and oxygen from the 6 polygons were significantly different ( $p \leq 0.0001$ , Table S3). Furthermore, there was an increase in salinity and oxygen in the west when moving from South polygon towards the North West polygon, while the eastern regions investigated were more uniform (Fig. 2).

### Dominant pelagic, mesopelagic, and demersal species

The most abundant larval species were categorized based on their adult habitats, i.e., pelagic, mesopelagic, and demersal. Among the identified pelagic species, *Selar crumenophthalmus*, *Dipterygonotus balteatus*, *Decapterus russelli*, *Sardinella* spp. (*S. albella*, *S. gibbosa*, and *S. sindensis*), and anchovy *Encrasicholina punctifer*, dominated the larval fish catches (Table 1, Figs. 3a, 4). The carangid *S. crumenophthalmus* was observed in Central East, South East, South West, and North West polygons (Fig. 4c). The mottled fusilier *D. balteatus* was mainly distributed in South East and offshore waters of North West polygons (Fig. 4e). Another carangid *D. russelli* was

abundant in the Central East (Fig. 4d), South East and South West polygons while all sardines (*Sardinella* spp.) and anchovy (*E. punctifer*) were concentrated in the North West (Fig. 3a).

Deep sea mesopelagic and bathypelagic species were dominated by drift fishes (Nomeidae), myctophids (Myctophidae), deep sea smelts (Bathylagidae), and codlets (Bregmacerotidae). *Cubiceps pauciradiatus* was the most abundant deep sea species in the larval catches being mainly distributed in the North East, Central East, South West, and North West regions (Fig. 3b). Among Myctophids, *Benthoosema fibulatum* and *Diaphus garmani* were dominant (Table 1, Fig. 3b). *Bathylagoides argyrogaster* was present in the South East, South West, and North West with highest abundance in the South West. The codlets *Bregmaceros* spp. were commonly found in all regions with varying abundance except for South East. Although the sequence identity for *Bregmaceros* spp. was low (Table S4), the genus was confirmed by their morphological characteristics (Fig. 5h).

Demersal fish species were mainly dominated by *Halichoeres zeylonicus*, *Amblyeleotris wheeleri*, *Lutjanus* spp. (*L. fulviflamma*, *L. johnii*, *L. lutjanus*, *L. notatus*, and *L. quinquelineatus*), *Upeneus* spp. (*U. guttatus*, *U. margarethae*, and *U. randalli*), and *Nemipterus* spp. (*N. furcosus* and *N. randalli*) (Table 1, Figs. 3c, 4). The gobies (Gobiidae) consisted of four species, i.e., *A. wheeleri*, *Oxyurichthys papuensis*, *Valenciennesa puellaris*, and *Valenciennesa wardii* (Table 1) which showed a similar distribution pattern as wrasses. Among gobies, *A. wheeleri* was the dominant species and restricted to the South East shelf (Fig. 3c). Most snappers including *Lutjanus* spp. (Lutjanidae) were concentrated in the South East. Four species of threadfin breams (Nemipteridae) were recorded in coastal waters of South East, and in offshore waters in South West and North West polygons. The Goldstripe wrasse, *H. zeylonicus* (Labridae) was abundant in the Central East, South East, South, and South West polygons (Fig. 4a). Another wrasse, *Oxycheilinus* spp., was found in the Central East and South polygons with low abundance and all 5 individuals belonging to this genus were assigned to a single OTU, with low sequence identity (Table S4). This genus was also confirmed through their morphological features (Fig. 5g).

### Larval tuna composition and distribution

Five larval tuna species were recorded in the current survey, *Auxis rochei*, *Auxis thazard*, *Euthynnus affinis*, *Katsuwonus pelamis*, and *Thunnus albacares* (Table 1, Figs. 5b, 5e and 6). Among these, the Bullet tuna *A. rochei* was restricted to the Central East shelf region (Fig. 6). The Frigate tuna *A. thazard* was distributed in the South East, South and North West, whereas *E. affinis* was distributed in South East shelf and South shelf region (Figs. 5c, e). The Skipjack tuna *K. pelamis* dominated in the North East and Central East.



**Table 1** Larval fish identified to species level (>97% sequence identity) in this study. Number of individuals (No.) and regions where individuals were found are given in parenthesis. Habitat of the adults and occurrence in the Indian Ocean (IO) were obtained from literature. North East (NE), Central East (CE), South East (SE), South (S), South West (SW), North West (NW)

