Intra-Annual and Family-Specific Assemblage of Fish Larvae in the Straits of Malacca

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ABSTRACT

Fish larvae are marine environmental indicators in the nearshore ecosystem. Identifying environmental factors influencing their assemblages offers insights into ecosystem dynamics and supports effective management of commercial fish stocks. We assessed the effects of intra-annual water quality and monsoon-related months on fish density in a tropical nearshore ecosystem in the Straits of Malacca. The study was conducted during the inter-monsoon (INTM) period (March-April) and the northeast monsoon (NEAM) period (October-November) in 2021. Using the Akaike Information Criterion (AIC) to rank general linear models, we discovered that pH, temperature, total dissolved solids, and monsoon period interactively influenced fish larvae density. These parameters appeared in the top four models ($\Delta AIC \leq 2$) out of 37 tested. The larval fish families Engraulidae, Ambassidae, Blennidae, and Gobiidae had an occurrence rate of >50% and were classified as 'common'. Fourteen families were classified as ‘rare’, with 12 found only in NEAM samples and two in INTM samples. The fish larvae’s affinity for a narrow range of water quality and specific monsoon conditions informs intra-annual fisheries management and conservation strategies in nearshore marine ecosystems.

Keywords: Akaike information criterion, Fisheries management and conservation, General linear model, Monsoon, Nearshore marine ecosystem

INTRODUCTION

Understanding how environmental factors influence fish spawning and larval recruitment provides insights into marine zooplankton ecology, commercial fish stock management and environmental indicators. The insights enhance the accuracy of marine ecosystem assessments, particularly in evaluating population recruitment status (Santos *et al*., 2017). Recruitment patterns in marine ecosystems vary temporally with seasonal changes and wind directions and spatially between offshore and nearshore enviroments (Félix-Hackradt *et al*., 2013). Water quality is closely tied to these spatiotemporal variations, with its effects on larval fish assemblages potentially lasting for months, shaping spawning events and seasons (Álvarez *et al*., 2012).

The spatial and temporal distribution of fish larvae is driven by a complex interplay of environmental factors and ecological processes. These assemblages reflect the location of spawning sites, the availability of nursery habitats, and oceanographic conditions such as currents and temperature gradients (Perry *et al*., 2019; Martinho, 2022). Understanding these patterns is crucial for effective marine management and conservation efforts, as they help identify key habitats and inform strategies to sustain fish populations.

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Larval assemblage structures provide insights into marine ecosystem health and dynamics, as they are directly linked to reproductive success of adult fish and the quality of spawning habitats, often influenced by monsoon seasons (Trindade-Santos and Freire, 2015). Monsoons play a crucial role in shaping tropical marine ecosystems by influencing sea surface temperatures, nutrient upwelling, and salinity, which in turn impact the distribution and abundance of marine species (Sadatzki *et al*., 2016; Nyadjro, 2021). Seasonal monsoon shifts, such as the southwest and northeast monsoons in the Indian Ocean, can drive significant changes in fish populations and spawning activities (Lo *et al*., 2010), impacting larval dispersal and habitat connectivity (Jones *et al*., 2009).

Spawning temperature preferences vary among species, with some requiring precise thermal conditions for successful reproduction (Arantes *et al*., 2010). Water temperature and salinity fluctuations can significantly affect larval distribution and survival, leading to distinct spatial patterns (Wang *et al*., 2023). Even minor variations in water quality parameters can influence spawning and migration behaviors, ultimately shaping larval assemblages (Rijnsdorp *et al*., 2010; Pfauserová *et al*., 2022).

Given the importance of water quality in nearshore ecosystems, it is a key factor in predicting the abundance and assemblage patterns of marine organisms. This study aims to assess the effects of monsoon seasons and water quality on larval fish recruitment in a nearshore ecosystem. We hypothesised that larval fish density is influenced by water quality, which is inherently linked to seasonal monsoon winds.

MATERIALS AND METHODS

Sample collection

A total of 52 larval fishes and water quality samples were collected from eight stations along a coastline portion of the west coast of Peninsular Malaysia (Figure 1). The overall depth of the sampling area was between 1 and 5 m during the lowest tide, and 3 to 9 m during the highest tide (chart catalogue no. MAL 5230; National Hydrographic Centre Malaysia, 2023).

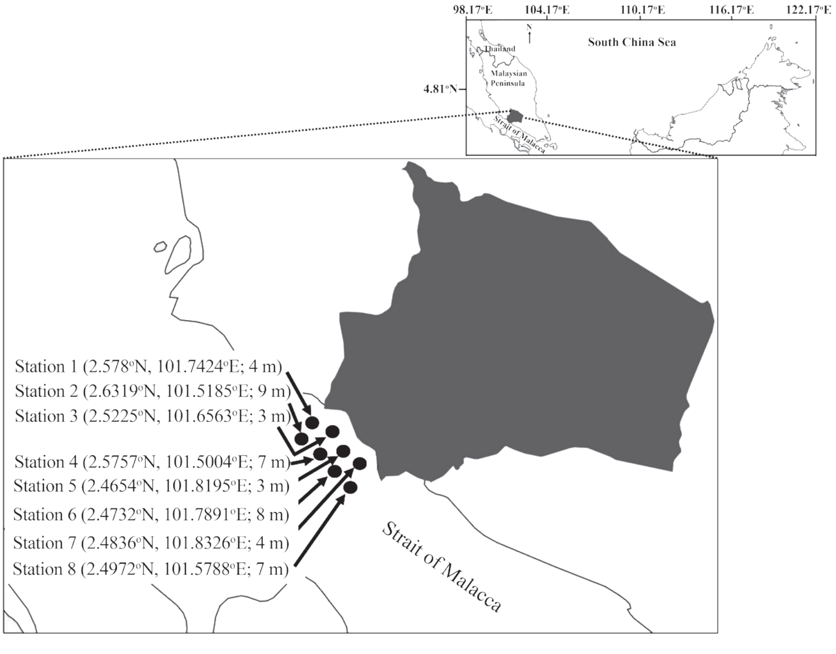

Figure 1. Sampling stations along the Negeri Sembilan coastline in the Strait of Malacca, with numbers in brackets represent latitude, longitude, and depth.

The samples were collected during two fieldwork occasions corresponding to monsoon seasons in the Southeast Asian region. Fieldwork was carried out between March and April 2021 during the inter-monsoon (INTM) season (n = 32) and between October and November 2021 during the northeast monsoon (NEAM) season (n = 20). The imbalance in sample size between the two periods was due to routine fieldwork serving two separate objectives (unpublished). The datasets from both seasons were combined to evaluate the potential effects of monsoon variation on the sampled larval fish assemblages.

All field samples were collected during peak spring tide, shortly after the new lunar (NL) and full lunar (FL) phases, to minimize tidal influence on larval fish assemblages. Boat trips were scheduled to depart from shore when the tide was at or near its highest point. Day trips began approximately 8:00 a.m., 7:00 p.m. each lasting four hours and concluding before the tide receded to low levels.

A Bongo net with a 0.6 m diameter circular ring inlet and a 3 m-long net was used for larval fish collection. The net had a mesh size of 300 µm. It was towed horizontally at a depth of approximately 1.5 m below the water surface, maintained at an angle of 30° to 45° to prevent it from dragging too close to the bottom or remaining near the surface. Sampling was conducted from a moving boat at a constant speed of 2.5 $km \cdot h^{-1}$ and lasted for 10 min for each tow.

