

Microscale Dynamics of Larval Fish Assemblages in the Straits of Malacca Nearshore Coincided with Lunar Phases

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ABSTRACT

Marine fish larvae are an integral part of the marine environment because their abundance can become an ecological indicator. The abundance is dependent on the environmental variations that include but are not limited to lunar phases and diel changes, both of which predictably influence them to drift between inshore and outshore of the nearshore system. This study determined the effects of those environmental variations at the spatio-temporal level on the larval fish abundance along the Negeri Sembilan coastline of the Straits of Malacca, Malaysia. Samples were collected using a Bongo net of 300 µm in mesh size during the inter-monsoon season of March through April 2021 ($n = 32$). Larval fish density for the 32 samples ranged between 1 and 31 larvae/m³. There were 18 larval fish families identified from the study, with the most sampled larvae of Engraulidae, contributing to 24.20% of 892 total fish larvae identified. Other families with notable abundance were Gobiidae (16.30%), Blennidae (13.15%), Ambassidae (10.40%), Apogonidae (9.95%), and Leiognathidae (3.73%). The larval fish abundance was significantly higher during the new lunar phase than the full lunar phase ($P < 0.01$). Although there were marginal differences between the night and day as well as between outshore and inshore in some of the samples,

there was no significant difference within both diel changes and shore distances. The study indicated that the dynamics in the larval fish assemblages in the study area were markedly attributed to lunar phases.

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INTRODUCTION

Larval fish life history is distinguished by specific eco-morphological characteristics that the larvae are adapted to during the early fish life stages (Catalán et al., 2020). Biotic and abiotic factors influence the adaptations. The biotic factors include but are not limited to prey and predator availability (Ferreira et al., 2020), digestive tract development, visual acuity, and swimming performance of larvae (Makrakis et al., 2005). At the same time, the abiotic factors can include habitats (Ara et al., 2020), daylight cycle (Picapedra et al., 2018), and water quality (Colombano et al., 2021; McGeady et al., 2021). The adaptations during the initial stage of the life cycle are critical because the survival rate is relatively as low as 10% and reduces to around 2–3% as the larvae start their first feeding (Ferreira et al., 2020).

In the marine ecosystem, fish larvae drift in the nearshore littoral zone during the ontogenetic developmental stage (Polte et al., 2017), where varying challenges affect their survival rate (Ridho et al., 2020). Natural circadian rhythms also influence larval fish assemblages in the coastal marine water. The nearshore coastal region fits the larval retention hypothesis in that it is an important nursery ground due to high bioavailability, low predation risk, and suitable physio-chemical characteristics (Díaz-Astudillo et al., 2017; Patrick & Strydom, 2014a).

Activities around the area are also affected by diel patterns. During this stage, fish larvae depend on the light given the less developed eyes in their early development. Nearshore depths between 0 and 100 m

harbor the highest larvae concentrations, where zooplankton density increases during the night, attributed to the lunar cycle (Olivar et al., 2018).

The lunar illumination cycle is the key driving element in the dispersion of fish larvae in the water column. It is the factor that affects vertical migration of the fish larvae in the marine ecosystem resulting in diel variation in the larval assemblages (Wang et al., 2022). The migration is mainly due to feeding, where they move to the epipelagic zone at night before returning to the mesopelagic zone to digest the food and excrete waste (Dove et al., 2021; Irigoien et al., 2014).

The lunar phases also cause cyclical variations in nighttime illumination (moonlight intensity), geomagnetic fields, gravitational pull, tidal amplitude, hormonal secretion, and gene expression for the cryptochrome gene (Ikegami, Takeuchi, Hur, et al., 2014). Melatonin hormone secretion can induce larval fish activity at night during the lunar phase. Hormone secretion occurs greatly at night during the new moon phase compared to the full moon phase (Ikegami, Takeuchi, & Takemura, 2014).

