

## Evidence of spawning migration of protandrous longtail shad (*Tenualosa macrura*) in the Siak River estuarine, Indonesia

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### ABSTRACT

Longtail shad (*Tenualosa macrura*), an endemic species of Siak River estuary, Riau is feared to be on the brink of extinction, driven by the apparent recruitment overfishing and degradation of its habitat over the past decades. Mature females were massively caught during their migration to the spawning area, specifically for their eggs which have high economic value for the export market. Despite the effort from the Indonesian government to control the level of exploitation through open-close season and area, the infringements keep happening partly due to weak supervision from law enforcers. Moreover, there was a strong indication that the current harvest control rule is not backed with robust scientific evidences, especially on where and when the spawning migration occurred. These uncertainties were bound to be answered through a hydro-acoustic study, using scientific echosounder SIMRAD EK-60, at a transducer frequency of 120 kHz, with a total area covered 173 nmi<sup>2</sup> (590 km<sup>2</sup>) and Elementary Sampling Distance Unit (ESDU) 0.1 nmi. In addition, repetitive (following the moon phase) oceanographic surveys were conducted during 2015–2016 on four prominent locations with a total of 16 observed stations. The result revealed a strong indication of spawning migration between the new moon and full moon, from April to November with different intensities every month. Mature males (*pias*) and females (*terubuk*) were seen in the spawning area during the waxing crescent phase in April, and movement was detected from Malaka Strait to the Siak River estuary. Largest schooling spotted at a swimming layer of 5–20 m depth and highest spawning event suspected occurred close to the water's depths bottom of the river bed during May to June. In contrast, emigration reached its peak in September. The generalised additive model (GAM) showed a linear relationship between abundance and some oceanographic parameters, with temperature and phase of the moon being the most integral factors. The occurrence of a high salinity and pH at spawning areas during high tides in the new moon and full moon phases, could certainly be the driving force for spawning migration.

### 1. Introduction

Two of the world's five known tropical scads species in the world can be found in Indonesian waters. The first, *Tenualosa macrura* (Bleeker, 1852) (*Alosinae: Clupeidae*), commercially known as longtail shad, is an endemic species of Bengkalis, Riau (Blaber et al., 2003, 1999). Whereas

the second, *Tenualosa ilisha* is widespread from the eastern part of North Sumatra to the western part of Kuwait in the west (Seygita et al., 2021). *T. macrura* is classified as protandrous hermaphrodite species, in which they develop as a pure male at their early reproduction stage and later shift as a pure female. This condition change of sex is usually triggered or happens at a certain size or age (Blaber et al., 2005; Suwarso et al.,

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2017). Given the endemic status, *T. macrura* has been declared as a protected species included in the appendix for international endangered species (Thamrin et al., 2021).

Mature females of *T. macrura* (>20 cm SL) are locally known as “Terubuk”, while juvenile/immature males (<20 cm SL) are commonly called “Pias”. Terubuk has been experiencing heavy exploitation since the 1950s, especially for their precious eggs (\$800/kg) (Nugroho et al., 2020; Suwarso et al., 2017). Therefore, it leads to a sharp decline in stock over the last five decades (Ahmad et al., 1995; Taryono, 2015). The condition has been worsening along with the economic development around their habitat, which put more pressure on the already-threatened stock (Amri et al., 2018; Brewer et al., 2001; Efizon et al., 2012). Until the late 1950s, the catch of Terubuk could easily reach up around 2000–3000 fishes per vessel (<5 GT). However, the numbers dropped significantly to just hundreds per trip in the late 1990’s (Merta et al., 1999; Suwarso and Merta, 1997).

The Indonesian government issued several regulations to prevent further decline, i.e., Ministry of Marine Affairs and Fisheries Decree No. KEP.59/MEN/2011, Ministerial Regulation No. PER.03/MEN/2010 and Government Regulation of the Republic of Indonesia No. 60/2007. The first emphasized on restricted protection through a fishing ban (close season and area) at the peak of spawning time (September–November). However, low compliance from fishers and weak supervision from law enforcers encourage infringements yearly. These violations usually take advantage of existing regulatory loopholes, caused by inaccurate data and information related to location, time, and spawning migration patterns.