Larval fish samples collected from the Bongo net were preserved in 5% borax-buffered formalin and transported to the laboratory for future analysis. Enumeration and taxonomic identification were performed using a camera-mounted light microscope (Zeiss Axioscope 1 and AxioCam ERc 5, Germany). Environmental parameters, including dissolved oxygen ($mg \cdot L^{-1}$), water temperature (°C), salinity (ppt), pH, and total dissolved solids ($mg \cdot L^{-1}$), were measured in situ using a YSI™ 556 multiparameter meter.

Larval fish identification

Larval fish were identified to the family level. Identification keys from Jeyaseelan *et al*. (1998), Kawaguchi (2003), Leis and Carson-Ewart (2004), Konishi *et al*. (2012) and Okiyama (2014) were used for classification. Larval fish density was calculated as the number of individuals per unit volume of water (m^3) that passed through the Bongo net. The identified larvae in each sample were counted to assess diversity indices, including relative abundance, dominance, and evenness using the following formula:

Simpson's index (1-D):

$$1\text{-}D = 1-\sum_{i=1}^{R}\left(\frac{n_i\,(n_i-1)}{N(N-1)}\right) \qquad \text{(Equation 1)}$$

where R = total number of families in the sample, n_i = number of individuals in family i, and N = total number of individuals in the sample (Simpson, 1949).

Shannon-Weiner (H′)

$$H' = \sum_{i=1}^{R} \ln(p_i) \qquad \text{(Equation 2)}$$

where R = number of individuals in family i, and p_i = proportions of individuals that belong to family i (Shannon, 1948).

Jaccard Evenness Index (J'):

$$J' = \frac{H'}{H'_{max}} \qquad \text{(Equation 3)}$$

where H' is derived from the Shannon-Wiener diversity index, and H'_{max} represents maximum possible value of H' (Pielou, 1966).

Data analysis

The occurrence of each larval fish family identified during the study period was measured by calculating its occurrence rate, expressed as a percentage (%). The occurrence rate was are calculated as follow:

The number of stations where a larval fish family was found out of 32 samples collected during the inter-monsoon sampling,
(Equation 4)

(b) the number of stations where a larval fish family was found out of 20 samples collected during the northeast monsoon sampling,
(Equation 5)

(c) the number of samples in which a larval fish family was present across both sampling occasions
(Equation 6)

A family with an occurrence rate ≥50% was considered as 'common,' while those with an occurrence rate of <50% is considered 'rare'.

Then, the effect of the monsoon fieldwork on the diversity indices Simpson's index (1-D), Shannon-Weiner Index (H'), and evenness was tested using one-way analysis of variance (ANOVA) at a 95% confidence interval ($\alpha = 0.05$).

Since families may be positively or negatively associated with each other, we analyzed family co-occurrence patterns using the 'cooccur' package in RStudio (Griffith *et al*., 2016). This package calculates the observed and expected frequencies of co-occurrence between each unique pair of larval fish families based on data from the 52 samples collected during both INTM and NEAM.

To examine the influence of monsoon and water quality on larval fish density, we tested 37 additive and interaction linear models. Model selection was conducted by ranking candidate models according to the Akaike Information Criterion (AIC) using the AICcmodavg package (version 2.3–3) in R (Mazerolle, 2023). Models with an AIC difference (ΔAIC) of ≤2 from the top-ranked model were considered as alternative explanations for larval fish density variation.

Model diagnostics were performed to evaluate the performance of the top multiple linear models in estimating fish larvae density, including:

(a) plotting observed against predicted values to assess model fit,

(b) examining residuals against predicted values and applying Breusch-Pagan test to check for homoscedasticity (constant variance),

(c) generating a Quantile-Quantile (Q-Q) plot to determine whether residuals follow a normal distribution, and

(d) analyzing residuals against each explanatory variable to test for independence assumption.

All statistical analyses and graphical visualizations were performed in RStudio (RStudio Team, 2023).

RESULTS

Diversity

A total of 30 larval fish families were identified in this study, with 18 families recovered from inter-monsoon (INTM) samples and 28 from northeast monsoon (NEAM) samples. Larval fish density varied between 0.2 and 30.4 individuals·m^{-3} for INTM samples, whereas NEAM samples exhibited a wider range, from 2.0 to 1,168 individuals·m^{-3}. Overall, the accumulated larval fish density for NEAM samples (1,710 individuals·m^{-3}) was approximately 10 times higher than that of INTM samples (176 individuals·m^{-3}). Notably, 68% of the NEAM catch was collected from a single sampling station (Station 1) which is located near a mangrove system, during a new lunar phase night. Within this station, Gobiidae accounted for 94% of the total sample, corresponding to a density of 1,097 individuals·m^{-3}. In terms of overall larval fish composition, pooled density data showed that Engraulidae, Gobiidae, and Blennidae were the dominant families in INTM samples. In contrast, NEAM samples were strongly dominated by Gobiidae, which contributed to more than half of the total fish larval fish density (Table 1).

Table 1. Pooled density of fish larvae (individuals·m^{-3}) sampled from all stations for inter-monsoon (INTM) and north-east monsoon (NEAM) seasons.

Family	**INTM**		**NEAM**	
	Density (individuals·m^{-3})	**Percentage (%)**	**Density (individuals·m^{-3})**	**Percentage (%)**
Ambassidae	97	11.3	312	5.7
Apogonidae	79	9.2	23	0.4
Belonidae	4	0.5	0	0.0
Blennidae	119	13.8	271	5.0
Carangidae	18	2.1	52	1.0
Clupeidae	43	5.0	36	0.7
Cynoglossidae	0	0.0	2	0.0
Eleotridae	3	0.3	0	0.0
Engraulidae	233	27.1	1,053	19.3
Gobiidae	175	20.3	3,410	62.4
Kyphosidae	3	0.3	4	0.1
Leiognathidae	40	4.6	138	2.5
Monacanthidae	0	0.0	3	0.1
Mullidae	0	0.0	12	0.2
Nemipteridae	22	2.6	43	0.8
Ophidiidae	2	0.2	4	0.1
Pomacentridae	1	0.1	20	0.4
Priacanthidae	0	0.0	2	0.0
Rachycentridae	0	0.0	1	0.0
Sciaenidae	4	0.5	1	0.0
Scombridae	16	1.9	29	0.5
Sillaginidae	0	0.0	10	0.2
Soleidae	0	0.0	1	0.0
Sphyraenidae	0	0.0	3	0.1
Syngnathidae	0	0.0	15	0.3
Synodontidae	0	0.0	6	0.1
Tetraodontidae	1	0.1	2	0.0
Trichontidae	0	0.0	2	0.0
Toxotidae	0	0.0	4	0.1
Uranoscopidae	1	0.1	3	0.1
Total	861	100	5,462	100

Although the INTM samples contained fewer families (18), compared to 28 families in the NEAM samples, the larval fish assemblages from the INTM samples tended to exhibit greater diversity than those from the NEAM samples (Figure 2). However, diversity measures were not significantly different between the two sampling periods due to the high variance observed in the NEAM samples. The lower diversity measures in the NEAM samples corresponded to disparities in density and dominance among families, as indicated by the evenness index. Similarly, the evenness index reflected the trends observed in the Simpson (1-D) and Shannon-Wiener (H') diversity indices, highlighting the uneven distribution of larval fish families during NEAM compared to INTM.