Species	Common name	No. & Region	Habitat	References
<i>Acanthurus mata</i>	Elongate surgeonfish	1 (SW)	Reef associated	De Bruin et al. 1994, Rajasuriya 2013
<i>Amblyeleotris wheeleri</i>	Gorgeous prawn-goby	4 (SE)	Benthic/reef associated	Kumara and Dalpathadu 2012, Joshi et al. 2016
<i>Apogon crassiceps</i>	Transparent cardinalfish	1 (CE)	Reef associated	Froese and Pauly 2019
<i>Auxis rochei</i>	Bullet tuna	2 (CE)	Pelagic/neritic	De Bruin et al. 1994
<i>Auxis thazard</i>	Frigate tuna	8 (SE/S/NW)	Pelagic/neritic	De Bruin et al. 1994
<i>Bathylagoides argyrogastrus</i> *	Silver deepsea smelt	4 (SE/SW/NW)	Mesopelagic	Gloerfelt-Tarp T, Kailola PJ 1984, Cohen DM 1990
<i>Benthoosema fibulatum</i>	Spinycheek lanternfish	4 (NE/CE/SE)	Benthopelagic and mesopelagic	Dalpadado and Gjosaeter. 1993, Sebastine et al. 2013
<i>Benthoosema pterotum</i>	Skinnycheek lanternfish	1 (SE)	Benthopelagic and mesopelagic	Dalpadado and Gjosaeter 1993, Valinassab et al. 2007
<i>Caesio caeruleaurea</i>	Blue and gold fusilier	2 (CE)	Reef associated	De Bruin et al. 1994, Rajasuriya 2014
<i>Callionymus simplicicornis</i> **	Simple-spined dragonet	1 (SE)	Benthic/reef associated	No records from IO
<i>Caranx melampygus</i>	Bluefin trevally	1 (SE)	Demersal/reef associated	De Bruin et al. 1994
<i>Ceratias holboelli</i> *	Kroyer's deep-sea angler fish	1 (NE)	Mesopelagic and bathypelagic	Munroe et al. 2015
<i>Ceratoscopelus warmingii</i>	Warming's lantern fish	1(NE)	Mesopelagic	Dalpadado and Gjosaeter 1993
<i>Chanos chanos</i>	Milkfish	1 (SE)	Benthopelagic/amphidromous	De Bruin et al. 1994
<i>Cheilopogon furcatus</i>	Spotfin flyingfish	1 (NW)	Pelagic/neritic/oceanic	De Bruin et al. 1994
<i>Chirocentrus dorab</i>	Dorab wolf-hering	1 (NW)	Pelagic	De Bruin et al. 1994
<i>Cirrhitilabrus rubeus</i>	Ruby longfin fairy wrasse	1 (SE)	Reef associated	Victor 2016
<i>Coryphaena hippurus</i>	Common dolphinfish	1 (NW)	Pelagic	De Bruin et al. 1994
<i>Crossorhombus azureus</i>	Blue flounder	2 (SW/NW)	Benthic	De Bruin et al. 1994, Nair and Gopalakrishnan 2015
<i>Cubiceps pauciradiatus</i>	Bigeye cigarfish	15 (NE/CE/SW/-NW)	Epipelagic-mesopelagic	Potier et al. 2008
<i>Cynoglossus arel</i>	Largescale tonguesole	1 (SW)	Demersal	De Bruin et al. 1994
<i>Decapterus macrosoma</i>	Shortfin scad	1 (SW)	Pelagic, Oceanic and Neritic	De Bruin et al. 1994
<i>Decapterus russelli</i>	Indian scad	6 (CE/SE/SW)	Pelagic, oceanic, and Neritic	De Bruin et al. 1994
<i>Diaphus garmani</i>	Garman's lanternfish	8 (S/SW)	Benthopelagic and mesopelagic	Dalpadado and Gjosaeter 1993
<i>Diaphus thiollierei</i>	Thiolliere's lanternfish	3 (CE)	Mesopelagic	Dalpadado and Gjosaeter 1993
<i>Diodon holocanthus</i>	Longspined porcupinefish	1 (SE)	Benthopelagic/reef associated	De Bruin et al. 1994
<i>Diodon liturosus</i>	Black-blotched porcupinefish	1 (SE)	Benthopelagic/reef associated	Rajasuriya 2013
<i>Dipterygonotus balteatus</i>	Mottled fusilier	12 (SE/NW)	Reef associated/pelagic/neritic	De Bruin et al. 1994, Rajasuriya 2014
<i>Encrasicholina heteroloba</i>	Shorthead anchovy	1 (SW)	Pelagic/neritic	De Bruin et al. 1994
<i>Encrasicholina punctifer</i>	Buccaneer anchovy	3 (NW)	Pelagic/neritic	De Bruin et al. 1994
<i>Equulites sp.</i>	Pony fish	2 (NW)	Demersal	De Bruin et al. 1994
<i>Euthynnus affinis</i>	Kawakawa	4 (SE/S)	Pelagic/neritic	De Bruin et al. 1994
<i>Gazza minuta</i>	Toothpony	1 (SE)	Demersal	De Bruin et al. 1994
<i>Gempylus serpens</i>	Snake mackerel	2 (CE)	Epipelagic and mesopelagic	De Bruin et al. 1994
<i>Halichoeres zeylonicus</i>	Goldstripe/Ceylon wrasse	5 (CE/SE/S)	Reef associated	De Bruin et al. 1994, Rajasuriya 2014
<i>Katsuwonus pelamis</i>	Skipjack tuna	6 (NE/CE)	Pelagic/oceanic	De Bruin et al. 1994
<i>Lagocephalus guentheri</i> *	Diamondback puffer	1 (SE)	Demersal	Mishra et al. 2018
<i>Leiognathus lineolatus/Equulites lineolatus</i>	Ornate ponyfish	2 (SW/NW)	Demersal	De Bruin et al. 1994
<i>Lethrinus olivaceus</i>	Longface emperor	1 (SE)	Demersal	De Bruin et al. 1994
<i>Liza macrolepis/Planiliza macrolepis</i>	Largescale mullet	3 (S/SW)	Benthopelagic/neritic and estuarine	De Bruin et al. 1994
<i>Liza tade/Chelon planiceps</i>	Tade mullet	1 (NE)	Benthopelagic/neritic and estuarine	De Bruin et al. 1994
<i>Lutjanus fulviflamma</i>	Dory snapper	1 (CE)	Reef associated	Rajasuriya 2014
<i>Lutjanus johnii</i>	John's snapper	3 (SE)	Reef associated/oceanodromous	De Bruin et al. 1994
<i>Lutjanus lutjanus</i>	Bigeye snapper	1 (SE)	Reef associated	De Bruin et al. 1994, Rajasuriya 2014
<i>Lutjanus notatus</i> *	Bluestriped snapper	2 (SE)	Reef associated	Velamala et al. 2017