The variability in the biotic and abiotic in relation to larval assemblages indicates spawning occurrence in the nearshore environment. The information is important for fisheries management, especially when targeted fisheries and fishing ground limits are concerned. While acquiring gravid fishes as an indicator of the occurrence of spawning events at a specific time or locality can be challenging, deduction from larval fish assemblages should be able to provide

such information. Therefore, the objective of this study was to determine the effects of lunar phases, diel variations, and shoreline distance on larval fish assemblages in the Malacca Strait's nearshore marine ecosystem.

MATERIALS AND METHODS

Study Area

The study was carried out on the Negeri Sembilan coastline, which accounts for about 5% of Peninsular Malaysia's total coastline length of 48 km on the strait. The whole of Peninsular Malaysia is of tropical climate, where the coastal environment is largely affected by monsoon winds throughout the year, southwest and northeast monsoons. Fieldwork for this study was carried out during inter-monsoon of the transition monsoon between northeast and southwest, i.e., March until April 2022.

Selection of Sampling Stations

Sampling stations were primarily selected based on the following limits: (1) in Zone A fishing area, which is designated by the Department of Fisheries Malaysia (DOF), essentially within less than 2.5 km offshore, (2) spatially equal distance of 2 km from each station across the coastal limits of Zone A fishing area and Negeri Sembilan state maritime borders with Lukut and Tanjung Tuan as the extreme-most points, (3) four replicate stations that are associated with coastal towns and landmarks, and (4) two distances seaward from the nearest coastal towns or landmarks i.e., 0.5 km (hereafter inshore) and 2.5 km (hereafter offshore).

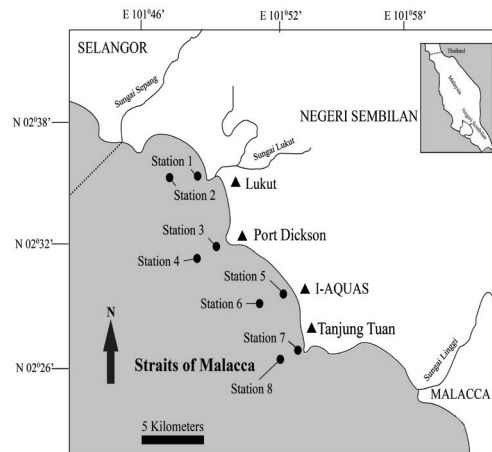


Figure 1. Sampling stations in the nearshore zone of the Straits of Malacca along the Negeri Sembilan shoreline.

Altogether, eight sampling stations were selected for the study based on the criteria (Figure 1). Sampling stations 1–4 are associated with the coastal towns of Lukut and Port Dickson, and sampling stations 5–8 are associated with landmarks of the International Institute of Aquaculture and Aquatic Sciences (IAQUAS) and Tanjung Tuan.

Broken lines perpendicular to Sungai Sepang and Sungai Linggi are arbitrary state maritime borders between Negeri Sembilan and other states

Fieldwork

Thirty-two (32) samples were collected during the inter-monsoon season of March through April 2021. All samples from the fieldwork were collected during spring tide to control for the effect of tides on larval fish assemblages. Altogether, the 32 samples consisted of samples from 2 lunar phases

× 2 distances from the shore × 2 diel × 4 replicate stations. The sampling scheme essentially culminated in eight spatio-temporal treatments, i.e.: (a) New Lunar + Inshore + Day, (b) New Lunar + Inshore + Night, (c) New Lunar + Outshore + Day, (d) New Lunar + Outshore + Night, (e) Full Lunar + Inshore + Day, (f) Full Lunar + Inshore + Night, (g) Full Lunar + Outshore + Day, and (h) Full Lunar + Outshore + Night.

Sample Collection and Preservation

Larval fish were collected by using a set of Bongo nets of 300 µm mesh size (mouth diameter 0.60 and 3 m long). The net was towed horizontally at the water sub-surface from a moving boat at a constant speed of 2.5 knots for 10 min. Larval fish samples collected from the tows were preserved in 5% formalin (Sigma-Aldrich, USA). The 5% formalin solution was buffered with sodium tetraborate de-carbohydrate, i.e., borax (Sigma-Aldrich, USA), to neutralize the pH (Joshi & Sreekumar, 2015). All collected samples were transported to the laboratory for taxonomic identification.