Occurrence and co-occurrence rates

With the exception of four families (Belonidae, Eleotridae, Apogonidae, and Scombridae), the occurrence rates of 26 other larval fish families were higher during NEAM compared to INTM. Engraulidae exhibited the highest occurrence rate, appearing in 91% of INTM samples and 100% of NEAM samples. Engraulidae, along with Ambassidae, Blennidae, and Gobiidae, were the only families with occurrence rates greater than 50% in both INTM and NEAM sampling periods (Figure 3). These families can be regarded as 'common' in the study area.

In contrast, 14 families appeared seasonally and were classified as 'rare', as they were either present only in one of the two sampling events or had an occurrence rate below 50%. Of these, 12 families were exclusive to NEAM samples and were absent from INTM samples. Conversely, Belonidae and Eleotridae were only found in INTM samples and were absent during NEAM. Overall, 16 out of the 30 identified larval fish families were present in both sampling events. Engraulidae had the highest occurrence rate of 94% during both sampling events.

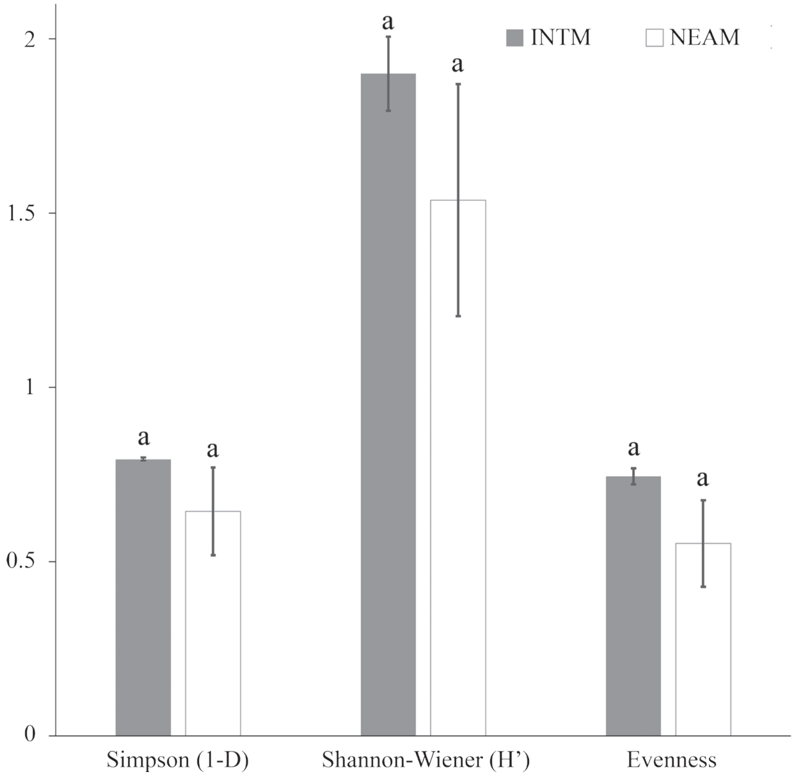

Figure 2. Mean diversity index ±SE of fish larvae sampled during inter-monsoon (INTM) and northeast monsoon (NEAM) seasons.

Note: Bars with the same lowercase letter indicate non-significant difference between mean values for each index.

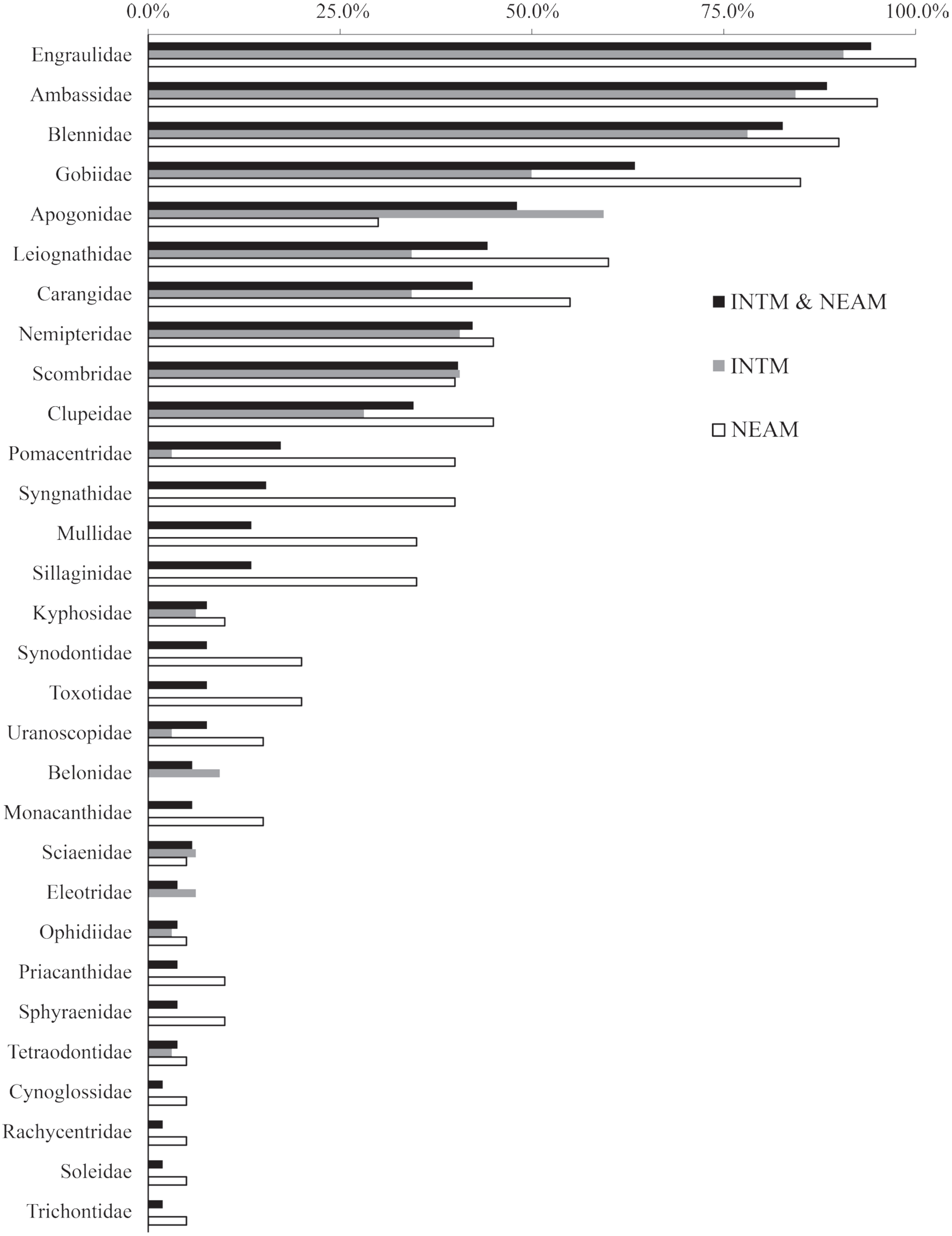

Figure 3. Occurrence rates for each larval fish family recovered from the inter-monsoon (INTM) and northeast monsoon (NEAM) sampling seasons.

The co-occurrence rate of each family pair was largely influenced by their individual occurrence probabilities. Fish larvae families with occurrence rate exceeding 40% also exhibited a high likelihood of co-occurring with one another (Figure 4). Conversely, families with low individual occurrence rates were also less likely to co-occur. Notably, no instances where a low probability of occurrence resulted in a high probability of co-occurrence, especially for families with an occurrence rate below 50%. For example, Nemipteridae and Leiognathidae, which exhibited a co-occurrence rate of 70%, had individual family occurrence rates of 43% and 48% across both seasons, respectively.