Extensive research on *T. macrura* has been conducted since the mid-1990s, including cooperation between CSIRO (The Commonwealth

Scientific and Industrial Research Organisation) and the Indonesian Government from 1997 to 1998. Blaber et al. (1999) investigated its biological aspect and life history, including its alleged migration. Several authors focused on its bio-ecology and population status (Nugroho et al., 2020; Suwarso and Merta, 1997; Suwarso et al., 2017), while its potential and distribution based on the moon phase was reported by Muchlizar et al. (2017). A study on the oceanographic conditions at the spawning area was initiated by Amri et al. (2018) and a more recent study related to the reproduction cycle was discussed by Thamrin et al. (2021). However, the spawning migratory movement pattern and the significance of oceanographic conditions have not been thoroughly examined.

This research used the results of hydro-acoustic studies and the oceanographic parameters that impacted spawning migration to provide evidence of the pattern and timing of spawning migration. This discovery was highly beneficial in developing policies for managing the most sustainable fisheries to avert its extinction. The objectives of this study were to investigate the evidence of spawning migration for *T. macrura* and to understand the environmental parameters that influence its spawning migration.

## 2. Materials and methods

### 2.1. Study area

The study commenced by in-situ method in the Siak River estuary, Bengkalis province, Riau, Indonesia which was established as a limited conservation area for *T. macrura*. Observation areas were categorized into sixteen stations which belong to four sub-areas, namely Bengkalis

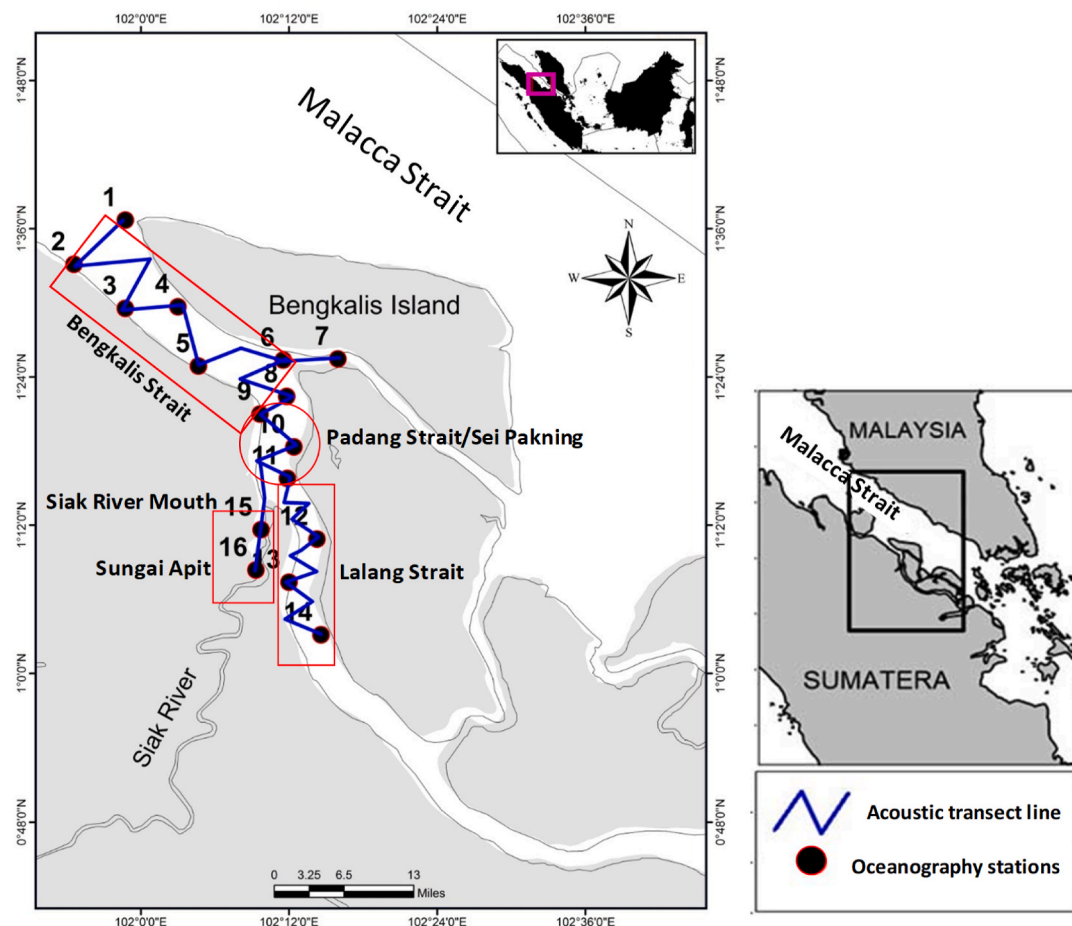


Fig. 1. Map of hydro-acoustic survey and in-situ oceanographic data collection around Bengkalis waters, Riau, Indonesia.