Water Quality and Diversity Indices

The following *in situ* environmental variables were measured using YSI™ 556 multi-parameter probes (USA) at every sampling station: seawater dissolved oxygen (mg/L), and water sub-surface temperature (°C), salinity (ppt), pH, and turbidity (mg/L).

Identified larvae for each sample were tallied to measure diversity indices based on the following formula:

- a. Relative abundance and its complement (complementary Simpson, 1-D), Simpson (1949), $1-D = 1 - \sum_{i=1}^R \left(\frac{n_i(n_i-1)}{N(N-1)} \right)$ where R = total number of family in the sample, n_i = number of individuals in family i , and N = total number of species in the sample.
- b. The proportion of larvae for each family of Shannon-Weiner H' , Shannon (1948), $H' = \sum_{i=1}^R \ln(p_i)$, where R = the number of individuals in the family i , and p_i = proportions of individuals that belong to species i .
- c. Evenness of the larvae over the number of families, Pielou (1966) $J' = \frac{H'}{H'_{max}}$, where H' = derived from Shannon-Wiener diversity index, and H'_{max} = the maximum possible value of H' .

Larval Fish Density and Abundance Estimation

Larval fish abundance was determined by quantifying the number of individuals per unit volume of water (larvae/m³). Dilution depends on the turbidity of the collected samples, where more turbid water requires a higher dilution factor as compared to the less turbid water samples. Then, taxonomic identification began with grouping a few preliminary water samples containing larval fish into generic groups based on their morphological characteristics: pre-flexion, flexion, and post-flexion. Larval fish were then identified to the lowest possible taxa by using identification keys provided by preceding researchers (Jeyaseelan & Ramamathan, 1998; Kawaguchi, 2003; Konishi et al., 2012; Lies & Carson-Ewart, 2004; Okiyama, 1989).

Data Analysis

The probability of occurrence of each identified family during the fieldwork was calculated based on tabulated presence and absence data from the 32 samples. Essentially, the probability of occurrence for each family is $p(\text{occurrence}) = \left(\frac{n_p}{N}\right)$, where n_p = number of samples, where at least one individual was present, and N = total number of samples analyzed in the study.

Overall differences in density and diversity indices were compared among the eight sampling stations to ascertain that the variation was due to chance. Three-way analyses of variance (ANOVA) were performed to evaluate the effect of lunar phases simultaneously, distance from the shore and diel variations, and their interactions on the larval fish density and diversity indices. The normality of response variables was tested prior to running the ANOVA tests by using the Shapiro-Wilk's lambda test. The homogeneity of variance of the tested groups was checked using Levene's test. Data that failed to meet the normality assumption were log-transformed in the analyses. Additionally, a one-way ANOVA was performed on eight spatio-temporal treatments of the combined factors to test whether there were differences in larval fish density among treatments. Significant ANOVA tests were subject to Tukey's honestly significant difference (HSD) post-hoc test to determine group differences.

Water quality parameters significantly different among the lunar phases were used as predictors in linear regression models to

determine their effects on larval fish density. All ANOVA tests were performed with $\alpha = 0.05$ or essentially at 95% confidence intervals in RStudio 2022.07.1 with relevant R packages (Team, 2020).

RESULTS

Fish Larvae Assemblage

There were 892 fish larvae recovered from the study, with 18 families identified from 32 samples. More than half of the 18 families, i.e., 10, were present at every level of each factor (Table 1). Three of the 18 families, i.e., Ophidiidae, Pomacentridae, and Sciaenidae, were absent from the inshore samples, while Eleotrida, Kyphosidae, Tetraodontidae, and Uranoscopidae were absent from the outshore samples. Pomacentridae was the only family that was absent during the new lunar phase.