Effects of monsoons and water quality of larval fish density

During the fieldwork, the inter-monsoon season (INTM) experienced relatively higher rainfall than the northeast monsoon (NEAM) within the study period and area. Although the seasonal differences were minor, water quality parameters varied between INTM and NEAM (Table 2).

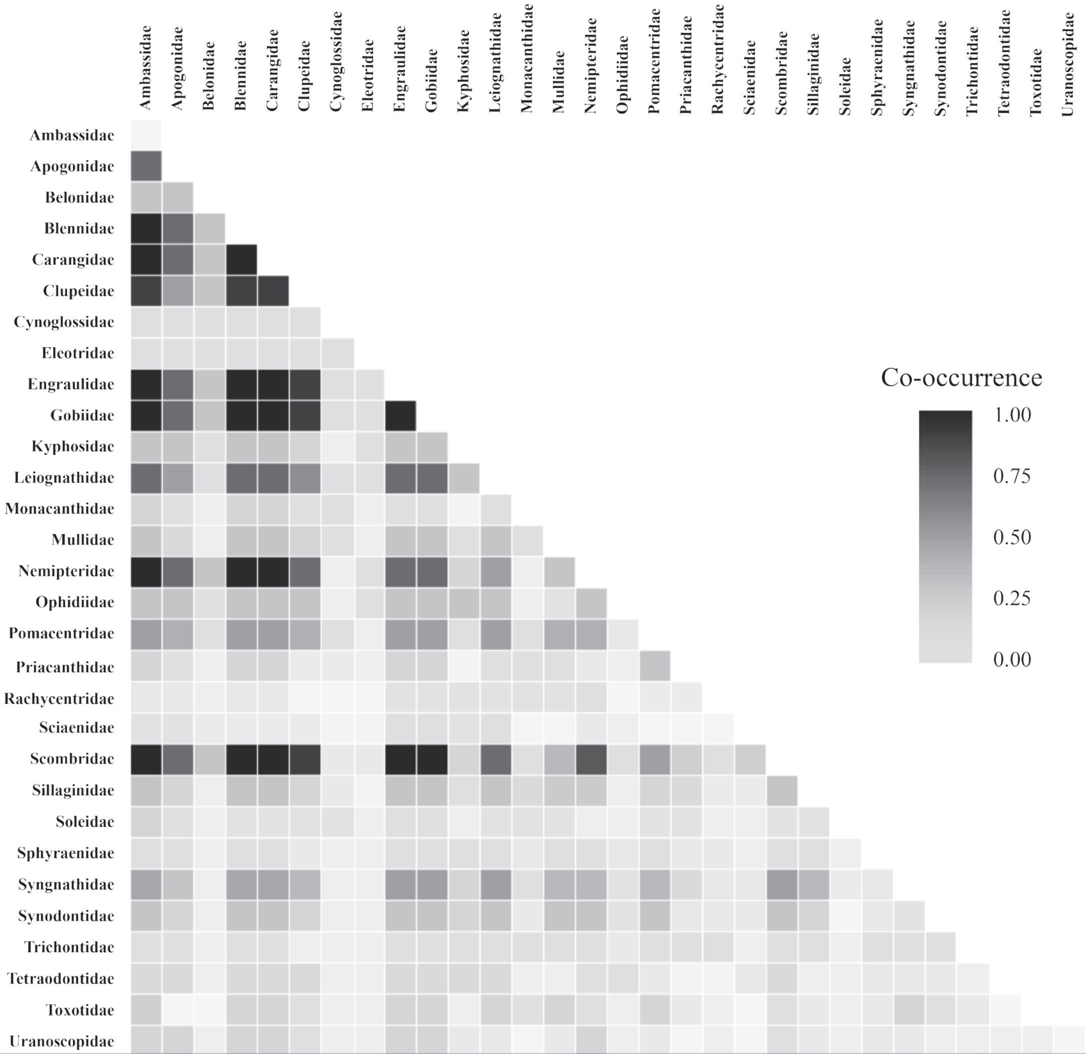

Figure 4. Co-occurrence rates of larval fish families from pooled inter-monsoon (INTM) and northeast monsoon (NEAM) samples (n = 52). The rates are expressed as decimal values.

Table 2. Mean±SE of water quality parameters measured during the inter-monsoon (INTM) and northeast monsoon (NEAM) sampling seasons.

Parameter	INTM	NEAM
pH	8.1±0.03	8.5±0.02
Temperature (°C)	29.3±0.06	30.0±0.12
Dissolved oxygen (mg·L^{-1})	6.1±0.09	6.4±0.06
Salinity (ppt)	29.9±0.02	28.9±0.29
Total dissolved solids (mg·L^{-1})	29.9±0.07	27.1±0.19

Specifically, pH, temperature, and dissolved oxygen were higher during NEAM, whereas salinity and total dissolved solids were higher during INTM. These seasonal differences in water quality may have influenced larval fish assemblages. Therefore, we incorporated these parameters into our candidate models.

An extreme outlier in larval fish density data from Station 1 during the NEAM sampling (new lunar phase) was removed prior to conducting the general linear models (GLM) analysis. As a result, the subsequent linear models were run using 19 samples instead of 20 for that sampling period. A total of 37 alternative models were proposed to explain larval density variation in the study area (Table 3). These models were ranked based on the support they provided for the observed patterns, using the Akaike Criterion Information (AIC) and its derivatives. Four models showed a ΔAIC of $\leq$2 compared to the top model, meaning they provided comparable explanatory power. Collectively, these four models account for 51% of the total AIC weight, indicating their relative importance. The key predictors identified in these models were pH, total dissolved solids (TDS), temperature and monsoon. In contrast, models incorporating salinity and dissolved oxygen provided less explanatory power, with the model using dissolved oxygen as a predictor offering the least support for the observed variation in larval density.

Three of the top four models included interaction between two factors. For instance, the best-supported model contained pH, and temperature, and an interaction between the two (pH×Temperature). Notably, when the interaction term was removed, the model's rank dropped to 27th, indicating the importance of this interaction in explaining larval density variation. Interestingly, models with a higher number of predictors were not necessarily better. The full model (base model), which included all five factors–monsoon, temperature, dissolved oxygen, salinity, and total dissolved solids–ranked only 9th in the model selection list. Paradoxically, the simplest model, which used monsoon as the sole predictor, ranked 16th, demonstrating that while monsoon influences larval density, additional environmental factors play a more significant role.

The parameter estimates from the top-ranked model indicated that pH and temperature significantly influenced larval fish density ($p<0.05$; Figure 5a). Predictions based on this model suggested that larval fish density increased with both pH and temperature (Figure 5b). At lower pH levels, fish larval density declined, with the decrease becoming more pronounced at higher temperatures. However, at lower temperatures, the rate of decline was less severe. The parameter estimates from the second-ranked model, which included temperature and total dissolved solids (TDS), indicated that only temperature had a significant effect on larval fish density ($p<0.05$; Figure 5c). Similar to the top model, larval fish density increased with temperature, with TDS further amplifying this trend. At temperatures below 30 °C, larval fish density remained low (Figure 5d).

Table 3. Candidate multiple linear regression models (MLR) models ranked according to the Akaike Criterion Information Creterion (AIC).