strait (Station No. 1 to 7), Padang Island/Sei Pakning strait (Station No. 8 to 10), Lalang strait (Station No. 11 to 14), and Siak river mouth (Station No. 15 to 16) (Fig. 1). At each station, water temperature (°C), salinity, pH, dissolved oxygen (mg/L) and transparency (m) were measured. To understand tidal patterns, we used an additional dataset of sea surface height obtained from Topex/Poseidon at one virtual station in the study area. *T. macrura* is known to have a timely migration period based on the lunar calendar (Blaber et al., 1999). Therefore, both sampling and hydro-acoustic surveys were conducted during each representation of the moon phase, namely: the full moon, new moon and crescent periods in 2015 (April, May, June, October and November) and in 2016 (June, August, September, and November) (Table 1).

2.2. Fish biomass

Hydro-acoustic soundings were commenced along the pre-determined track (Fig. 1) using scientific echosounder SIMRAD EK-60, at transducer frequency 120 kHz, with total area covered of 173 nmi<sup>2</sup> (590 km<sup>2</sup>) and Elementary Sampling Distance Unit (ESDU) 0.1 nmi. A target strength (TS) can be defined as the quotient between the value of the intensity of the noise coming about the target or backscattering cross-section ( $\sigma_{bs}$ ) and multiplied by the number of ten (10) (MacLennan and Simmonds, 1992) like the following formula:

$$TS = 10 \log_{10} (\sigma_{bs}) \tag{1}$$

Therefore, an area fish density ( $\rho_a$ , fish individuals/m<sup>2</sup>) could be calculated with the following equation:

$$\rho_a = \frac{N}{A} = \frac{s_a}{\sigma_{bs}} \tag{2}$$

where N is the number of individual fish, A is the square area of the layer, and  $s_a$  is the area backscattering coefficient.

To calculate volume density of fish ( $\rho_v$ , fish individuals/m<sup>3</sup>) in the layer between depth  $r_1$  and  $r_2$  following equation:

$$\rho_v = \rho_a(r_2 - r_1) \tag{3}$$

Since backscattering cross section ( $\sigma_{bs}$ ) can be explained as a quadratic term of fish length (L):

$$\sigma_{bs} = aL^2 \tag{4}$$

Therefore, we can substitute  $\sigma_{bs}$  from equation (1) with  $aL^2$  from equation (4) to produce Target Strength (TS) as follows:

$$TS = 20\log L + A \tag{5}$$

where A is the normalized target strength value for every centimetre of fish length (normalized). The value of target strength (TS) for each fish in hydro-acoustic was measured in decibels (dB), a measurement for sound level. According to (Hannachi et al., 2004) the value of normalized target strength for the small pelagic group (Clupeidae) was -73.97

**Table 1**  
A Detailed timeline of hydro-acoustic surveys and oceanographic parameters sampling.

| Year | No. | Gregorian Calendar |          | Moon shape | Moon Phases     |
|------|-----|--------------------|----------|------------|-----------------|
|      |     | Month              | Date     |            |                 |
| 2015 | 1   | April              | 15,16,17 | ☉          | Waxing Crescent |
|      | 2   | May                | 20,21,22 | ●          | New moon        |
|      | 3   | June               | 3,4,5    | ☉          | Full moon       |
|      | 4   | October            | 28,29,30 | ☉          | Full moon       |
|      | 5   | November           | 17,18,19 | ☾          | Waning Crescent |
| 2016 | 1   | June               | 1,2,3    | ☉          | Waxing Crescent |
|      | 2   | August             | 9,10,11  | ☾          | Third Quarter   |
|      | 3   | September          | 8,9,10   | ☾          | Third Quarter   |
|      | 4   | November           | 8,9,10   | ☾          | Waning Gibbous  |

dB, thus the relationship between TS and length from equation (5) becomes:

