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Larval fish assemblages in a tropical mangrove estuary and adjacent coastal waters: Offshore–inshore flux of marine and estuarine species

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ABSTRACT

A total of 92,934 fish larvae representing 19 families were sampled monthly from the Sangga Kecil estuary (Matang Mangrove Forest Reserve) and adjacent coastal waters from May 2002 to October 2003. Larval fish assemblages were numerically dominated by Gobiidae (50.1%) and Engraulidae (38.4%). Canonical Correspondence Analysis (CCA) revealed that the larval fish assemblages, including their ontogenetic stages, differed between the mangrove estuary and adjacent offshore waters, and that salinity, turbidity and zooplankton food are the major environmental factors structuring the larval fish assemblages. Estuarine preflexion gobiid larvae were ubiquitous in the coastal and estuarine waters. Larval stages of euryhaline species that were spawned in offshore waters, such as Engraulidae and Clupeidae, were largely advected into mangrove areas at the postflexion stages. Larvae of other euryhaline fishes (Sciaenidae, Blenniidae and Cynoglossidae) that may have been spawned inside the estuary were, however, exported to offshore waters. Given that the collective number of juvenile and adult fish families in the Matang estuary was 53, while the number of larval families was only 17, the former is quite disconnected from the existing larval fish population in the estuary.

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1. Introduction

Despite the large number of fish studies on mangrove wetlands due to their role as nursery and feeding areas (Faunce and Serafy, 2006), there are only a few published works that pertain to mangrove ichthyoplankton. These include those from Thailand (Janekarn and Boonruang, 1986), Malaysia (Blaber et al., 1997), India (Krishnamurthy and Jeyaseelan, 1981; Jeyaseelan, 1998), East Africa (Little et al., 1988), Brazil (Barletta-Bergan et al., 2002; Bonecker et al., 2009) and Puerto Rico (Austin, 1971). However, non-mangrove ichthyoplankton studies are substantial, including those from temperate (e.g. Moser et al., 1984; Neira et al., 1998; Aceves-Medina et al., 2004; Lo et al., 2010; Campfield and Houde, 2011) and tropical waters (e.g. Franco-Gordo et al., 2002; Katsuragawa et al., 2011). Nonetheless, ichthyoplankton studies in southeast Asian waters are few and include those in the coastal waters of Vietnam (Nguyen, 1999), the Philippines (Chiu et al., 1992), Indonesia (Soewito and Schalk, 1990; Suharti and Sugeha, 2008) and shelf waters of the Andaman Sea (Munk et al., 2004). In the Australasian region, larval fish studies have been carried out mainly in coral reefs (e.g. Leis, 1993; Kingsford, 2001; McIlwain, 2003).

The Matang mangrove of Malaysia is one good example of a specific single location where numerous studies have been carried out to elucidate its nursery-ground function for coastal fishes and invertebrates (Sasekumar et al., 1994; Chong et al., 2001; Ahmad Adnan et al., 2002; Kiso and Mahyam, 2003; Chong, 2007; Chew and Chong, 2011), yet none pertains to fish larvae. This is unfortunate because a complete understanding of the ecology of fish and their dependence on mangroves is not possible without a complete knowledge of their early life history. The latter includes the most fragile stages that are strongly influenced by the highly variable milieu of the estuary and ocean (Robertson and Blaber, 1992). Larval recruitment and survival in the mangrove will thus have a strong bearing on the structure and abundance of the juvenile fish community. The lack of ichthyoplankton studies are mainly due to the demands of sufficient sampling (to counter the problem of patchiness), the time-consuming examination of plankton samples, but most of all, the problem of identification due to the lack of larval fish identification keys. In most cases, fish larvae are at best identified to the family level.

Typically, only a few species of so-called permanent residents, such as gobiids, spawn within estuarine ecosystems (Blaber, 2000). Many fish species found in mangrove estuaries are however, commonly known to be euryhaline, and represent one phase of their life history pattern where the adult occurs in marine waters (Blaber and Milton, 1990; Chong, 2005). The few studies thus far suggested that most euryhaline fishes enter estuaries as

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juveniles or postlarvae after spending their larval stage in offshore waters where adults normally spawn (Bell et al., 1984; Little et al., 1988; Sarpedonti and Chong, 2008). However, studies have also shown that marine tropical fish may spawn in the estuary, for example, certain species of ariids (Singh, 2003), sciaenids (Yap, 1995), gray mullets (Chong, 1977), clupeids (Blaber et al., 1997), ambassids (Allen and Burgess, 1990) and centropomids (Moore, 1982). Most observations are however based on the presence of gravid females, and are not substantiated conclusively by the presence of spawned eggs or the early larval stages. The study of fish larvae and their ecology is thus crucial to defining spawning grounds as well as nursery grounds within the estuary, which will benefit management and conservation efforts to protect both fish and habitat from drastic changes.

The objectives of the present study are the following: (1) to identify and compare the ichthyo- assemblages in estuary and offshore waters, (2) to relate larval fish abundance to the physical and biotic characteristics of the estuary and coastal waters and (3) to determine the type and extent of estuarine use by fish species (e.g. spawning, feeding or/and nursing).

2. Methods

2.1. Area of study

The Matang Mangrove Forest Reserve (MMFR) covers an estimated forest area of 41,711 ha and another 8653 ha of estuarine waterways on the western shore of Peninsular Malaysia. It is an exemplary silvicultured production forest that has been sustainably managed since 1906. Tides are mesotidal and semi-diurnal, with tidal range of 1.6 and 0.6 m at spring and neap tidal periods, respectively (Chong et al., 1999). Malaysia's rainfall pattern is strongly influenced by the region's monsoon regime, the South-west Monsoon (May–September) and the North-east Monsoon (November–March), which are interceded by two short periods (inter-monsoon) of variable winds. At the study site, the NE monsoon however brings the heaviest rainfall (> 200 mm mo⁻¹), whereas the SW monsoon is comparatively drier (< 100 mm mo⁻¹).