Rank	**Family**	*K*	**AIC**	**ΔAIC**	**Relative likelihood**	**AIC$_{weight}$**
1	pH+temperature+(pH×temperature)	3	424	0	1.000	0.217
2	Temperature+(temperature×total dissolved solids)	3	425	1	0.607	0.132
3	pH+monsoon+(pH×monsoon)	3	426	2	0.368	0.080
4	Temperature+monsoon+(temperature×monsoon)	3	426	2	0.368	0.080
5	Monsoon+salinity	2	427	3	0.223	0.048
6	Temperature+total dissolved solids	2	427	3	0.223	0.048
7	Monsoon+dissolved oxygen+(monsoon+dissolved oxygen)	3	428	4	0.135	0.029
8	pH+total dissolved solids+(pH×total dissolved solids)	3	428	4	0.135	0.029
9	Monsoon+temperature+dissolved oxygen+salinity+total dissolved solids	5	428	4	0.135	0.029
10	Monsoon+temperature	2	428	4	0.135	0.029
11	Dissolved oxygen+total dissolved solids+(dissolved oxygen×total dissolved solids)	3	428	4	0.135	0.029
12	Salinity+total dissolved solids	2	428	4	0.135	0.029
13	Monsoon+dissolved oxygen	2	429	5	0.082	0.018
14	pH+salinity	2	429	5	0.082	0.018
15	pH+salinity+(pH×salinity)	3	429	5	0.082	0.018
16	Monsoon	1	429	5	0.082	0.018
17	Monsoon+salinity+(monsoon×salinity)	3	429	5	0.082	0.018
18	Temperature+salinity	2	429	5	0.082	0.018
19	Dissolved oxygen+total dissolved solids	2	429	5	0.082	0.018
20	Salinity+total dissolved solids+(salinity×total dissolved solids)	3	429	5	0.082	0.018
21	pH+total dissolved solids	2	430	6	0.050	0.011
22	pH+dissolved oxygen+(pH×dissolved oxygen)	3	430	6	0.050	0.011
23	total dissolved solids	1	430	6	0.050	0.011
24	pH+monsoon	2	431	7	0.030	0.007
25	Monsoon+total dissolved solids	2	431	7	0.030	0.007
26	Temperature+salinity+(temperature×salinity)	3	431	7	0.030	0.007
27	pH+temperature	2	432	8	0.018	0.004
28	Total dissolved solids+monsoon+(total dissolved solids×monsoon)	3	432	8	0.018	0.004
29	Temperature+dissolved oxygen+(temperature×dissolved oxygen)	3	432	8	0.018	0.004
30	Dissolved oxygen+salinity+(dissolved oxygen×salinity)	3	432	8	0.018	0.004
31	pH	1	433	9	0.011	0.002
32	Dissolved oxygen+salinity	2	433	9	0.011	0.002
33	pH+dissolved oxygen	2	434	10	0.007	0.001
34	Temperature	1	434	10	0.007	0.001
35	Temperature+dissolved oxygen	2	435	11	0.004	0.001
36	Salinity	1	437	13	0.002	0.000
37	Dissolved oxygen	1	445	21	0.000	0.000

The parameter estimates for the third- and fourth-ranked models indicated that the monsoon had a significant effect on larval fish density ($p<0.05$; Figure 6a and 6c). The prediction models further showed that fish larval density increased with NEAM, given the concurrent increase in pH and temperature (Figure 6b and 6d).

The Breusch-Pagan test for detecting heteroskedasticity in the regression models showed that the errors in the top four models exhibited constant variance. This indicated that these models did not violate the assumption of homoscedasticity, where significance values for the first-, second-, third- and fourth-ranked models of $p = 0.105$, $p = 0.054$, $p = 0.073$ and $p = 0.069$ respectively.

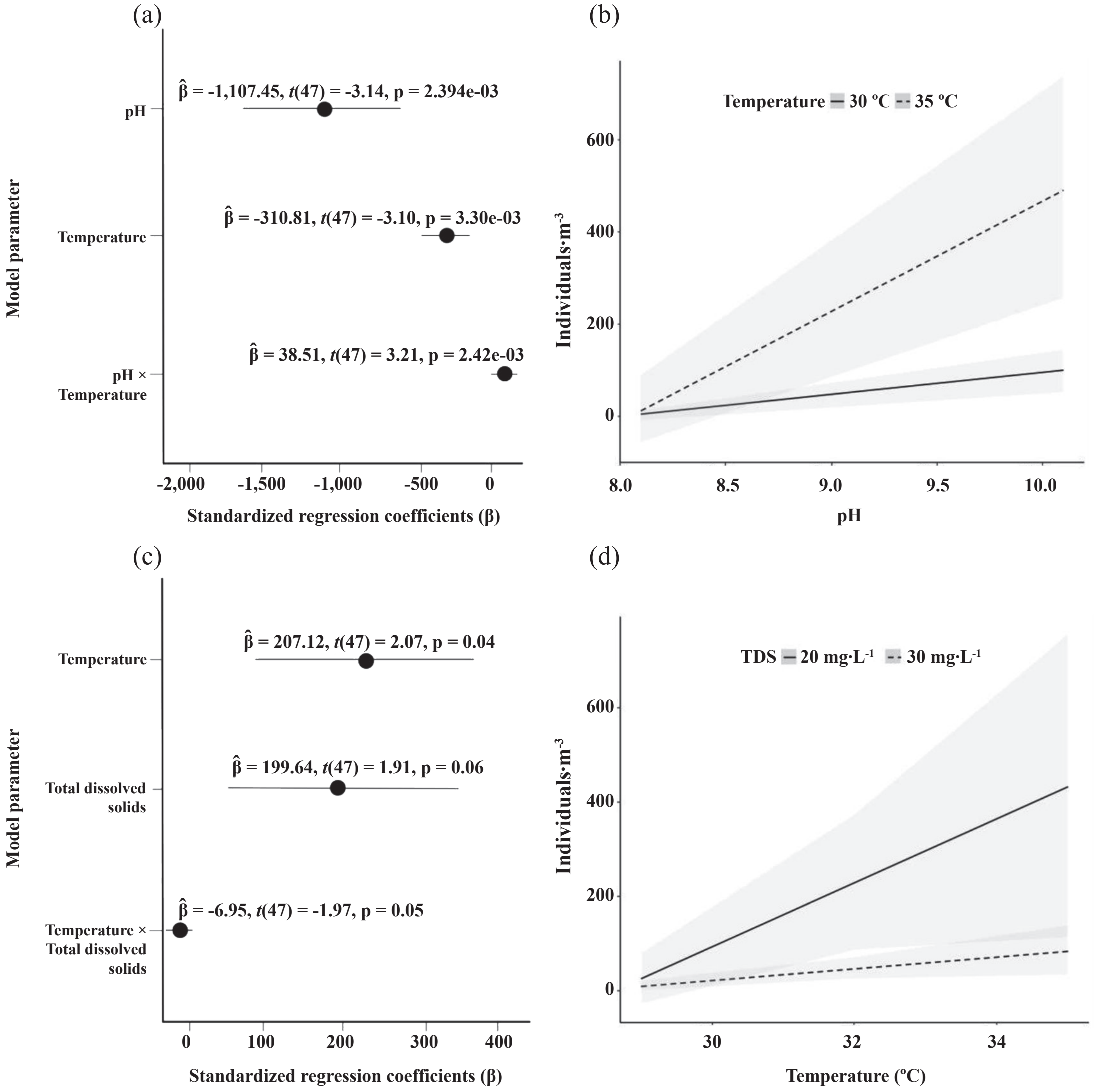

Figure 5. a-b) Parameter estimates (ß) and predictions of the first-ranked model multiple linear model (MLM); c-d) Parameter estimates (ß) and predictions of the first-ranked MLM. Bars across the model parameter estimate points are standard errors.