During the full lunar phase, more families were absent from the reenumeration, and they were Eleotridae, Kyphosidae, Ophidiidae, Sciaenidae, Tetraodontidae, and Uranoscopidae (Figure 2). As expected, more families were recovered from night samples as opposed to day samples, with Uranoscopidae being the only absent from the former samples. Engraulidae had the highest probability of occurrence, $p(\text{occurrence}) = 0.91$, while the lowest was Tetraodontidae, $p(\text{occurrence}) = 0.03$ (Figure 2). Apart from Engraulidae, Ambassidae ($p = 0.84$), Blennidae ($p = 0.78$), Apogonidae ($p = 0.59$), and Gobiidae ($p = 0.5$) are families with 50% occurrence from the 32 samples.

Table 1
 Checklist of fish larvae family identified from the samples by the three environmental factors tested in the study

Locality	Station / Shore distance	Lunar phase	Diel	Family																					
				Ambassidae	Apogonidae	Belonidae	Blennidae	Carangidae	Clupeidae	Eleotridae	Engraulidae	Gobiidae	Kyphosidae	Leiognathidae	Nemipteridae	Ophidiidae	Pomacentridae	Sciaenidae	Scombridae	Tetraodontidae	Uranoscopidae	Total Family			
Lukut	Station 1 (Inshore)	Full	Night	✓	×	×	✓	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	5		
			Day	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	✓	×	×	×	×	5	
		New	Night	✓	×	×	✓	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	5
			Day	✓	×	×	✓	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	5
	Station 2 (Outshore)	Full	Night	✓	✓	✓	✓	✓	✓	×	×	×	×	×	×	×	×	×	×	×	×	×	×	10	
			Day	×	✓	×	✓	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	3
		New	Night	✓	✓	×	✓	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	9
			Day	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	1
Port Dickson	Station 3 (Inshore)	Full	Night	✓	✓	×	✓	✓	✓	×	×	×	×	×	×	×	×	×	×	×	×	×	8		
			Day	✓	×	×	✓	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	4	
		New	Night	✓	✓	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	5	
			Day	✓	✓	×	✓	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	4	
	Station 4 (Outshore)	Full	Night	✓	×	×	✓	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	6	
			Day	✓	✓	×	✓	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	5	
		New	Night	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	✓	12	
			Day	✓	✓	×	✓	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	×	6	