**Table 1** (continued)

Species	Common name	No. & Region	Habitat	References
<i>Lutjanus quinquelineatus</i>	Five-lined snapper	1 (NW)	Reef associated	De Bruin et al. 1994, Rajasuriya 2013
<i>Mene maculata</i>	Moonfish	3 (SW/NW)	Semi-demersal	De Bruin et al. 1994
<i>Mugil cephalus</i>	Flathead mullet	2 (SW)	Benthopelagic/neritic and estuarine	De Bruin et al. 1994, Rajasuriya 2013
<i>Nemipterus furcosus</i>	Forktail threadfin bream	2 (SE/SW)	Demersal	De Bruin et al. 1994
<i>Nemipterus randalli</i>	Randall's threadfin bream	1 (NW)	Demersal	De Bruin et al. 1994
<i>Notolychnus valdiviae</i>	Topside lampfish	1 (NW)	Mesopelagic	Dalpadado and Gjosaeter 1993
<i>Oxyporhamphus micropterus</i>	Bigwing halfbeak	1 (NW)	Pelagic/oceanic	Nair and Kumar 2018
<i>Oxyurichthys papuensis</i>	Frogface goby	1 (SE)	Benthic	Pezold and Larson 2015
<i>Parablennius thysanurus</i>	Tasseled blenny	1 (NW)	Benthic/reef associated	Williams 2014
<i>Planiliza subviridis</i>	Greenback mullet	1 (NW)	Benthopelagic/neritic and estuarine	De Bruin et al. 1994
<i>Pomacentrus caeruleus</i>	Caerulean damsel	2 (NE/SE)	Reef associated	Kumara and Dalpathadu 2012
<i>Pseudanthias marcia</i> *	Marcia's anthias	3 (NE/CE/S)	Reef associated	Nair 2008
<i>Pterocaesio tessellata</i>	One-stripe fusilier	2 (CE/SE)	Reef associated	De Bruin et al. 1994
<i>Rastrelliger kanagurta</i>	Indian mackerel	2 (SW)	Pelagic/neritic	De Bruin et al. 1994
<i>Rhabdamia gracilis</i>	Luminous cardinalfish	1 (CE)	Reef associated	Froese and Pauly 2019
<i>Sardinella albella</i>	White sardinella	1 (NW)	Pelagic/neritic	De Bruin et al. 1994
<i>Sardinella gibbosa</i>	Goldstripe sardinella	2 (NW)	Pelagic/neritic	De Bruin et al. 1994
<i>Sardinella sindensis</i>	Sind sardinella	1 (NW)	Pelagic/neritic	Karunasinghe et al. 2000, Di Dario 2018
<i>Sargocentron punctatissimum</i>	Speckled squirrelfish	1 (SE)	Reef associated	De Bruin et al. 1994
<i>Scolopsis bimaculata</i>	Thumbprint monocle bream	1 (SE)	Demersal	De Bruin et al. 1994, Rajasuriya 2014
<i>Scolopsis xenochrous</i>	Oblique-barred monocle bream	1 (SE)	Demersal	Rajasuriya 2014
<i>Selar crumenophthalmus</i>	Bigeye scad	19 (SE/SW/NW)	Semidemersal/reef associated/neritic	De Bruin et al. 1994
<i>Sphyrna jello</i>	Pickhandle barracuda	1 (SW)	Pelagic/neritic	De Bruin et al. 1994
<i>Sufflamen chrysopteron</i>	Halfmoon triggerfish	1 (SE)	Reef associated	De Bruin et al. 1994
<i>Synanceia verrucosa</i>	Stonefish	1 (CE)	Benthic/reef associated	Motomura et al. 2018
<i>Terapon jarbua</i>	Jarba terapon	1 (SW)	Benthopelagic/estuarine	De Bruin et al. 1994
<i>Thunnus albacares</i>	Yellowfin tuna	1 (CE)	Pelagic/neritic	De Bruin et al. 1994
<i>Trachinocephalus myops</i>	Snakefish	2 (NW)	Benthic/reef associated	De Bruin et al. 1994
<i>Trichiurus auriga</i>	Pearly hairtail	2 (NW)	Benthopelagic/mesopelagic	Ganga et al. 2015
<i>Trichonotus setiger</i>	Spotted sand-diver	1 (SE)	Benthic	De Bruin et al. 1994
<i>Upeneus guttatus</i>	Two-tone goatfish	1 (SW)	Demersal/reef associated	De Bruin et al. 1994, Uiblein and Heemstra 2010
<i>Upeneus margarethae</i>	Margaretha's goatfish	3 (S/NW)	Demersal/reef associated	De Bruin et al. 1994, Uiblein and Heemstra 2010
<i>Upeneus randalli</i> *		5 (NW)	Demersal/reef associated	Uiblein and Heemstra 2010
<i>Valenciennea puellaris</i>	Maiden goby	1 (SE)	Benthic	Long et al. 2010, Hoese and Larson 1994, Larson 2016a
<i>Valenciennea wardii</i> *	Ward's sleeper	1 (SW)	Benthic	Larson 2016b

\* Species previously not recorded from Sri Lankan waters

\*\* Species not previously recorded from the Indian Ocean

Skipjack tunas were present in both shelf and offshore regions of the North East while concentrated in the shelf region of Central East. The Yellowfin tuna *T. albacares* was restricted to the Central East deep (Fig. 5d).