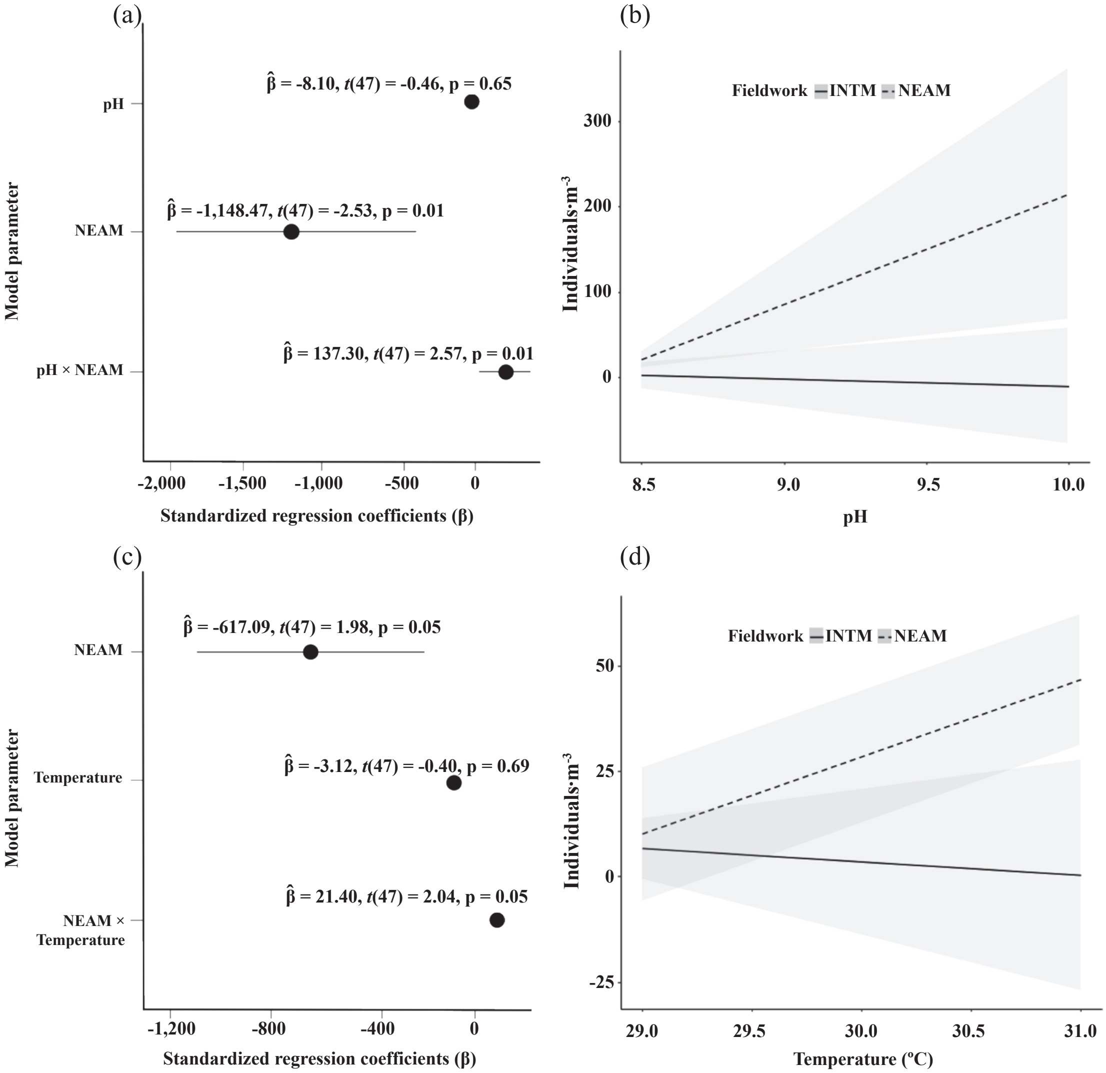

Figure 6. a-b) Parameter estimates (ß) and predictions of the third-ranked multiple linear regression model (MLR); c-d) Parameter estimates (ß) and predictions of the fourth-ranked MLR. Bars across the model parameter estimate points represent standard errors.

DISCUSSION

Fish larvae, being planktonic drifters, rely on natural currents for dispersal and redistribution within nearshore ecosystems shortly after hatching. However, their dispersal and survival are influenced by micro-scale variations in water quality, particularly temperature, total dissolved solids, and pH, as well as by seasonal weather patterns like the monsoon. These larval assemblages also undergo annual fluctuations, largely driven by family-specific reproductive activities and environmental conditions.

Our models provide evidence that larval recruitment in the tropics is closely related to intra-annual variations in water quality and monsoon seasons within nearshore ecosystems. The findings suggest that water quality, particularly temperature and pH, plays a critical role in shaping larval fish recruitment and assemblage structure in tropical nearshore habitats. Water quality parameters had a greater influence than the lunar phase on the structure and composition of nearshore fish larvae (Díaz-Astudillo *et al*., 2017). Temperature influences fish both directly and indirectly, affecting the availability of essential resources such as phytoplankton and zooplankton, which vary in importance among different fish families. Families such as Bothidae and Gobiidae require higher concentrations of these biomass resources. While Bothidae and Gobiidae depend on higher biomass availability, other families, including Scaridae, Scombridae, and Gonostomatidae, can thrive under lower biomass conditions (Souza and Junior, 2019).

Fluctuations in pH, often driven by ocean acidification, can have various direct and indirect impacts on larval fish assemblages. Larval fish are particularly sensitive to changes in pH, as it affects the biochemical processes essential for their growth. Lower pH levels can impair the development of sensory systems, skeletal structures, and metabolic functions in larval fish (Baumann *et al*., 2019). Acidified conditions have been shown to slow down growth rates and alter morphological features, potentially reducing the ability of larvae to compete for resources and survive in early life stages (Frommel *et al*., 2012). A decline in pH can also increase larval fish mortality by disrupting osmoregulation and acid-base balance (Melzner *et al*., 2009). Larvae exposed to acidified waters often experience higher mortality rates due to physiological stress, leading to reduced recruitment and altered population dynamics (Baumann *et al*., 2019). For example, studies have demonstrated that pH levels below 7.8 significantly increase marine larval mortality, particularly in species that rely on calcification during development (Kroeker *et al*., 2013). Indeed, predictions from our top-ranked model, which included pH, indicated that the larval density increased with this water quality parameter.

Seasonal-selective distribution of marine fishes has been well-documented in temperate ecosystems (Ahern *et al*., 2018). However, in the tropical climate, rather than temperature, the monsoon is expected to play a confounding role in fish distribution, especially for species that experience planktonic life stages. Interannual monsoon winds have been identified as a key driver of small pelagic fisheries in the marine ecosystem of East Africa (Jebri *et al*., 2020). The presence of certain larval fish families exclusively during NEAM samples suggests that the monsoon, rather than the lunar phase, influences spawning patterns. For example, Sphyraenidae was absent during INTM (conducted during spring tides of full and new lunar phases), but was detected during NEAM (spring tide of the full moon and neap tide of the third-quarter moon). This suggests that pelagic fish may migrate from the east coast of Peninsular Malaysia, which faces the South China Sea, to the west coast along the Strait of Malacca for spawning, driven by monsoon-influenced migratory patterns on their migratory patterns (Longhurst and Pauly, 1987; Bensam, 1999).