Five sampling stations were established along the main water channels of the Sepetang (Station 1), Sangga Besar (Station 2) and Sangga Kecil (Stations 3, 4 and 5) rivers within the MMFR, and another two stations in the adjacent coastal waters (Stations 6 and 7) (Fig. 1). Upstream distances from the river mouth (Station 5) for Stations 1, 2, 3 and 4 were 10.6, 7.0, 3.5 and 2.8 km, respectively. Offshore distances from the river mouth for Stations 6 and 7 were 8.0 and 16.0 km, respectively. Mean depths at each station were as follows: Station 1 (3.81 ± 1.62 m), Station 2 (3.46 ± 0.71 m), Station 3 (7.25 ± 1.21 m), Station 4 (7.05 ± 1.98 m), Station 5 (5.75 ± 0.56 m), Station 6 (3.30 ± 0.74 m) and Station 7 (7.04 ± 0.86 m).

2.2. Field collection

Zooplankton was regularly sampled by horizontally towed bongo nets during neap tide each month from May 2002 to October 2003. In addition, eight 24-hour studies following the moon phases were carried out in July 2003 and November 2003. However, the main results from the diel studies are not reported here.

The MARMAP bongo net system comprised of two 45-cm diameter net frames, fitted with pre-calibrated flow meters and twin nets of 363 and 180 μ m mesh sizes. The nets sampled surface waters at approximately 0.5 m depth for 10-min durations. Oblique tow of the entire water column was not done due to the shallow depths (up to 7 m), which were also variable along the tow path. However, the diel studies using a 24 in.mouth Clarke–Bumpus at Station 5 had demonstrated no large



Fig. 1. Sampling stations (numbered 1–5) in the Sepetang, Sangga Besar and Sangga Kecil rivers (Matang Mangrove Forest Reserve), and offshore waters (numbered 6 and 7), Perak, Malaysia.

discrepancy in larval fish catches, as well as zooplankton biomass, between top and bottom waters during daytime or nighttime (Ooi et al., 2005).

Duplicate samples were taken at each station during the day, one on the sea-bound journey and the other on the return. The collected zooplankton samples were immediately preserved in 10% buffered formaldehyde in 500-ml plastic bottles. During plankton tows, water parameters including temperature, salinity, pH, turbidity and dissolved oxygen were measured by a metered YSI 3800 multi-parameter sonde, and in later months by a Hydrolab 4a. Water samples were also collected for chlorophyll *a* analysis in the laboratory.

2.3. Laboratory analysis

In the laboratory, zooplankton samples from both 363 and 180 μ m bongo nets were washed and sieved through a stack of 500, 250 and 125 μ m Endecott sieves under running tap water. The sieved zooplankton fractions were transferred onto pre-weighed steel gauze and excess moisture was removed using blotting paper before the wet weight of each size fraction was determined by a fine balance. The zooplankton fractions were immediately resuspended in 80% alcohol and stored in separate 100-ml vials.

All fish larvae were sorted out from the 250-500 and > 500 μ m size fractions collected by the 363 μ m bongo net. The $125-250 \,\mu\text{m}$ size and $< 125 \,\mu\text{m}$ size fractions were ignored because preliminary examination of 100 samples of the former did not yield any fish larvae. Fish larvae were identified to the lowest taxon possible using the available information from Okiyama (1988), Leis and Trnski (1989), Jeyaseelan (1998), Termvidchakorn (undated) and Leis and Carson-Ewart (2000). Identification of larval stages of species or genus not available in the published literature was attempted using the series method (Leis and Trnski, 1989). The number of individuals per taxon was counted from the entire sample and fish density was calculated based on a standard volume of 100 m³. Teleost eggs were enumerated but not identified. Chlorophyll *a* concentrations of collected water samples were determined by fluorometry, using a Quantech Turner fluorometer Model FM109530-33, after spectrophotometric calibration based on extracted microalgal chlorophyll a.

2.4. Data analyses

Analysis of variance (ANOVA) was used to compare differences in total fish larvae ($N100 \text{ m}^{-3}$) among months and stations. The data was logarithmically transformed [$\log_{10}(x+1)$] to achieve normality and homogeneity of variance before analysis (Zar, 1998). All statistical analyses were performed using Statistica Version 9.0 Software Package. The level of significance was tested at the 5% level.

CCA was performed to determine the relationships between the abundance of total fish larvae and environmental variables. This was done using the CANOCO for Windows Version 4.5 software (Ter Braak and Smilauer, 2002). One hundred and eighteen samples containing 19 major larval fish families were related to nine environmental parameters, namely, salinity, pH, temperature, dissolved oxygen, turbidity, chlorophyll *a* concentration and plankton biomass of size fractions > 500, 250–500 and 125–250 µm. Plankton biomass was based on plankton collected from the 180 µm bongo net. Developmental stages of the most abundant families, like Gobiidae, Engraulidae, Clupeidae, Sciaenidae, Ambassidae and Blenniidae, were also related to the environmental variables. CCA biplots of the abundance of taxa or developmental stage with the environmental variables were illustrated.

3. Results

3.1. Environmental factors

The average monthly precipitation recorded at Taiping (4°51′N 100°44′E), the town nearest to the study area, showed very wet weather conditions in November–December and relatively drier weather conditions from May–July, corresponding to the onsets of the North-east and South-west Monsoon, respectively (Fig. 2). Both monsoons are however characterized by dry and wet spells, for instance, in January and July/September, respectively. The period of variable winds or the inter-monsoons, in April and October, are also relatively wetter months.