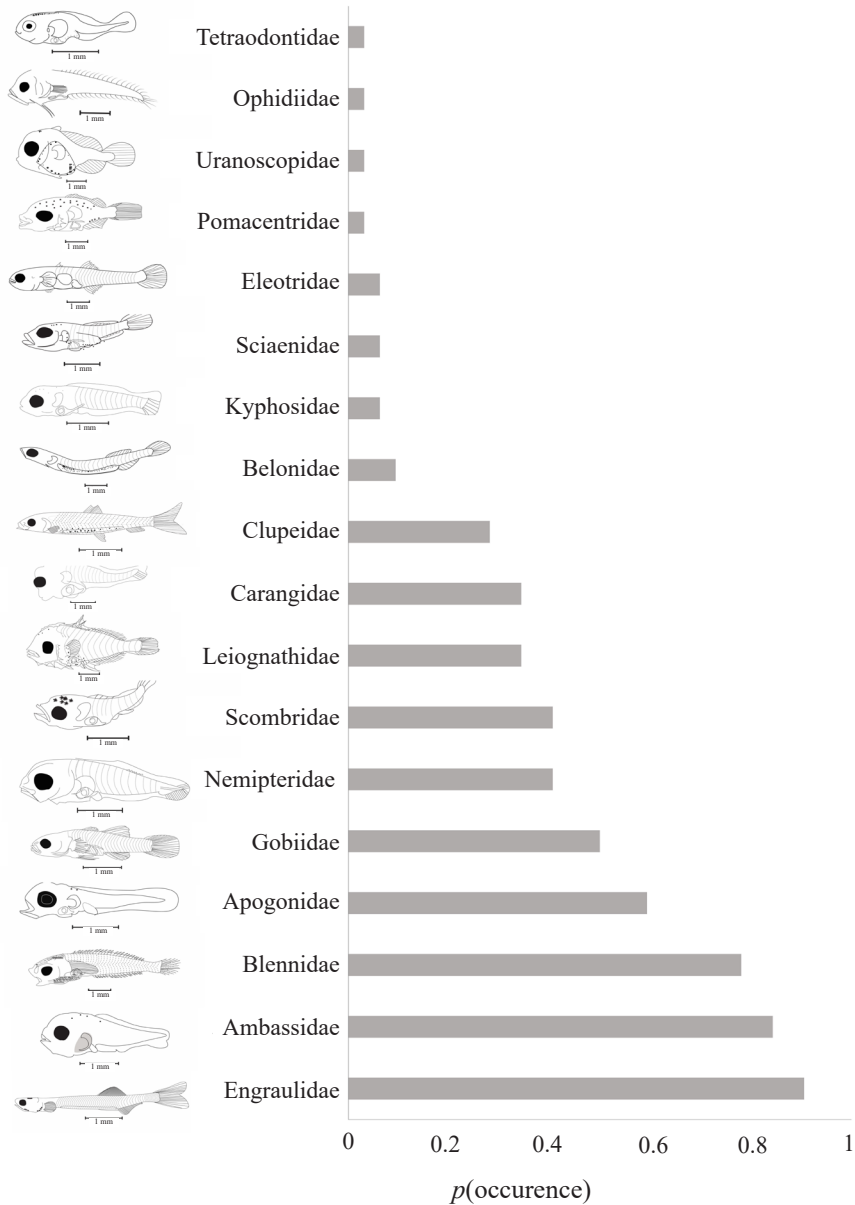


Figure 2. Probability of occurrence for identified larval fish family from all samples ($n = 32$)

Larval fish density for the 32 samples ranged between 1 and 31 larvae/m³. Comparison among stations revealed that the diversity indices corroborated the larval fish density despite no significant differences (Figure 3). The F statistic and p -

value for larval fish density was $F_{7,24} = 0.64$, p -value = 0.72, whereas diversity indices comparison of Shannon was $F_{7,24} = 0.81$, p -value = 0.59, Simpson $F_{7,24} = 0.96$, p -value = 0.48, and Evenness $F_{7,24} = 1.24$, p -value = 0.32. The outcomes indicated that larval