The northeast monsoon results in heavy rainfall on the east coast but not on the west coast due to the presence of a mountain range, i.e., the Titiwangsa range, which blocks the wind from traveling further south (Suhaila *et al*., 2010). Species diversity is significantly reduced during the monsoon season compared to non-monsoon periods, as fish migration occurring during the monsoon is mediated by environmental factors (Sreekanth *et al*., 2017). Precipitation impacts resource availability, leading to seasonal use of nearshore ecosystems.

Seasonal utilization of nearshore ecosystem by Clupeiformes and Perciformes has been recorded in insular beaches, whereas Anterhiniformes and Perciformes occupy continental ecosystems year-round (Pereira *et al*., 2015). Season-specific spawning can occur at the species level. During the intense rainfall, increased runoff reduces water transparency, mixing debris from coastal upwelling and enriching nearshore waters with nutrients. This enhances larval food availability while simultaneously reducing predator visibility, improving ichthyoplankton survival rates. In the Persian Gulf, seasonal variations in water quality influenced ichthyoplankton abundance, with Clupeidae, Gobiidae, and Sillaginidae peaking in April and declining in December (Chermahini *et al*., 2021).

Co-occurrence analysis showed no strong negative correlations suggesting inter-familial competition among larval fish. Instead, seasonal variations in tropical fish assemblages appear to be driven by opportunistic marine and estuarine species that exploit areas with higher environmental variability across both dry and rainy seasons (Molina *et al*., 2020). Our top four models support the hypothesis that water quality and monsoons are interdependent drivers of larval fish assemblage in the study area (McGeady *et al*., 2021). These four models were significantly better (ΔAIC$\leq$2) than the others in explaining the observed patterns. Moreover, our diversity index analysis indicated that the northeast monsoon intensified fish spawning across most families toward the end of the year.

The remaining models, which included total dissolved solids (TDS) and dissolved oxygen (DO) did not best explain larval fish assemblages during the study period. However, TDS and DO are essential water quality parameters that significantly impact fish larvae in marine ecosystems. Elevated TDS levels increase salinity and ionic concentrations, challenging the osmoregulatory mechanisms of fish larvae. Inadequate osmoregulation leads to physiological stress, negatively affecting growth and survival (Weber-Scannell and Duffy, 2007). Similarly, low DO levels can alter larval behaviour, reducing their ability to avoid predators, locate food, and migrate. These behaviour shifts increase vulnerability to predation and decrease survival rates (Wang *et al*., 2023). The simultenous effects of TDS and DO fluctuations create challenges for fish larvae in finding suitable habitats for growth and development, ultimately reducing recruitment and altering population dynamics.

While the current study's coarse taxonomic resolution limits the depth of its insights, identifying larvae at the genus or species level would provide more detailed and actionable information for fisheries and conservation management. The absences of certain families across different sampling periods suggests that larval distribution and spawning patterns are influenced by seasonal factors that vary not only at the species or genus level but also at the family level. This underscores the need for finer-scale taxonomic analyses to better understand the ecological dynamics at play and to refine management strategies accordingly.

CONCLUSIONS

This study provides evidence that larval fish assemblages in the Straits of Malacca vary in response to monsoon seasons and water quality, with assemblages being family-specific. Examining how monsoon patterns and fluctuation in water quality influence the composition and distribution of fish larvae–particularly across different times of the year and among different families can yield valuable insights into larval behaviour and survival. These findings are particularly relevant in the context of climate change and human activities affecting coastal systems where these larvae drift and assemble.

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LITERATURE CITED

Ahern, A.L.M., J. Gómez-Gutiérrez, O. Aburto-Oropeza. 2018. DNA sequencing of fish eggs and larvae reveals high species diversity and seasonal changes in spawning activity in the southeastern Gulf of California. **Marine Ecology Progress Series** 592: 159–179. DOI: 10.3354/meps12446.

Álvarez, I., I.A. Catalán, A. Jordi, M. Palmer, A. Sabatés and G. Basterretxea. 2012. Drivers of larval fish assemblage shift during the spring-summer transition in the coastal Mediterranean. **Estuarine, Coastal and Shelf Science** 97: 127–135. DOI: 10.1016/j.ecss.2011.11.029.

Arantes, C.C., L. Castello, D.J. Stewart, M. Cetra and H.D. Queiroz. 2010. Population density, growth and reproduction of arapaima in an Amazonian river-floodplain. **Ecology of Freshwater Fish** 19(3): 455–465. DOI: 10.1111/j.1600-0633.2010.00431.x.

Baumann, L., H. Segner, A. Ros, D. Knapen and L. Vergauwen. 2019. Thyroid hormone disruptors interfere with molecular pathways of eye development and function in zebrafish. **International Journal of Molecular Sciences** 20(7): 1543. DOI: 10.3390/ijms20071543.

Bensam, P. 1999. Spawning migration of Indian shad (*Hilsa ilisha*) in the rivers of Eastern India: Review. **Journal of the Marine Biological Association of India** 41(1–2): 1–20.

Chermahini, M.A., A. Shabani, R. Naddafi, R. Ghorbani, M. Rabbaniha and M. Noorinejad. 2021. Diversity, distribution, and abundance patterns of ichthyoplankton assemblages in some inlets of the Northern Persian Gulf. **Journal of Sea Research** 167: 101981. DOI: 10.1016/j.seares.2020.101981.

Díaz-Astudillo, M., M.I. Castillo, M.A. Cáceres, G. Plaza and M.F. Landaeta. 2017. Oceanographic and lunar forcing affects nearshore larval fish assemblages from temperate rocky reefs. **Marine Biology Research** 13(10): 1015–1026. DOI: 10.1080/17451000.2017.1335872.

Félix-Hackradt, F.C., C.W. Hackradt, J. Treviño-Otón, M. Segovia-Viadero, A. Pérez-Ruzafa and J.A. García-Charton. 2013. Environmental determinants on fish post-larval distribution in coastal areas of south-western Mediterranean Sea. **Estuarine, Coastal and Shelf Science** 129: 59–72.

Frommel, A.Y., R. Maneja, D. Lowe, A.M. Malzahn, A.J. Geffen, A. Folkvord, U. Piatkowski1, T.B.H. Reusch and C. Clemmesen. 2012. Severe tissue damage in Atlantic cod larvae under increasing ocean acidification. **Nature Climate Change** 2(1): 42–46. DOI: 10.1038/nclimate1324.

Griffith, D.M., J.A.Veech and C.J. Marsh. 2016. Cooccur: probabilistic species co-occurrence analysis in R. **Journal of Statistical Software** 69: 1–17. DOI: 10.18637/jss.v069.c02.

Jebri, F., Z.L. Jacobs, D.E. Raitsos, M. Srokosz, S.C. Painter, S. Kelly and E. Popova. 2020. Interannual monsoon wind variability as a key driver of East African small pelagic fisheries. **Scientific Reports** 10(1): 13247. DOI: 10.1038/s41598-020-70275-9.

Jeyaseelan, M.P., N. Ramanathan and M. Vannuci. 1998. **Manual of Fish Eggs and Larvae from Asian Mangrove Waters.** Unesco Publishing, Paris, France. 187 pp.

Jones, G.P., G.R. Almany, G.R. Russ, P.F. Sale, R.S. Steneck, M.J.H. van Oppen and B.L. Willis. 2009. Larval retention and connectivity among populations of corals and reef fishes: History, advances and challenges. **Coral Reefs** 28: 307–325. DOI: 10.1007/s00338-009-0469-9.