In the mangrove estuary, mean salinity was 21.9 ± 4.8 ppt, while it was 29.2 ± 2.8 ppt in the offshore waters. The monthly mean salinity in offshore waters was quite consistent, whereas in the mangrove, it ranged from 15.4 to 27.8 ppt (Fig. 2). Mean water temperatures in the mangrove estuary and offshore waters were 30.9 ± 0.98 and 30.4 ± 0.81 °C, respectively. In the mangrove estuary, mean turbidity ranged from 9.8 ± 2.1 to 165.8 ± 141.7 NTU. The highest surface turbidity recorded inside the mangrove estuary in January was due to high riverine inputs of planktonic and detrital particulates. Offshore waters were generally less turbid with mean of 22.2 ± 29 NTU. The mean pH in the mangrove was 7.4 ± 0.3 but rose to 7.9 ± 0.2 in offshore waters. Mean dissolved oxygen measured in the mangrove and offshore waters were 5.1 ± 1.5 and 5.9 ± 0.8 mg L⁻¹, respectively.

3.2. Taxa composition and abundance

A total of 92,934 fish larvae representing 19 families were collected between May 2002 and October 2003. A total of 15 and 17 families were recorded from the mangrove and offshore waters, respectively. The larval fish assemblages in the mangrove estuary and offshore stations were numerically dominated by four families that made up 97.5% of the total abundance (Table 1). Gobiidae was the most abundant family comprising 50.1% of the catch, with a mean of 158.1 ± 433.8 individuals (*N*) 100 m⁻³, followed by Engraulidae, $122.6 \pm 263.1N$ 100 m⁻³ (38.4%), Clupeidae, $17.9 \pm 123.4N100$ m⁻³ (5.8%), and Sciaenidae, $11.6 \pm 64.4N100$ m⁻³ (3.2%). Other families that were



Fig. 2. Monthly mean rainfall and surface water parameters recorded in Matang mangrove estuary and offshore waters. Rainfall, from January 2002 to December 2003; others, May 2002–October 2003. Vertical thread lines indicate SD.

less represented and contributed less than 1% were Ambassidae, Blenniidae, Syngnathidae, Scatophagidae, Cynoglossidae, Carangidae, Bregmacerotidae, Platycephalidae, Scorpaenidae, Leiognathidae, Terapontidae, Trichonotidae, Triacanthidae, Mullidae and Mugilidae. Another two families that were not found during monthly samplings, but were recorded in the mangrove during the diel studies, were Belonidae and Tetraodontidae. Unidentified fish larvae make up 0.37% of the total larval fish abundance.

The mean number of larval fish families differed very significantly among stations (F=3.706; P < 0.01) and among months (F=8.941; P < 0.01), with significant station x month interaction (P < 0.05). Mean total abundance of fish larvae differed but not significant (P > 0.05) among the seven stations, viz. Station 1 (472 ± 874N100 m⁻³), Station 2 (213 ± 265N100 m⁻³), Station 3

Table 1

Numbers of sampled fish larvae and their mean density ($N100 \text{ m}^{-3}$) by family and station, Matang mangrove estuary (Stations 1–5) and adjacent coastal waters (Stations 6 and 7).

Family	Total no. of larvae		Station							Overall mean
			1	2	3	4	5	6	7	
Gobiidae	46,562	Mean	464.98	138.90	203.28	215.38	127.82	32.98	28.00	158.06
		\pm SD	871.25	212.05	390.31	563.34	408.47	82.10	112.64	433.76
Engraulidae	35,671	Mean	3.91	68.82	99.64	201.48	164.00	149.99	124.22	122.58
		\pm SD	4.39	122.42	232.48	441.68	244.80	240.20	255.41	263.10
Clupeidae	5401	Mean	0.63	2.33	1.38	2.92	1.86	20.00	98.47	17.91
		\pm SD	1.73	11.88	3.59	10.37	3.62	59.54	319.34	123.35
Sciaenidae	2958	Mean	1.26	0.43	2.26	2.96	3.96	35.73	32.89	11.59
		\pm SD	3.38	1.58	7.55	14.00	8.11	129.42	101.21	64.37
Cynoglossidae	554	Mean	0.00	0.02	0.02	0.15	0.38	4.74	10.27	2.22
		\pm SD	0.00	0.14	0.12	0.46	1.42	20.38	29.28	13.78
Ambassidae	674	Mean	0.65	0.21	1.80	0.37	1.12	7.79	2.43	2.13
		\pm SD	2.13	1.02	9.50	1.72	2.46	15.33	3.43	7.66
Blenniidae	558	Mean	0.04	0.83	2.26	2.99	3.22	3.98	0.17	2.07
		\pm SD	0.20	1.43	5.02	7.28	8.50	11.48	0.48	6.69
Scorpaenidae	67	Mean	0.00	0.02	0.00	0.00	0.00	0.51	1.50	0.29
		\pm SD	0.00	0.10	0.00	0.00	0.00	1.93	5.78	2.30
Syngnathidae	44	Mean	0.04	0.17	0.33	0.36	0.16	0.05	0.00	0.17
		\pm SD	0.18	0.45	0.70	0.90	0.45	0.20	0.00	0.53
Carangidae	46	Mean	0.00	0.02	0.07	0.02	0.02	0.03	0.91	0.15
-		\pm SD	0.00	0.15	0.43	0.13	0.10	0.17	4.00	1.50
Platycephalidae	26	Mean	0.00	0.00	0.00	0.00	0.00	0.69	0.03	0.11
		+ SD	0.00	0.00	0.00	0.00	0.00	3.45	0.14	1.36
Scatophagidae	11	Mean	0.00	0.02	0.00	0.16	0.02	0.03	0.03	0.04
		\pm SD	0.00	0.14	0.00	0.72	0.10	0.15	0.14	0.30
Leiognatidae	5	Mean	0.00	0.00	0.09	0.02	0.00	0.00	0.00	0.02
		+ SD	0.00	0.00	0.40	0.12	0.00	0.00	0.00	0.16
Bregmacerotidae	5	Mean	0.03	0.00	0.00	0.00	0.00	0.05	0.05	0.02
0		+ SD	0.13	0.00	0.00	0.00	0.00	0.20	0.18	0.11
Terapontidae	2	Mean	0.00	0.00	0.00	0.04	0.00	0.00	0.00	0.01
1		\pm SD	0.00	0.00	0.00	0.26	0.00	0.00	0.00	0.10
Trichonotidae	1	Mean	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.003
		+ SD	0.00	0.00	0.00	0.00	0.00	0.00	0.13	0.05
Triacanthidae	1	Mean	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.004
		+ SD	0.00	0.00	0.00	0.00	0.00	0.15	0.00	0.06
Mullidae	2	Mean	0.03	0.00	0.00	0.00	0.00	0.03	0.00	0.01
		+ SD	0.16	0.00	0.00	0.00	0.00	0.15	0.00	0.08
Mugilidae	1	Mean	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.003
5		+ SD	0.00	0.00	0.00	0.00	0.00	0.00	0.11	0.039
Unidentified	345	Mean	0.54	0.90	0.21	0.11	0.55	2.67	2.94	1.14
		+ SD	1.55	4.39	0.71	0.45	1.68	9.12	4.85	4.52
		<u> </u>								
Total	92,934	Mean	472.11	212.67	311.34	426.97	303.11	259.30	301.96	318.51
		\pm SD	873.93	264.86	459.48	862.56	515.28	318.31	554.95	570.38