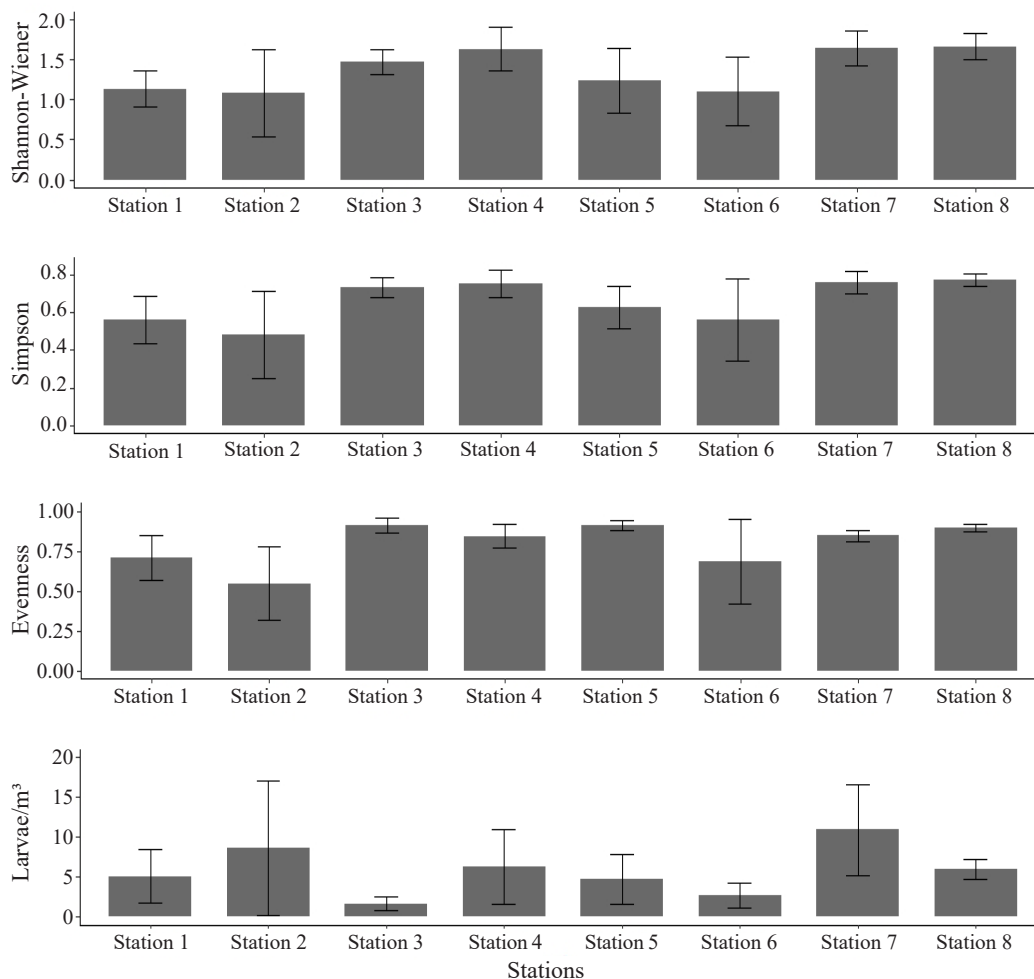


Figure 3. Mean \pm SE for diversity indices, (a) Shannon-Wiener, (b) Simpson, (c) Pielou's Evenness, and (d) larval fish density

fish density in the study area was random and not inherent in their locality within the geo-limit of the study.

Effects of Lunar Phase, Shore Distance, and Diel Change on Larval Fish Density and Diversity

Three-way ANOVA analyses using original and log-transformed data (equal variance, Levene's $s_{7,24} = 0.478$, p -value = 0.841) revealed the same outcomes (Table 2). The lunar phase was the only factor that showed

a significant difference ($p < 0.001$). Mean \pm standard error density for samples collected during the new lunar phase (10 ± 1 larvae/m³) was nine times higher than during the full lunar phase (2 ± 3 larvae/m³). There were no significant two-way or three-way interactions among the main effects ($p > 0.05$). The outcome essentially revealed the significant role of lunar phases over other spatial factors in determining larval fish density.

Table 2

Three-way analysis of variance outputs for main effects of shore distance, lunar phase, diel factors, and their interactions. Similar outputs were obtained for log-transformed data (numbers in brackets)

Effect	F-statistic <i>df</i> ₁ =1, <i>df</i> ₂ =24	p-value
Distance	0.015 (0.026)	0.902 (0.874)
Lunar phase	14.565 (21.373)	0.000837* (0.000108*)
Diel	2.341 (0.44)	0.139 (0.514)
Distance × Lunar phase	0.012 (0.093)	0.914 (0.762)
Distance × Diel	0.724 (0.044)	0.403 (836)
Lunar phase x Diel	2.195 (1.106)	0.151 (0.303)
Distance × Lunar phase × Diel	1.515 (1.359)	0.23 (0.255)

Note. * = Significant result at 95% confidence intervals

A follow-up analysis of one-way ANOVA on the spatio-temporal treatments using original and log-transformed data resulted in the same significant outcome, $F_{7,24} = 3.052$, p -value = 0.019 vs. 0.010, respectively. The post-hoc analysis further revealed that the combined factor of new lunar phase, inshore, and night treatment

significantly marked the highest density, while the combined factor of full lunar phase, inshore, and day treatment significantly resulted in the lowest density (Figure 4). Overall, samples from new lunar phase fieldwork recorded higher larval fish mean density than those of the full lunar phase.