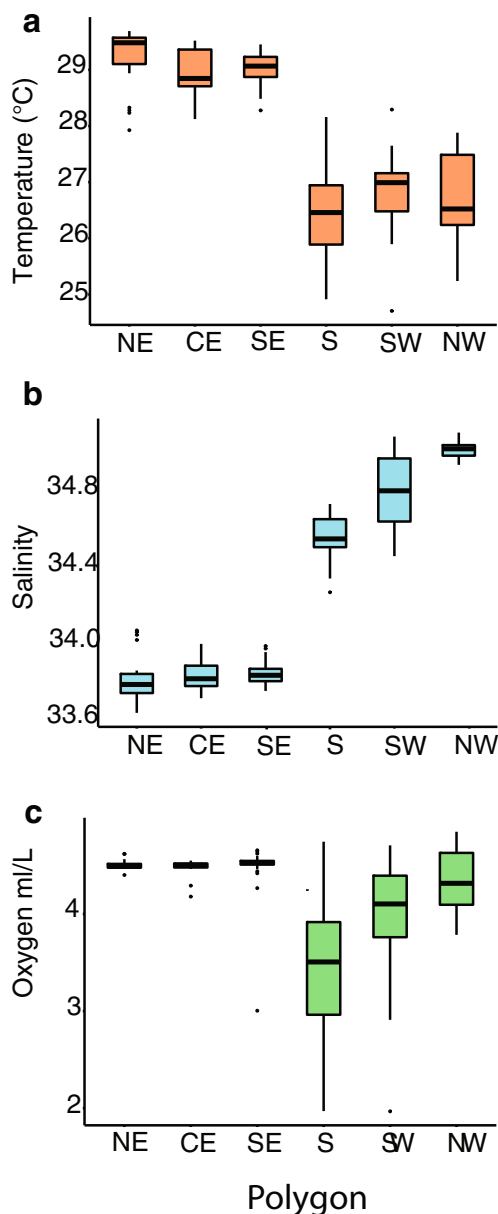
### New records of occurrences

The results from DNA barcoding revealed new records of species in the Indian Ocean and Sri Lankan waters (Table 1). To our knowledge, *Callionymus simplicicornis* (South East shelf) was not previously reported from the Indian Ocean. Several additional species including *Bathylagoides argyrogaster*

(South East shelf, South West deep, and North West deep), *Ceratias holboelli* (North East shelf), *Lagocephalus guentheri* (South East shelf), *Lutjanus notatus* (South East shelf/deep), *Upeneus randalli* (North West shelf), *Pseudanthias marcia* (North East/ Central East/ South deep), and *Valenciennea wardii* (South West shelf) were not previously recorded from Sri Lankan waters.

### Size structure and developmental stage

The average size (total length) of dominant pelagic larvae, i.e. *Selar crumenophthalmus*, was larger in the east than the west



**Fig. 2** Box plots of temperature (a), salinity (b), and oxygen (c) at 0–25 m in the 6 polygons around Sri Lanka: North East (NE), Central East (CE), South East (SE), South (S), South West (SW), and North West (NW). The boxes are divided by the median value and framed by the upper and lower quartiles. The whiskers extend to the highest and lowest observations in each direction. Outliers are shown by separate points

(5.7 mm and 3.8 mm, respectively). Within pelagic larval fish, for *Dipterygnotus balteatus*, the average size was ca. 5 mm in both regions (SD 2.1). The dominant mesopelagic larvae *Cubiceps pauciradiatus* in both east and west regions had an average length 5.5 mm (east SD=1.5 and west SD=1.2). Most demersal larvae of *Lutjanus* spp. and *Halichoeres zeylonicus* recorded in this study were in the late post flexion stage, indicating they are nearing juvenile stage. *Lutjanus* spp.

were in general much larger, ranging in size up to 26 mm, whereas *H. zeylonicus* varied from 7.8 to 13.5 mm.

### Family diversity, species composition, and spatial distribution

Shannon–Weaver diversity index showed a high larval fish family diversity with some variations among stations and regions. The highest larval diversities were observed in the South East ( $H=2.96$ ,  $E=0.72$ ), followed by South West ( $H=2.80$ ,  $E=0.78$ ), North West ( $H=2.78$ ,  $E=0.78$ ), and North East ( $H=2.50$ ,  $E=0.83$ ) polygons. The lowest diversity was recorded from the Central East ( $H=1.57$ ,  $E=0.5$ ) and South ( $H=2.14$ ,  $E=0.66$ ) polygons.

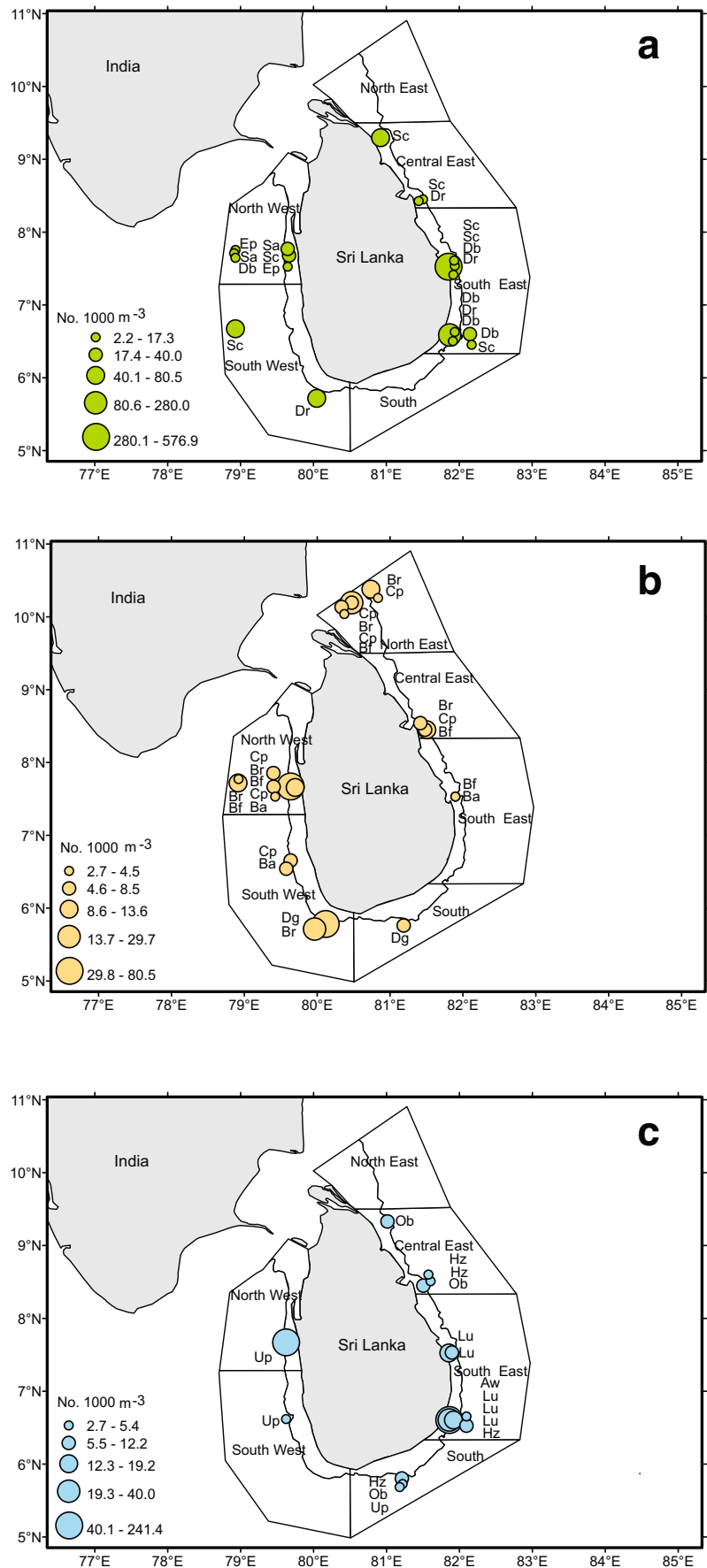
Among the 551 larval fish analyzed following the molecular approach, 305 individuals were successfully identified (55%) and divided into two different categories based on sequence identity threshold when compared to the databases (Table 1, Table S4). In total 65% of the individuals (80 species) were identified at >97% sequence identity (Table 1), while 35% (53 operational taxonomic units (OTUs)) were assigned at a lower identity (Table S4). Morphological identification of larval fish was successful to family level for up to 70% of the total samples.