 $(311 \pm 460N100 \text{ m}^{-3})$, Station 4 $(426 \pm 863N100 \text{ m}^{-3})$, Station 5 $(303 \pm 515N100 \text{ m}^{-3})$, Station 6 $(259 \pm 318N100 \text{ m}^{-3})$ and Station 7 $(302 \pm 555N100 \text{ m}^{-3})$. Thus, the estuarine mangrove stations (Stations 1–5) generally showed the highest total abundance, but also the most variable as compared to the offshore stations (Stations 6 and 7). Nevertheless, an analysis of abundance by family showed significant differences among stations for some families, such as Gobiidae, Engraulidae, Clupeidae, Sciaenidae, Cynoglossidae, Ambassidae, Blenniidae, Scorpaenidae and Syngnathidae.

3.3. Spatio-temporal abundance of major families

Distribution of larval fish at different ontogenetic stages varied spatially and temporally suggesting preference for certain estuarine or offshore conditions and differences in recruitment time. For instance, although Gobiidae larvae were ubiquitous and present all year round, they appeared to prefer estuarine waters and were more abundant in certain months. On the other hand, engraulid and clupeid larval distribution appeared to be ontogenetically dependent, with the oldest larvae inside the estuary. Detailed descriptions of the major families and their identifiable species or genus are given below.

3.3.1. Gobiidae

This family was recorded at all stations. The larvae were mostly small and very difficult to identify due to the co-presence of at least 17 species from 14 genera (Then, 2008). Based on the presence of young juveniles, the most common species were *Glossogobius giuris*, with less common species such as *Oxyurichthys microlepis*, *Parapocryptes seperaster*, *Pseudacryptes elongates*, *Trypauchen vagina* and *Ctenotrypauchen microcephalus*.

Inside the mangrove estuary, total Gobiidae density ranged from 15 to 1228N100 m⁻³, with a mean of $207 \pm 502N100$ m⁻³. At Station 1, Gobiidae was the most abundant family, at $465 \pm 871N100$ m⁻³ (Fig. 3a), constituting 98% of the total abundance. However, their density decreased towards offshore waters where at Station 7, larval density reached $28 \pm 112N100$ m⁻³ (9% of the total abundance). In offshore waters, mean density of gobiids ranged from 0 to 183N100 m⁻³.

Preflexion gobiid larvae were consistently observed at all stations (> 80%, see Fig. 3a) and months (generally > 40%, with nine out of 18 months showing > 90%) (Fig. 4a). The data suggests continuous or year-round spawnings by gobiid fishes in the mangrove estuary. In March and October 2003, Gobiidae accounted for 93% (921.9 \pm 1013.1N100 m $^{-3}$) and 63.8% (625.4 \pm 944.9N100 m $^{-3}$) of the total abundance, respectively.



Fig. 3. Spatial distribution of developmental stages of six dominant fish families: (a) Gobiidae, (b) Engraulidae, (c) Clupeidae, (d) Sciaenidae, (e) Ambassidae and (f) Blenniidae. Numerals above histograms indicate mean larval density, N100 m⁻³. Standard deviation (SD) in parentheses.

3.3.2. Engraulidae

In the mangrove estuary, mean larval density of *Stolephorus* (*S. baganensis* and *S. indicus*) and *Thryssa* (*T. kammalensis*, *T. hamiltonii* and *T. mystax*) were $70 \pm 187N100 \text{ m}^{-3}$ and $26 \pm 150N100 \text{ m}^{-3}$, respectively. Less *Thryssa* larvae were recorded at the offshore waters $(4 \pm 17N100 \text{ m}^{-3})$, as compared to *Stolephorus* larvae $(51 \pm 122N100 \text{ m}^{-3})$. However, in contrast to Gobiidae, Engraulidae were relatively more abundant at Stations 6 $(150 \pm 240N100 \text{ m}^{-3})$ and 7 $(124 \pm 255N100 \text{ m}^{-3})$ in offshore waters where they constituted 58% and 41% of the total larvae, respectively. Offshore stations had a larger proportion of preflexion stage, whereas mangrove areas had a larger proportion of postflexion stage (> 60%) (Fig. 3b). Postflexion stages and early juveniles were only observed in mangrove waters.

Mean density of the engraulids was the highest $(564 \pm 448N100 \text{ m}^{-3})$ in August 2002 (Fig. 4b) when 88% of the total engraulids were in the preflexion stage in both mangrove and offshore waters. In offshore waters, more than 70% of the total engraulids consisted of preflexion larvae from May to December 2002 with the highest abundance in September 2002 (99%). The data thus suggested that major spawnings of engraulids occurred from May to September.