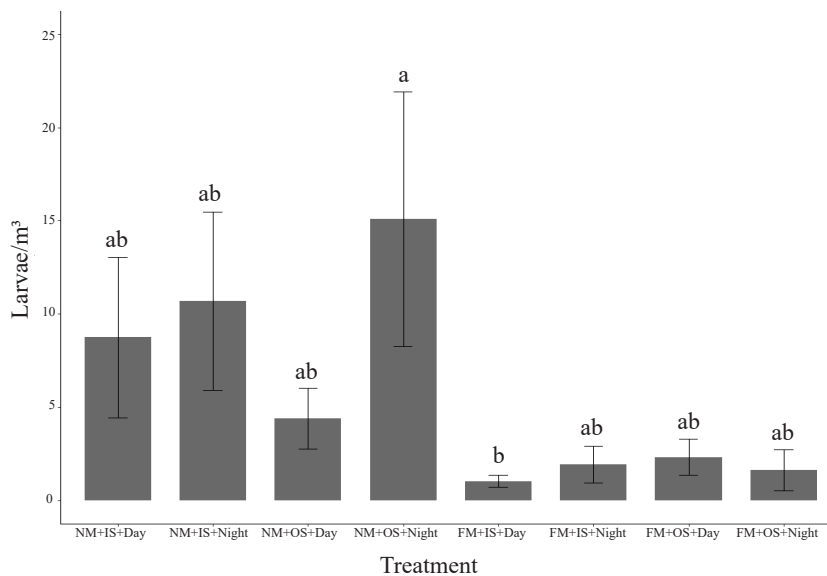


Figure 4. Mean ± SE larval fish density for eight spatio-temporal treatments of three factors with two levels each. The same scripts on top of the upper error bars indicate Tukey's honestly significant difference in post-hoc results.

Note. NM = New lunar; FM = Full lunar phase; IS = Inshore; OS = Outshore

Variation in Water Quality Parameters

Except for water temperature and total dissolved solids (TDS), all other water quality parameters measured during the study (pH, salinity, and dissolved oxygen) were not significantly different between the two levels of each factor (lunar phases, diel changes, and shore distance) tested in this study. Lunar phase ($F_{1,30} = 5.55$; p -value = 0.03) and shore distance ($F_{1,30} = 7.66$; p -value = 0.01) were significant factors that affected water temperature and TDS, respectively. The mean \pm SE water temperature during the full lunar phase ($29.4 \pm 0.07^\circ\text{C}$) was significantly higher than that

of the new lunar phase ($29.2 \pm 0.09^\circ\text{C}$). Additionally, the TDS of offshore water was significantly higher than inshore water (30.1 ± 0.01 mg/L vs. 29.7 ± 0.13 mg/L).

However, multiple linear regression, water temperature, and TDS were not significant factors in predicting larval fish density during the study period (Table 3). The coefficient of determination of the linear model of both water quality parameters was low in that those predictors insignificantly explained only 2.3% of the variance in the larval fish density ($F_{2,29} = 0.343$, p -value = 0.713, $R^2 = 0.023$).

Table 3

Parameter estimates of multiple linear regression on larval fish density

Effect	Estimates	Standard error	<i>t</i> -value	<i>p</i> -value
Intercept	112.47	138.00	0.82	0.42
Temperature ($^\circ\text{C}$)	-2.96	3.97	-0.75	0.46
Total dissolved solids (mg/L)	-0.67	3.44	-0.19	0.85

DISCUSSION

Numerous marine fishes use the nearshore coastal habitats, including the inshore regions of the continental shelf, as an important habitat for at least part of their life cycles. A wide variety of fish species inhabit the oceanic regions, from large pelagic fish such as tuna that migrate to reproduce close to the littoral zone to those that spend their entire lives in the open ocean (Olivar et al., 2018). For example, Carangidae were abundant in spring and summer in seas less than 60 m deep (Chen & Li, 2003), whereas the majority of Nemipteridae larvae occupied sediment bottoms between 60 and

80 m deep (Guobao et al., 2002). Diverse fish need varying depths for spawning, where the depth influences the geographical distribution of spawning grounds and larval occurrence (Feng et al., 2021; Lelièvre et al., 2014). Due to the absence of a swimbladder and incomplete fin development, larval fish involuntarily change their habitat through drifting or along with water currents, ocean waves, and diel vertical migration. The drifting behavior explains why larval fish density decreases with depth or distance from the shoreline.