Overall, Carangidae was the most abundant family among the identified larval fish. It was followed by Myctophidae Lutjanidae, Scombridae, and Caesionidae. Myctophidae and Scombridae with six different species, Lutjanidae with five species, while Caesionidae, Carangidae, Clupeidae, Gobiidae, Mugilidae, and Nemipteridae contained four species (Table 1).

### Clustering analysis

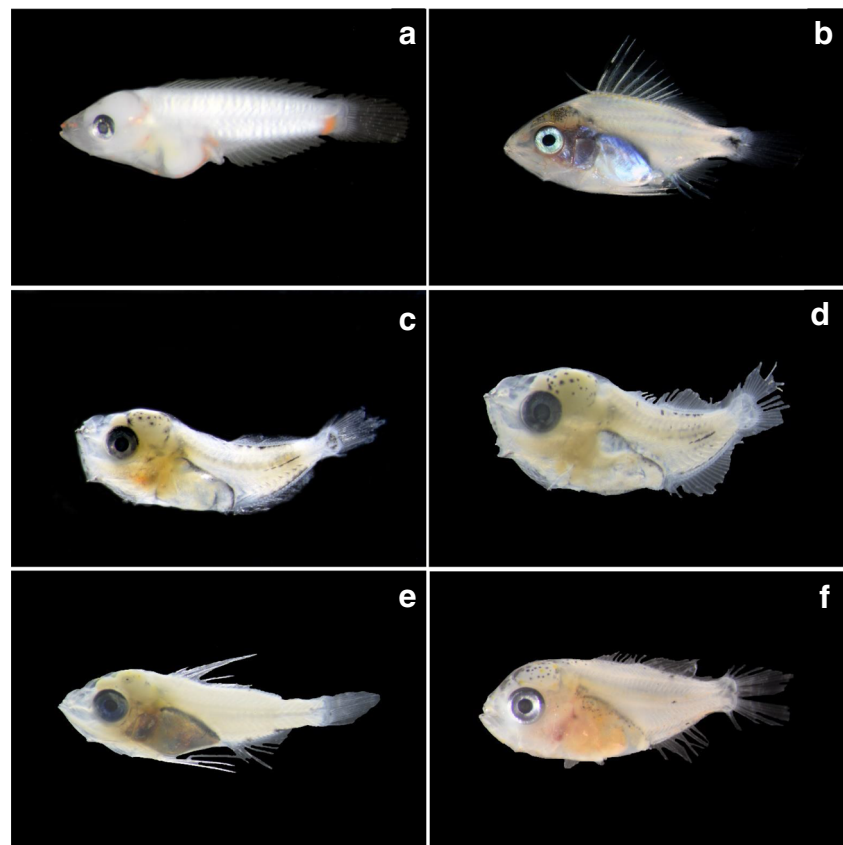
The first two axes of the PCA together explained ~67% of the variance in the data set across stations (Fig. 7). The PCA analysis showed a clear separation of eastern and western stations along the PC1 axis, which explained most of the variance (~44%). Increasing PC1 scores are associated with decreasing salinity and increasing temperature. Hence, we find eastern stations associated with warmer less saline waters on the right-hand side of the PCA biplot (Fig. 7, in red), while western stations characterized by cooler and more saline waters with less oxygen and higher productivity are found on the left-hand side of the biplot (Fig. 7, in blue). Mesopelagic larvae loadings are explained by both PC1 (being associated predominantly in cooler, less oxygenated waters in the west) and PC2 (correlated with depth). The demersal and pelagic larval abundances were associated with PC2 axis (which explains ~23% of the variance) likely driven by their high