3.3.3. Clupeidae

The clupeid larvae had not been identified to the lowest level, but based on the presence of their youngest juveniles in the area, they comprised of the following species, ranked by abundance: Anodontostoma chacunda, Escualosa thoracata, Nematolosa nasus and Sardinella gibbosa. The clupeids were more abundant in offshore waters where the highest abundance $(99 \pm 319N100 \text{ m}^{-3})$ was recorded from Station 7 where preflexion larvae contributed 92.3% of the total clupeids (Fig. 3c). Mean density of the clupeids increased from April to its peak in June 2003 ($175 \pm 477N100 \text{ m}^{-3}$) when preflexion stage constituted 98% of the total clupeids (Fig. 4c). The month of June 2003 could be their main spawning period. Preflexion larvae dramatically decreased in abundance towards the estuary, which recorded almost entirely of postflexion larvae at less than $3N100 \text{ m}^{-3}$.

3.3.4. Sciaenidae

This family is one of the most diverse in the study site, comprising 14 species and 8 genera with *Johnius* (7 species) being the most speciose (Then, 2008). The collected larvae of different ontogenetic stages were very difficult to distinguish even to the generic level; the recorded genera were *Johnius*, *Dendrophyssa*, *Nibea*, *Otolithes*, *Otolithoides*, *Aspericorvina*, *Panna* and *Pennahia*.

Sciaenid larvae were more abundant in offshore areas, with mean abundance of $36 \pm 129N100 \text{ m}^{-3}$ and $33 \pm 101N100 \text{ m}^{-3}$ at Stations 6 and 7, respectively, as compared to the mangrove estuary with mean of less than $4N100 \text{ m}^{-3}$ (Fig. 3d). At Station 6, 99% of the total sciaenids consisted of preflexion larvae, while at Station 7 the sciaenids comprised 47% preflexion and 52% postflexion larvae.



Fig. 4. Temporal distribution of developmental stages of six dominant fish families: (a) Gobiidae, (b) Engraulidae, (c) Clupeidae, (d) Sciaenidae, (e) Ambassidae and (f) Blenniidae. Numerals above histograms indicate mean larval density, N100 m⁻³. Standard deviation (SD) in parentheses.

Sciaenid preflexion larvae were present throughout the year (Fig. 4d). In the mangrove estuary, sciaenids, which occurred mainly as preflexion larvae, were found to be abundant in August 2002 (23N100 m⁻³). In the following month, preflexion larvae in the offshore areas also recorded the highest density (275N100 m⁻³). The results suggested that August and September 2003 were their main spawning period. Postflexion larvae comprised 88% (138 ± 276N100 m⁻³) of the total larvae in October 2003 in the offshore areas.

3.3.5. Ambassidae

Most of the ambassid larvae comprising *Ambassis gymnocephalus* were found at Station 6 where 96% of them were postflexion larvae $(8 \pm 15N100 \text{ m}^{-3})$. The abundance of ambassid larvae in offshore areas, for all ontogenetic stages, were significantly (P < 0.05) higher than inside the mangrove estuary. Although there was no clear spatial separation of ontogenetic stages, the uppermost station (Station 1) contained more than 60% preflexion larvae and later stage larvae were found more towards offshore waters (Fig. 3e).

Mean density of ambassids appeared to be the highest in June 2002 and 2003 (Fig. 4e). Postflexion larvae dominated most of the catch throughout the year, while preflexion larval abundance was the highest in December and May.

3.3.6. Blenniidae

Blenniids (*Omobranchus* spp.) were present at all stations in low numbers but most were encountered from Station 3 to Station 6, with mean density that ranged from 2.3 to $4N100 \text{ m}^{-3}$ (Fig. 3f). Most larvae were preflexion larvae. Monthly abundance of blenniids ranged from 0 to 5.9N100 m⁻³ (absent in two out of 18 months) and preflexion stage made up the most by station and month (Fig. 4f).

3.3.7. Other families

Cynoglossidae comprising four Cynoglossus spp. (C. bilineatus, C. lingua, C. puncticeps and C. cynoglossus), whose larval stages have yet to be positively identified, was recorded at all stations except Station 1. They were abundant at the offshore areas especially at Station 7 (10.3 \pm 29.3*N*100 m⁻³). All cynoglossids caught were at the preflexion stage. Cynoglossidae was abundant in September 2002 $(17.4 \pm 34.4N100 \text{ m}^{-3})$ and October 2003 $(12.4 \pm 42.7N100 \text{ m}^{-3})$. Carangids were also found at all stations except Station 1. Most of the Carangidae (Scomberoides and Caranx spp.) were of preflexion stage in offshore areas. The highest density of Syngnathidae was in October 2003, occurring mainly in the mangrove estuary. Around 85% of Syngnathidae caught was pipefish (Ichthyocampus carce), the rest was seahorse (*Hippocampus trimaculatus*). *Scatophagus argus* (Scatophagidae) was found mainly in the mangrove waters except in May 2002 and August 2003. Interestingly, larvae of the reportedly deepwater spotted codlet, Bregmaceros mcclellandi (Bregmacerotidae), were caught in the offshore waters in June and July 2002, and March and August 2003. Leiognathidae (L. brevirostris, L. equulus and two species of Secutor) larvae were recorded inside the mangrove waters, only at Stations 3 and 4. They were only caught in January, March and October 2003, and were mainly postflexion larvae. Most of the Scorpaenidae (likely Vespicula trachinoides) were observed in offshore stations. The larval mullid, Upeneus sulphureus, was recorded at Station 1 in April 2003 and Station 6 in September 2003. Platycephalidae (Platycephalus indicus), Trichonotidae (Trichonotus sp.), Triacanthidae (Tripodichythes



Fig. 5. CCA biplots of larval fish abundance (various symbols) in relation to environmental factors (arrows). Gobiidae, Engraulidae, Clupeidae, Sciaenidae, Ambassidae and Blenniidae are presented by developmental stages. Legend to larval fish families and developmental stages are given in right boxes. Sal—salinity, Temp—temperature, DO—dissolved oxygen, Turb—turbidity, Chl a—Chlorophyll a, Zoo 500—wet weight of '> 500 µm' zooplankton, Zoo 250—wet weight of '250–500 µm' zooplankton, Zoo 125—wet weight of '125–250 µm' zooplankton.