Engraulidae were the greatest family composition found in all stations in

the study area, followed by Gobiidae, Blennidae, Ambassidae, Apogonidae, and Leiognathidae. A previous study stated that Engraulidae fish larvae were found mostly in waters less than 20 m deep in the Yangtze River Estuary (Li et al., 2018). The abundance of larval fish was greater inshore than in the deepest offshore area (Tiedemann & Brehmer, 2017). However, the current study has not found any evidence to indicate that inshore larval fish distribution, abundance, and density are significantly higher than offshore. Another study found that inshore catches were Gobiidae, and offshore catches were Engraulidae mainly (Patrick et al., 2021). In this study, Gobiidae occurred only in the Mangrove Lukut estuarine habitat as it is an estuarine resident species (Chu et al., 2019; Vorsatz et al., 2021). However, in the current study, larval fish density in nearshore and offshore has no significant difference due to micro spatial sampling as it is still in fishing Zone A. Larval fish movement is regulated by the day and night variation.

Diel vertical migration of larval fish is an exogenous process. The highest abundance and richness are higher during the night (Arévalo-Frías & Mendoza-Carranza, 2015). The highest catches of larvae and early juveniles have been made during the night and ebb tide. Engraulidae dominates larvae at night during the dry or summer season and mostly in pre-flexion larvae (Patrick & Strydom, 2014b). Larval fish abundance and density are higher during the nighttime than during the daylight hours (Islam et al., 2007; Olivar & Beckley,

2022; Wang et al., 2022). The current study corroborated the past findings. Another study supported that diel variation did not show any significant trends in a study carried beach surf zone in southwest Spain (Gutiérrez-Martínez et al., 2021).

The fish larvae were abundant at night because when daylight decreases in intensity during nightfall, the condition stimulates larval migration toward surface layers. After all, the fish larvae respond to increased illumination from the full moon, as opposed to during daylight, when they move deeper waters (Picapedra et al., 2015). During this crepuscular period of low light levels, the risk of predation is reduced but, at the same time, enables vision of food in the surface layers. This activity is viewed as a multi-adaptive approach that confers advantages in terms of predator avoidance, bioenergetic efficiency, and zooplankton foraging (Mehner, 2014).

The phases of the moon cause cyclical variations in nighttime illumination (moonlight intensity), geomagnetic fields, gravitational pull, tidal amplitude, hormonal secretion, and gene expression for the cryptochrome gene (Ikegami, Takeuchi, & Takemura, 2014). Melatonin hormone secretion can induce larval fish activity at night during the lunar phase, where the inducement is greater during the new than the full lunar phase (Ikegami, Takeuchi, Hur, et al., 2014). There are mixed findings with regard to the role of lunar phases on larval fish assemblages. However, there was evidence to indicate that the increased abundance was not significant during the

new lunar phase (Mwaluma, 2014); at least two studies corroborated with our findings that larval fish abundance is significantly highest during the lunar phase (Jaxion-Harm & Speight, 2016; Pattrick et al., 2022). However, the assemblages may vary among families as Engraulidae were seen the highest during the third quarter and full lunar phases (Díaz-Astudillo et al., 2017), while Ambassidae, Apogonidae, Gobiidae, and Leiognathidae were present during new and full lunar nights (Krumme et al., 2015). The selective presence of these families during certain lunar phases indicates that their spawning may be associated with the atmospheric cycle as well.

CONCLUSION

The new lunar phase appeared to augment larval fish assemblages in the Straits of Malacca along the Negeri Sembilan shoreline in Malaysia. It was possibly because of spawning events during the previous full lunar phase. Diel variation and coastal area within the Department of Fisheries Malaysia's Zone A fishing ground had a trivial influence on the aggregation of early development of marine fishes in the study area. Despite numerous research on fish larvae in the straits, ours was the first to demonstrate lunar phases as a possibly non-random element influencing larval fish assemblages in the nearshore zone.

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