**Fig. 3** Most abundant (No. 1000 m<sup>-3</sup>) larval fish species categorized based on adult habitats: **a** pelagic, **b** mesopelagic, and **c** demersal. Note that overlapping stations are placed slightly apart, for better visualization of the species composition. Species are listed in abbreviated form according to descending abundance at sampling locations. Pelagic: *Selar crumenophthalmus* (Sc), *Decapterus russelli* (Dr), *Dipterygonotus balteatus* (Db), *Encrasicholina punctifer* (Ep), *Sardinella* spp. (Sa); mesopelagic: *Cubiceps pauciradiatus* (Cp), *Bathylagoides argyrogaster* (Ba), *Benthoosema fibulatum* (Bf), *Diaphus garmani* (Dg), *Bregmaceros* spp. (Br); and demersal: *Halichoeres zeylonicus* (Hz), *Amblyeleotris wheeleri* (Aw), *Lutjanus* spp. (Lu), *Oxycheilinus* spp (Ob), *Upeneus* spp (Up)





**Fig. 4** Images of few abundant fish species recorded during the survey 24 June to 16 July 2018. Their total length (TL) and % sequence identity (ID) are given: **a** *Halichoeres zeylonicus* (Hz) 15 mm TL, 100% (ID); **b** *Lutjanus notatus* (Ln), 14 mm TL, 100% (ID); **c** *Selar crumenophthalmus* (Sc), 7.1 mm TL, 100% (ID); **d** *Decapterus russelli* (Dr), 6.3 mm TL, 100% (ID); **e** *Dipterygonotus balteatus* (Db), 8.2 mm TL, 98.2% (ID); **f** *Cubiceps pauciradiatus* (Cp) 5.8 mm TL, > 99% (ID). The images were taken on fresh specimens



abundances in the shallower South West and South East shelf stations (stations 10, 13 and 18).

## Discussion

The current study provides an insight into the larval fish diversity and structuring in a sparsely studied area of the central Indian Ocean. In our study, morphological identification of larval fish was successful up to family level in 70% of the samples. Visual identification to genus and species levels, however, was only possible for a few species with distinct morphological features or those that are well documented due to their commercial importance such as *Mene maculata*, *Coryphaena hippurus*, *Auxis thazard*, *Euthynnus affinis*, *Katsuwonus pelamis*, and *Thunnus albacares* (see Fig. 5). All the above-mentioned species were cross validated with DNA barcoding.

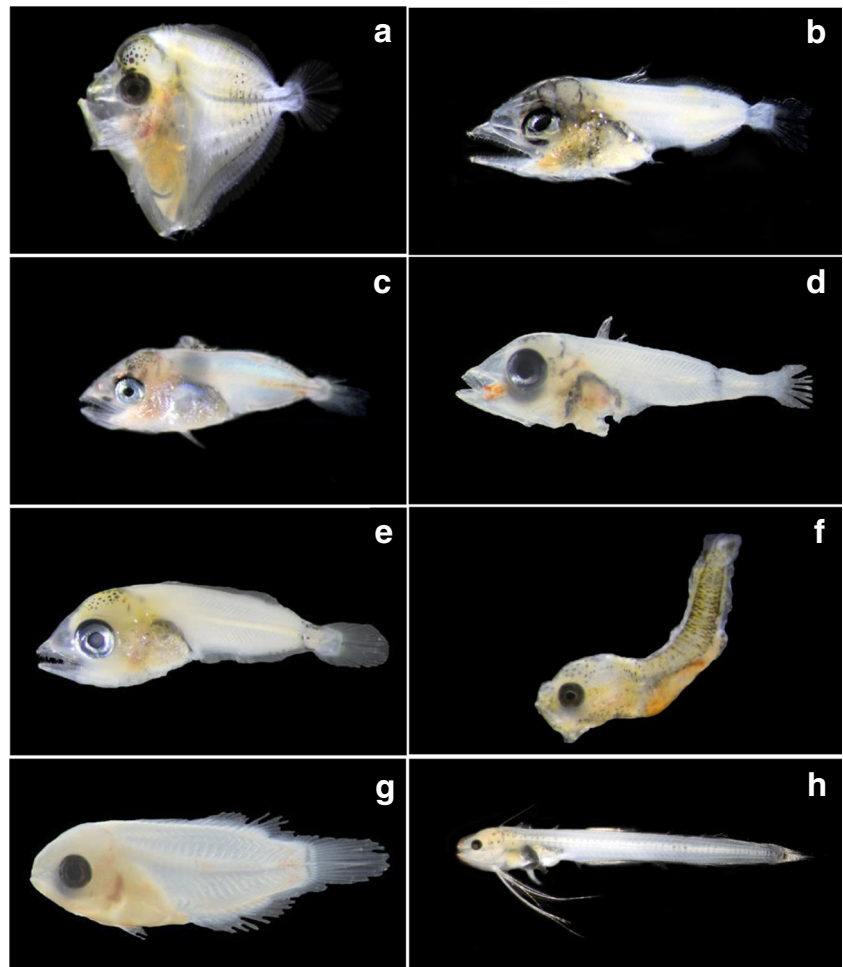
Molecular barcoding is a powerful tool for identification of larval fish species (Hubert et al. 2015; Ayala et al. 2016; Ahern et al. 2018), and required to thoroughly monitor larval recruitment and year class-strength (Steinke et al. 2016). Combining morphological and DNA barcoding allowed identification of 80 species of larval fish belonging to 69 families in our study, demonstrating a very high diversity in the tropical central Indian Ocean and exceeding previously reported

numbers from this region. Morphological approaches alone are much more challenging for accurate identification of larval fish species compared to adults, highlighting the urgent need for using molecular approaches in taxonomic investigations from this region (Collet et al. 2017).

Carangidae was the most abundant family observed. Studies on the reproductive cycles of the two most dominant carangids *Selar crumenophthalmus* and *Decapterus russelli* showed a prolonged spawning season from ca. April to November in the south west Indian Ocean and south west coast of India (Balasubramanian and Natarajan 2000; Roos et al. 2007). Although no records of spawning of *D. russelli* and *S. crumenophthalmus* on the Sri Lankan shelf are available, our results indicate that their spawning also takes place in Sri Lankan shelf areas.