Fig. 6. CCA attribute biplots of larval Gobiidae abundance (bubble plots) in relation to environmental factors (arrows), (a) preflexion stage, (b) flexion stage, and (c) postflexion stage. Sal—salinity, Temp—temperature, DO—dissolved oxygen, Turb—turbidity, Chl a—Chlorophyll a, Zoo 500—wet weight of '> 500 µm' zooplankton, Zoo 250—wet weight of '250–500 µm' zooplankton, Zoo 125—wet weight of '125–250 µm' zooplankton.

blochii or *Triacanthus biaculeatus*) and Mugilidae (*Liza melinoptera* or *L. subviridis*) were only recorded from the offshore stations.

3.4. Fish family in relation to water parameters and plankton

The abundance of fish larvae was related to five water parameters (salinity, temperature, dissolved oxygen, pH and turbidity) and two indicators of fish food abundance (zooplankton and chlorophyll *a*) using Canonical Correspondence Analysis (CCA). The first two CCA axes accounted for 69.3% of the variance in the correlation of species-environmental parameters. Salinity appeared to be the most significant factor influencing the distribution and abundance of most larval fish. Mugilid, sciaenid, cynoglossid, triacanthid and platycephalid larvae generally preferred more saline, well oxygenated offshore waters in spite of the lower zooplankton abundance (Fig. 5). All larval stages of the Gobiidae and the postflexion and postlarvae of Engraulidae, Syngnathidae and Mullidae were more abundant in the less saline, zooplankton richer water inside the mangrove. Also in the mangrove were the Leiognathidae and Terapontidae, which preferred the more turbid, cooler and greener water.

In particular, the preflexion larvae of gobiids were ubiquitous, being quite spread out over the coastal belt although higher densities were observed in the more turbid water inside the mangrove estuary (Fig. 6a). The larger flexion and postflexion larvae were more abundant inside the mangrove estuary where their numbers were strongly related to the abundance of zooplankton, which may be their primary food source (Fig. 6b and c). Preflexion and flexion ambassid larvae preferred the warmer and clearer waters of both coastal and estuarine waters. In the estuary, their abundance correlated well with higher zooplankton abundance. More postflexion larvae were however encountered in warmer, well oxygenated and higher salinity water (Fig. 5).

The preflexion larvae of engraulids were preponderant in coastal waters where they were likely spawned (Fig. 7a). However, these larvae entered the mangrove areas at the flexion and postflexion stages, which showed high affinity for turbid and greener water (Fig. 7b and c). Both the postflexion and in particular the postlarval stage showed greater preference for zooplankton inside the estuary (Fig. 7d). Clupeid larvae similarly spawned in less turbid, warmer and well oxygenated offshore waters (Fig. 5). Although they tend to maintain their position in



Fig. 7. CCA attribute biplots of larval Engraulidae abundance (bubble plots) in relation to environmental factors (arrows), (a) preflexion stage, (b) flexion stage, (c) postflexion and (d) postlarvae stage. Sal—salinity, Temp—temperature, DO—dissolved oxygen, Turb—turbidity, Chl a—Chlorophyll a, Zoo 500—wet weight of '> 500 µm' zooplankton, Zoo 250—wet weight of '250–500 µm' zooplankton, Zoo 125—wet weight of '125–250 µm' zooplankton.

offshore waters, postflexion clupeid larvae did enter mangrove waters, presumably to feed on the richer zooplankton resources.

Preflexion larvae of sciaenids also occurred mainly in coastal waters although they were also present inside the estuary where zooplankton were abundant (Fig. 8a). Some of the more developed flexion and postflexion larvae inside the estuary seemed to move towards more saline offshore waters (Fig. 8b and c). Nevertheless, it is possible that larvae of certain sciaenid species do not show ontogenetic movement since the sciaenid species were not identified in this study.

4. Discussion

The ichthyoplankton diversity of the mangrove system in Matang was low since only 19 families were recorded, and of these, four families (Gobiidae, Engraulidae, Clupeidae and Sciaenidae) cumulatively make up 97.5% of the total larval abundance. Some rarely caught families accounted for less than 1% of the total larvae. This type of situation has been similarly reported in other estuarine larval fish populations. For example, 25 families (54 taxa) were identified in North Brazilian mangrove creeks (Barletta-Bergan et al., 2002), 25 families in the mangrove creeks of East Africa (Little et al., 1988) and 26 families (56 taxa) in Sabah and Sarawak estuaries, Malaysia (Blaber et al., 1997).

The mean total fish densities of 22 to $1247N100 \text{ m}^{-3}$ in Matang estuary from the present study were comparable to those reported in the estuaries of Sabah and Sarawak, which ranged from 3 to $920N100 \text{ m}^{-3}$ (Blaber et al., 1997). In an east African mangrove creek, the mean total fish larvae ranged from 120 to $200N100 \text{ m}^{-3}$ (Little et al., 1988), while in the St. Lucia estuary of KwaZulu-Natal (South Africa), the fish larvae density ranged from 15 to $1003N100 \text{ m}^{-3}$ (Harris and Cyrus, 1995). Generally, the number of larval fish taxa and their densities among studies vary greatly, which may be due to differences in sampling methods, sampling time, abiotic environment, habitat heterogeneity and the level of positive larval identification.

As was also reported by Kuo et al. (1999) and Robertson and Duke (1990), the present study shows that the spatial rather than temporal factor contributed more to the differences in larval



Fig. 8. CCA attribute biplots of larval Sciaenidae abundance (bubble plots) in relation to environmental factors (arrows): (a) preflexion stage, (b) flexion stage and (c) postflexion stage. Sal—salinity, Temp—temperature, DO—dissolved oxygen, Turb—turbidity, Chl a—Chlorophyll a, Zoo 500—wet weight of '> 500 µm' zooplankton, Zoo 250—wet weight of '250–500 µm' zooplankton, Zoo 125—wet weight of '125–250 µm' zooplankton.

assemblage structure. The ANOVA results indicate that 60% of the total variability in families was due to spatial differences while the temporal (month) differences accounted for 25%. Although the distance between the river mouth and the nearest offshore station was short (8 km), fish assemblages and their ontogenetic stages were quite distinct between the mangrove and offshore waters. Variable larval tolerance to different physical, chemical and biological factors, as well as their nursery habitat requirements (Kuo et al., 1999; Peters et al., 1998), could result in the observed spatial difference.