Kawaguchi, K. 2003. **Guide for Sampling and Identification of Fish Larvae in the Straits of Malacca.** Universitas Riau Press., Riau, Pekanbaru, Indonesia. 66 pp.

Konishi, Y., R. Chayakul, C. Chamchang and T. Duangdee. 2012. **Early Stages of Marine Fishes in Southeast Asian Region.** Southeast Asian Fisheries Development Center, Bangkok, Thailand. 262 pp.

Kroeker, K.J., R.L. Kordas, R. Crim, I.E. Hendriks, L. Ramajo, G.S. Singh and J.P. Gattuso. 2013. Impacts of ocean acidification on marine organisms: quantifying sensitivities and interaction with warming. **Global Change Biology** 19(6): 1884–1896. DOI: 10.1111/gcb.12179.

Leis, J.M. and B.M. Carson-Ewart. 2004. **The Larvae of Indo-Pacific Coastal Fishes: An Identification Guide to Marine Fish Larvae,** Volume 2. Brill, Leiden, Netherlands. 850 pp.

Lo, W.T., H.Y. Hsieh, L.J. Wu, H.B. Jian, D.C. Liu and W.C. Su. 2010. Comparison of larval fish assemblages between during and after northeasterly monsoon in the waters around Taiwan, western North Pacific. **Journal of Plankton Research** 32(7): 1079–1095. DOI: 10.1093/plankt/fbq034.

Longhurst, A.R. and D. Pauly. 1987. **Ecology of Tropical Oceans.** Academic Press INC, New York, USA. 389 pp.

Martinho, F. 2022. **Nursery areas for marine fish.** In: Life Below Water (eds. W. Leal Filho, A.M. Azul, L. Brandli, A. Lange Salvia and T. Wall), pp 1–11. Encyclopedia of the UN Sustainable Development Goals, Springer International Publishing, Cham, Swizerland. DOI: 10.1007/978-3-319-71064-8_42-1.

Mazerolle, M.J. 2023. **AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c).** https://cran.r-project.org/package=AICcmodavg. Cited 1 Apr 2024.

McGeady, R., C. Lordan and A.M. Power. 2021. Shift in the larval phenology of a marine ectotherm due to ocean warming with consequences for larval transport. **Limnology and Oceanography** 66(2): 543–557. DOI: 10.1002/Ino.1162.

Melzner, F., M.A. Gutowska, M. Langenbuch, S. Dupont, M. Lucassen, M.C. Thorndyke, M. Bleich and H.O. Pörtner. 2009. Physiological basis for high CO_2 tolerance in marine ectothermic animals: pre-adaptation through lifestyle and ontogeny?. **Biogeosciences** 6(10): 2313–2331. DOI: 10.5194/bg-6-2313-2009.

Molina, A., G. Duque and P. Cogua. 2020. Influences of environmental conditions in the fish assemblage structure of a tropical estuary. **Marine Biodiversity** 50(1): 5. DOI: 10.1007/s12526-019-01023-0.

National Hydrographic Centre Malaysia. 2023. **Integrated MAL chart catalogue.** https://hydro.gov.my/ehydrov2/. Cited 7 Jul 2023.

Nyadjro, E.S. 2021. Impacts of the 2019 Strong IOD and monsoon events on Indian Ocean Sea surface salinity. **Remote Sensing in Earth Systems Sciences** 4: 158–171. DOI: 10.1007/s41976-021-00054-1.

Okiyama, M. 2014. **An Atlas of Early-Stage Fishes in Japan,** 2nd ed. Tokai University Press, Tokyo, Japan. 1154 pp.

Pereira, H.H., L.M. Neves, M.R. da Costa and F.G. Araújo. 2015. Fish assemblage structure on sandy beaches with different anthropogenic influences and proximity of spawning grounds. **Marine Ecology** 36(1): 16–27. DOI: 10.1371/journal.pone.0219325.

Perry, F.A., A. Atkinson, S.F. Sailley, G.A. Tarling, S.L. Hill, C.H. Lucas and D.J. Mayor. 2019. Habitat partitioning in Antarctic krill: Spawning hotspots and nursery areas. **PLoS ONE** 14(7): e0219325. DOI: 10.1371/journal.pone.0219325.

Pielou, E.C. 1966. The measurement of diversity in different types of biological collections. **Journal of Theoretical Biology** 13: 131–144. DOI: 10.1016/0022-5193(66)90013-0.

Pfauserová, N., M. Brabec, O. Slavík, P. Horký, V. Žlábek and M. Hladík. 2022. Effects of physical parameters on fish migration between a reservoir and its tributaries. **Scientific Reports** 12(1): 8612. DOI: 10.1038/s41598-022-12231-3.

Rijnsdorp, A.D., C.J.V. Damme and P.R. Witthames. 2010. Implications of fisheries-induced changes in stock structure and reproductive potential for stock recovery of a sex-dimorphic species, North Sea plaice. **ICES Journal of Marine Science** 67(9): 1931–1938. DOI: 10.1093/icesjms/fsq049.

RStudio Team. 2023. **RStudio: integrated development environment for R.** http://www.rstudio.com/. Cited 25 Aug 2024.

Sadatzki, H., M. Sarnthein and N. Andersen. 2016. Changes in monsoon-driven upwelling in the South China Sea over glacial Terminations I and II: a multi-proxy record **International Journal of Earth Sciences Geologische Rundschau** 105: 1273–1285. DOI: 10.1007/s00531-015-1227-6.

Santos, R.V.S., S. Ramos and A.C.T. Bonecker. 2017. Can we assess the ecological status of estuaries based on larval fish assemblages? **Marine Pollution Bulletin** 124(1): 367–375. DOI: 10.1016/j.marpolbul.2017.07.043.

Shannon, C.E. 1948. A mathematical theory of communication. **The Bell System Technical Journal** 27: 379–423.

Simpson, E.H. 1949. Measurement of diversity. **Nature** 163: 688. DOI: 10.1038/163688a0.

Souza, C.S.D. and P.O.M. Junior. 2019. Large-scale spatial and temporal variability of larval fish assemblages in the tropical Atlantic Ocean. **Anais Da Academia Brasileira de Ciencias** 91(1): e20170567. DOI: 10.1590/0001-3765201820170567.

Sreekanth, G.B., N.M. Lekshmi and N.P. Singh. 2017. Temporal patterns in fish community structure: environmental perturbations from a well-mixed tropical estuary. **Proceedings of the National Academy of Sciences, India Section B: Biological Sciences** 87: 135–145. DOI: 10.1007/s40011-015-0581-2.

Suhaila, J., S.M. Deni, W.Z.W. Zin and A.A. Jemain. 2010. Trends in Peninsular Malaysia rainfall data during the southwest monsoon and northeast monsoon seasons: 1975–2004. **Sains Malaysiana** 39(4): 533–542.

Trindade-Santos, I. and K.D.M.F. Freire. 2015. Analysis of reproductive patterns of fishes from three large marine ecosystems. **Frontiers in Marine Science** 2: 38. DOI: 10.3389/fmars.2015.00038.

Wang, D., J. Yu, Z. Lin and P. Chen. 2023. Spatial-temporal distribution of fish larvae in the Pearl River estuary based on habitat suitability index model. **Biology** 12(4): 603. DOI: 10.3390/biology12040603.

Weber-Scannell, P.K. and L.K. Duffy. 2007. Effects of total dissolved solids on aquatic organisms: a review of literature and recommendation for salmonid species. **American Journal of Environmental Sciences** 3(1): 1–6. DOI: 10.3844/ajessp.2007.1.6.