The mottled fusilier *Dipterygonotus balteatus* is abundant in the Indian Ocean inhabiting coral reefs as juveniles, whereas adults are captured together with other nearshore pelagic fish such as sardines and anchovies (Carpenter 1988). In our study, this species dominated throughout the coastal waters of South East and offshore waters of North West. Although this species extends its distribution from western Indian Ocean into the western Pacific (Holleman et al. 2013), its spawning sites in the Indian Ocean are unknown (Holleman et al. 2013).

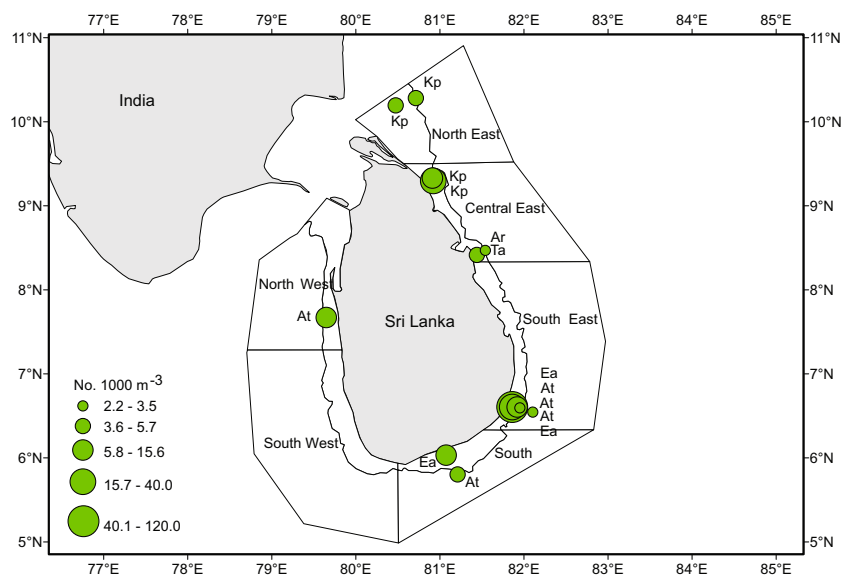
**Fig. 5** Images of fish species and genera with special morphological characteristics including tuna species recorded during the survey 24 June to 16 July 2018. Their total length (TL) and % sequence identity (ID) are given: **a** *Mene maculata* (Mm), 7 mm TL, 100% (ID); **b** *Katsuwonus pelamis* (Kp), 9.1 mm TL, 100% (ID); **c** *Euthynnus affinis* (Ea), 9.2 mm TL, 100% (ID); **d** *Thunnus albacares* (Ta), 9.0 mm TL, 99.8% (ID); **e** *Auxis thazard* (At), 8.4 mm TL, 100% (ID); **f** *Coryphaena hippurus* (Ch), 5.2 mm TL, 99.8% (ID); **g** *Oxycheilinus* spp. (Ob) 8.5 mm TL, 93.3% (ID); **h** *Bregmaceros* spp. (Br) 16.8 mm TL, 94% (ID). The images were taken on fresh specimens

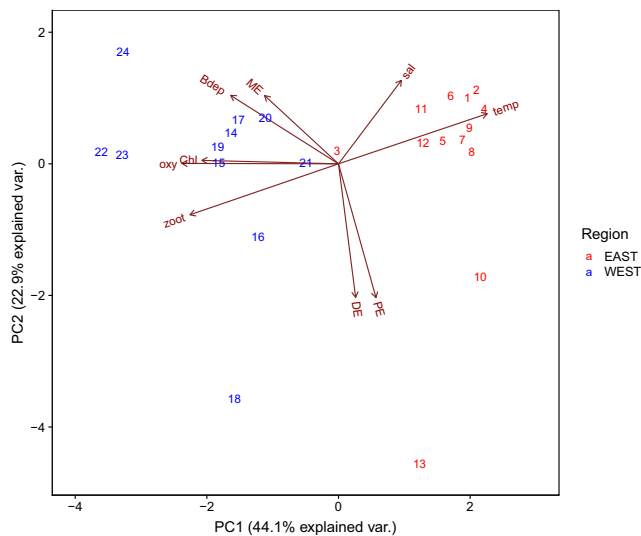


The larger pelagic tunas spawn at sea surface temperatures above 20 °C (Reglero et al. 2014), suggesting that waters around Sri Lankan are suitable spawning grounds. The spawning of Skipjack (*Katsuwonus pelamis*) is relatively high

in the northern and central Indian Ocean during September through April (Pillai and Silas 1979), while the Yellowfin tuna, *Thunnus albacares*, spawns off Sri Lanka from April to June (Stequert and Marsac 1989). The smaller Frigate tuna,

**Fig. 6** Distribution of most abundant larval tuna species. Note that overlapping stations are placed slightly apart, for better visualization of the species composition. Species are listed in abbreviated form according to descending abundance at sampling location. *Katsuwonus pelamis* (Kp), *Thunnus albacares* (Ta), *Auxis thazard* (At), *Auxis rochei* (Ar), *Euthynnus affinis* (Ea)





**Fig. 7** PCA biplot separating the different stations (1–24). Abiotic variables: temperature (temp), salinity (sal), and oxygen (oxy), bottom depth (Bdep) and biotic variables: chlorophyll *a* (Chl), zooplankton total biomass (zoot), larval fish abundance for demersal (DE), pelagic (PE), and mesopelagic (ME). See Table S3 for more details on corresponding survey station for each PCA station. The PCA biplot is designated in two colors: left side in “blue” and the right side in “red”

*Auxis thazard*, spawns in Sri Lankan waters from May to August (Pillai and Satheeskumar 2012; Herath et al. 2019) overlapping the period of Kawakawa tuna *Euthynnus affinis* (Pillai and Satheeskumar 2012). This dominance of larval tuna in coastal regions off Sri Lanka indicates that they are likely drifted with the surface currents (Fig. S1) from spawning sites into nursery areas with good feeding conditions (Krakstad et al. 2018). All fish stocks that live in areas characterized by stable current systems have genetic predispositions to secure their survival within a geographical area (Harden-Jones 1968). The author outlines a life cycle with an upstream spawning area and a downstream nursery area and the general applicability of this theory has been proven for numerous fish stocks in several geographical areas such as in the North Atlantic (ICES 2019) and South African coast bordering both south Atlantic and Indian Ocean (Hutchings et al. 2002). The study by Hutchings et al. (2002) showed that most pelagic and demersal fish species have evolved highly selective reproductive strategies, among other that fish conduct spawning migrations to upstream areas from where the offspring are transported with the currents to suitable nursery areas, such as productive retention and broader shelf areas.