Larval fish diversity of the Matang mangrove estuary was lower as compared to the adjacent coastal waters, whereas larval abundance was generally higher inside the estuary (see Table 1). The higher abundance was attributable to the consistently abundant Gobiidae, which are typical estuarine residents that include the familiar mudskippers. Gobiid larvae are likely to dominate estuarine waters because they form the most speciose family of estuarine and marine fishes (Nelson, 2006) and have a relatively long larval phase of approximately 40 days (Thresher, 1984). In the present study, gobiid larvae of all ontogenetic stages were found throughout the mangrove estuary, indicating their use of the mangrove estuary as feeding, spawning as well as nursery ground. Other larval studies have recorded similar findings, for examples, Little et al. (1988) recorded 69% gobiids in an East African mangrove creek, while in the Lupar and Lassa estuaries of Sarawak (Malaysia), gobiids constituted 38% and 34%, respectively (Blaber et al., 1997). Janekarn and Boonruang (1986) reported that gobiid larvae accounted for 60% of their collected larvae from the Andaman Sea. Kuo et al. (1999) reported 18 species of Gobiidae, which was identified as the most diverse family in the mangrove creeks of the western coast of Taiwan. In Matang waters, 13 species of juvenile and adult gobies have so far been recorded (Chong, 2005; Then, 2008).

Euryhaline fishes such as the Sciaenidae may spawn inside the estuary and also in adjacent coastal waters. Their larvae are exported outside to the adjacent coastal waters or into the estuary irrespective of their developmental stage. Of the 14 species of sciaenids recorded from Matang mangrove estuary, 11 species have also been found in offshore waters (Chong, 2005; Then, 2008). This explains the appearance of preflexion larvae in both the estuary and adjacent coastal waters. Their year-round presence could be due to their dietary flexibility for which Yap et al. (1994) had recorded monthly dietary changes involving 12 prey taxa for seven major sciaenid species occurring in Matang waters.

Sasekumar et al. (1994) however reported that as high as 87% of the fishes in Matang mangrove waterways and 83% in adjacent

mudflats were sexually immature or juveniles; from this, they suggested that the mangrove estuary plays a bigger role as nursery ground than as a spawning ground. The present study showed the importance of the mangrove estuary as nursery site for marine migrants belonging to especially the Engraulidae, Clupeidae and Ambassidae, that enter the estuary at predominantly the postflexion and postlarval stages. The engraulid Stolephorus baganensis is a multiple spawner, spawning all year round in clearer and relatively deep coastal waters (Sarpedonti and Chong. 2008). Their postflexion larvae (ca. 10 mm SL) then move towards the shallower and more turbid waters where they remain until the juvenile stage (three month old). Sasekumar et al. (1994) also observed a similar migration pattern for another engraulid species, Thryssa kammalensis, which moves into the Matang estuary as early juveniles. Their upstream migration and taking residence in the estuary has been viewed as a migratory behavior that enhances juvenile survival (Blaber, 1997).

The various studies of juvenile and adult fish fauna in the Matang estuary have so far yielded 53 families (Table 2), while the present larval study recorded only 17 families. This big discrepancy in numbers clearly shows that the juvenile fish assemblage is guite disconnected from the existing larval fish populations in the mangrove estuary as well as nearshore waters. The study suggests that except for those species that spawn in upstream waters and those with non-planktonic larvae, many of the euryhaline species that visit the mangrove estuaries and nearshore waters are likely to spawn farther offshore (i.e. beyond 16 km) in marine waters. Quinn and Kojis (1985) recorded a similarly low number of species from the Labu estuary, Papua New Guinea (PNG), and suggested that the diversity of the mangrove ichthyofauna is not directly related to the diversity of the coastal waters in spite of the fact that PNG lies within the Indo-Malayan region, which supports the highest diversity of reef fishes. In a study of the nearshore larval fish assemblage off the St. Lucia estuary, South Africa, Harris et al. (1999) reported not only a high diversity of fish (89 families, 186 species), as opposed to 44 families (85 species) in the St. Lucia estuary (Harris and Cyrus, 1995), but also larval dominance (90% abundance) of marine spawners that were not dependent of estuaries. They attributed these to local spawning populations in the shelf waters and mesopelagic larvae transported from deep slope waters by the prevailing currents.

The present study substantiates the importance of the mangrove as nursery area for marine euryhaline species (76% of estuarine fish population), which seek mangroves mainly at the juvenile stage (Chong, 2005). Blaber (2000) reported very few

Table 2

Life history stages of fish families in Matang mangrove estuary and adjacent coastal waters, Malaysia.

No.	Family	Mangrove	estuary		Offshore (< 16 km)			
		Larvae ^a	Juvenile ^c	Adult ^{b,c}	Larvae ^a	Juvenile ^c	Adult ^c	
1	Ambassidae	•	•	•	•	•	•	
2	Apistidae			•				
3	Ariidae		•	•		•	•	
4	Bagridae		•	•				
5	Batrachoididae		•	•				
6	Belonidae	•		•	•			
7	Blenniidae	•			•			
8	Bregmacerotidae	•			•	•	•	
9	Callionymidae		•	•			_	
10	Caraligidae	•	•	•	•	•	•	
11	Centropolitidae		•	•				
12	Cichlidae		•	•				
14	Chirocentridae		•	•				
15	Clupeidae	•	•	•	•	•	•	
16	Cynoglossidae						•	
17	Cyprinodontidae	•	•	•	•	•	•	
18	Dasvatidae		•	•		•	•	
19	Drenanidae		•	•		•	•	
20	Eleotridae		•	•		•	•	
21	Elopidae			•				
22	Engraulidae	•	•	•	•	•	•	
23	Ephippidae					•	•	
24	Gerreidae		•	•				
25	Gobiidae	•	•	•	•	•	•	
26	Haemulidae		•	•		•	•	
27	Hemiramphidae			•				
28	Hemiscylliidae					•	•	
29	Latidae		•	•				
30	Leiognathidae	•	•	•		•	•	
31	Lobotidae					•	•	
32	Lutjanidae		•	•		•	•	
33	Megalopidae		•	•				
34	Mugilidae		•	•	•	•	•	
35	Mullidae	•	•	•	•	•	•	
36	Muraenesocidae		•	•		•	•	
37	Ophichthidae					•	•	
38	Paralichthyidae		•					
39	Platycephalidae		•	•	•	•	•	
40	Plotosidae		•	•		•	•	
41	Polynemidae		•	•		•	•	
42	Pristigasteridae		•	•		•	•	
43	Scatophagidae	•	•	•	•	•	•	
44	Scombridge	•	•	•	•	•	•	
46	Scornsenidse	•	•	•	•	•	•	
40	Serranidae	•			•	•	•	
48	Sillaginidae					•	•	
49	Siganidae		•	•		•	•	
50	Soleidae		-	•		-	-	
51	Sphyraenidae		•	•		•	•	
52	Stegostomatidae		•	•		•	•	
53	Stromateidae			•		•	•	
54	Syngnathidae	•			•			
55	Synodontidae		•	•		•	•	
56	Terapontidae	•	•	•		•	•	
57	Tetradontidae	•	•	•		•	•	
58	Toxotidae			•				
59	Triacanthidae		•	•	•	•	•	
60	Trichiuridae			•			•	
61	Trichonotidae				•			

^a This study.

^b Chong (2005).

^c Then (2008).

marine euryhaline migrate into estuaries to spawn. The few exceptions include certain species of the Mugilidae, Ariidae, Sciaenidae, Ambassidae and Dasyatidae (Chong, 1977; Singh, 2003; Yap, 1995). Nonetheless, larval absence in the water despite

actual spawning may be due to post-spawning behavior as displayed by most ariids. The male practices oral or buccal incubation of spawned eggs until a time when the young are released once capable of active feeding (Rimmer and Merrick, 1982). Adult ovoviviparous stingrays (*Himantura walga*) caught in the mangrove have been observed to bear young in their uterus (personal observation). On the other hand, while larval Blenniidae were caught in the present study, previous studies in the mangrove estuary had never reported any juvenile or adult blennies. Adult blennies were not caught perhaps due to their burrowing or benthic nature and/or their close association with reefs, pilings or tidal pools. Inside the mangrove forest floor, some species of *Omobranchus* hide in the crevices of dead branches and logs and among mangrove roots (H. Larson, Darwin, personal communication).

Environmental factors greatly affect the ichthyoplankton assemblages of mangrove estuaries. In KwaZulu-Natal estuaries and nearshore coastal habitats of South Africa, the larval fish assemblages apparently depend on environmental conditions such as salinity, temperature and turbidity at the time of recruitment (Harris and Cyrus, 1995; Harris et al., 1999). In Taiwan, Huang and Chiu (1998) showed that the abundance of Acanthopagrus schlegelii larvae was negatively correlated with water temperature and positively correlated with salinity and dissolved oxygen. In the Ganges estuary, mudskippers of three genera spawned during the monsoon period when the salinity was low, and turbidity, temperature and plankton biomass were high-a strategy adopted to ensure sufficient food while reducing predation (Clayton, 1993). Increased turbidity inside the mangrove estuary may decrease the predation risk for small fishes and is believed to have positive effect on fish abundance (Blaber, 2000). The present study also shows a similar strategy adopted by gobiids in the Matang mangrove where all larval stages showed preference for low salinity, high turbidity and higher plankton food (see Fig. 5). Flexion, postflexion and juveniles of engraulid larvae were also closely associated with higher turbidity and their plankton food (see Figs. 5 and 7). Fish stomach content analysis revealed that 10 of the 26 major species of examined small and juvenile fishes in the Matang estuary depended heavily on copepod as food (Chew et al., 2007). The fish diet comprised 47 taxa of prey food, but copepods and Acetes shrimps constituted 53% and 16%, respectively. Notwithstanding, the response of fish larvae to environmental variables is likely species specific, and hence may not equally apply to all species within a family (see Tzeng and Wang, 1992).

5. Conclusions

The larval fish assemblage in the Matang estuary is generally similar to those found in adjacent offshore waters except for two families. This is due to larval flux between estuary and coastal waters, whereby postflexion larvae or young juvenile of euryhaline migrant species are imported into the estuary, while yolk and preflexion larvae of resident species are exported out of the estuary. Although larval advection into or off the estuary is tidal, the final result of advection appears to be modulated by salinity and turbidity gradients, larval food availability, as well as larval stage and possibly larval behavior. Based on their larval presence, Matang fishes could be classified as follows: (1) estuarine group, those that utilize the mangrove estuary (including nearshore water) as spawning and nursery ground, e.g. Gobiidae, Syngnathidae and Ambassidae; (2) marine euryhaline group, those that spawn in the sea but their larvae utilize the estuary and adjacent coastal waters as nursery ground; there are two types, those that (a) enter as larvae, e.g. Engraulidae, Clupeidae and Leiognathidae, Scatophagidae, Terapontidae, Scorpaenidae, Sciaenidae, Blenniidae, Platycephalidae, Carangidae and Mullidae, and (b) enter as juveniles, e.g. Lutjanidae and Serranidae; (3) stenohaline group, which spawn only in the offshore waters and their larvae may enter the estuary during the dry season, e.g. Cynoglossidae, Bregmacerotidae, Trichonotidae and Triacanthidae.

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