Myctophids are the most diverse and common group in oceanic waters (Lirdwitayaprasit et al. 2008; Ayala et al. 2016; Isari et al. 2017; Beckley et al. 2019). Recent studies highlighted the large contribution of Myctophidae to the mesopelagic vertebrate biomass (> 50%) and their importance in the midwater food web (Martin et al. 2018; Batta-Lona et al. 2019 and references therein). Though their high biomass in the Indian Ocean has been known for several decades (FAO

2001), yet until recently there has been comparatively little research activity on the mesopelagic zone (Hildago and Browman 2019). Myctophidae were the second most abundant family in this study associated with high saline, cooler, less oxygenated, deeper waters in the south and west regions (South, South West, and North West). Myctophids are known to exhibit adaptations to oxygen minimum zones (Catul et al. 2011), hence, likely their success in the Indian Ocean. The oxygen minimum layer (< 0.5 ml/L) off Sri Lanka is below 100 m (Krakstad et al. 2018); hence, the myctophids we observed in our study are likely to experience low oxygen zones. A study by Olivar et al. (2018) showed that the vertical distribution of larval mesopelagic fish varied from 0 to 200 m in the tropical and equatorial Atlantic depending on the species. Another study in the Kuroshio Current region exhibited larval myctophid species to occupy different depth strata (Sassa et al. 2002). Their study showed that larvae belonging to subfamily Lampanyctinae occupied shallower waters (0–30 m) than those in the subfamily Myctophinae (50–150 m).

The majority of the demersal larval fish species identified (*Lutjanus notatus*, *L. lutjanus*, *L. johnii*, *Halichoeres zeylonicus*, *Oxycheilinus* spp., and *Upeneus margarethae*) recorded in this study in the South and South East are consistent with rocky reef habitats favorable for adults of these species (Krakstad et al. 2018). The adult habitat and spawning behavior seem to explain the spatial patterns of the demersal larval fish assemblages in Sri Lankan waters. Similar to our findings, Hubert et al. (2015) using molecular tools for ichthyoplankton identification in the Indo-Pacific region revealed that most of the species identified in larval pools reflected the local contribution from the adult pools of demersal fish in the neighboring reefs. Sakaue et al. (2016) also revealed that the larvae of some Lutjanidae species were found near adult spawning aggregations, supporting our observations.

Furthermore, the use of molecular barcoding in this study revealed a new species *Callionymus simplicicornis* that has not been reported before in the Indian Ocean. The simple-spined dragonet *C. simplicicornis* is found in southeast Asian waters, i.e., Philippine waters, Palau/Belau islands (Fricke 2002). There is a possibility that this species known to occur in the Pacific have entered the Indian Ocean through the “Indonesian Throughflow (ITF)” (Tomczak and Godfrey 1994). According to these authors, water exchange between the Indian Ocean and the Pacific Oceans occurs through the ITF, where water from the Pacific flows into the Indian Ocean, as a narrow band of low salinity water. A branch of the ITF water penetrates the northern Indian Ocean via Somali Current further into the Arabian Sea during boreal summer (Song et al. 2004). During summer monsoon, the Southwest Monsoon Current transfers Arabian Sea waters eastward to offshore areas around the southern tip of India and Sri Lanka (Hood et al. 2017). The simple-spined dragonet is a small demersal reef associated species inhabiting coastal waters. As a non-commercial small

species and due to the lack of taxonomic studies, these fish could be considered as “overlooked species”.

Majority of the larvae were in flexion and post flexion developing stages, indicating that they use the waters around Sri Lanka as nursery grounds. It is likely that some of the larvae especially in early development stages are dispersed by the South Monsoon Current from the west to the eastern regions (Fig. S1). Studies by Beldade et al. (2006) and Borges et al. (2007) on larval fish assemblages in nearshore waters have described that particularly postflexion stages, close to the bottom, are less susceptible to transport hence, contained close to adult habitats. The late post flexion larvae of demersal families in the east region seem to indicate that they remain close to where adult spawning occurs.

In conclusion, our study shows that combined morphological and molecular approaches can reveal vast species diversity. Dominance of several larval fish species in the east during the survey seem to indicate that oligotrophic areas in the east can also sustain high diversity. Findings from this study exhibit that Sri Lankan waters act as valuable nursery grounds for a wide range of fish species.

**Supplementary Information** The online version contains supplementary material available at <https://doi.org/10.1007/s12526-021-01169-w>.

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## Declarations

**Conflict of interest** The authors declare that they have no conflict of interest.

**Ethical approval** All applicable international, national, and/or institutional guidelines for the care and use of animals were followed by the authors.

**Sampling and field studies** All necessary permits for sampling and observational field studies have been obtained by the authors from the competent authorities and are mentioned in the acknowledgements.

**Data availability** All data generated or analyzed during this study are included in this published article.

**Author contributions** Project coordination PD. In situ data collection and database management MIGR, HBUW, RPPKJ, JOK, PD. DNA barcoding AMR, RSM. Analytical tools and visualization AMR, MIGR, PD. Writing – original draft MIGR, AMR, PD. Writing – review & editing MIGR, AMR, RSM, HBUW, RPPKJ, JOK, PD.

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