$$TS = 20\log L - 73.97 \tag{6}$$

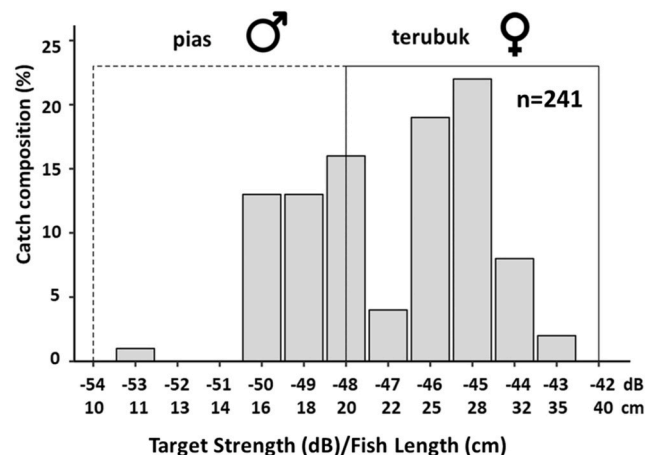
A total of 241 length data of *T. macrura* samples were collected during hydro-acoustic tracking. Samples were collected by random sampling from gillnet catch. By using the samples taken from gillnet catch, the cubic length-weight (LW) relationship formula,  $W = 0,005 \cdot L^{3,379}$  was determined. The constant a and b from LW relationship were used to estimate the biomass by converting the length to weight. By combining length frequency distribution and equation (6), the target strength for *pias* was distributed between -54 dB and -48 dB (L = 10–20 cm, weight 12–122 g). Target strength for *Terubuk* on the other hand were distributed from -48 dB to -43 dB (L = 20–35 cm, weight 122–854 g) (Fig. 2). The result was confirmed by a previous study from (Muchlizar et al., 2017), which showed that the catch comparison between *pias* and *terubuk* from gillnet fishery was almost 1:1 with length ranging from 14 to 20 cm and 22–28 cm, respectively.

2.3. Identifying spawning ground and migration route

Hydro-acoustic survey data (TS) distribution combined with the current direction described the geographical position and possible migration route of *pias* and *terubuk* based on their sizes. By tabulating and plotting its aggregated data, we could identify the potential time and migration pattern, and its oceanographic condition at that particular area and event. The occurrence of *pias* and *terubuk* in the same area indicated the location of their spawning process.

2.4. Correlation between abundance and oceanographic parameters

The relationship between the abundance of *T. macrura* and oceanographic parameters was analyzed using the Generalised Additive Model (GAM) semi-parametric statistical approach under mgcv package (Wood, 2017) in R 4.2.0 (R Core Team, 2021). This model was utilised because it did not require the data distribution's normality. Moreover, the non-linearity nature of this method could be used to reduce the weakness of the assumption of a normal distribution in the observed environmental parameters and the absence of a linear relationship among variables. To measure any increasing regression coefficient variances affected by collinearity we used variance inflation factors (VIF) and fairplot, which were declared in  $1/(1-R^2)$ . In addition, no collinearity was shown by VIF value less than 3 (Zuur et al., 2007). We employed a stepwise approach to model selection, which started with a null model with no dependent variable. It then expanded by adding



**Fig. 2.** Estimated catch-at-size composition for *pias* and *terubuk* from gillnet fishery.

additional variables one by one. The method was repeated until we got the lowest Akaike Information Criterion value (AIC) (Akaike, 1974). The initial models' construction was listed as follows:

$$Terubuk \cong \mu + Pias + s(Temp) + s(Sal) + s(pH) + s(DO) + MoonPhase + \epsilon \tag{7}$$

where:

- Terubuk*: Total abundance of mature female *T. macrura* (ind/nm<sup>2</sup>) from each station
- Pias*: Total abundance of immature male (ind/nm<sup>2</sup>)
- Temp*: Surface temperature (°C)
- Sal*: Salinity (‰)
- pH*: Power of hydrogen to measure the level of acidity in the water column
- DO*: Dissolved oxygen (mg/L)
- Moon Phase*: Categorized into 8 (eight) phases of the moon, i.e., new moon, waxing crescent, first quarter, waxing gibbous, full moon, waning gibbous, third quarter, waning crescent.
- $\mu$ : intercept
- s*: smoothing term in generalised additive model (GAM)
- $\epsilon$ : error term

### 3. Results

#### 3.1. The abundance of *terubuk* and *pias*

Based on verified target strength (*TS*), the highest approximated density of *T. macrura* (*terubuk* and *pias* combined) was discovered during the full moon in October 2015, as much as 206 ind/km<sup>2</sup> (~122,274 ind). In contrast, the lowest occurred during waning gibbous in November 2016, with just around 46 individuals or close to zero per km<sup>2</sup> (Table 2). There was a significant shift of sex ratio between the years of the survey, in which a large part of *pias* (74–89%) was found in 2015, while *terubuk* was the dominant component of 37–76% in 2016 (Fig. 3).

#### 3.2. The dynamic of oceanographic parameters

Mean salinity values varied from 5 to 30.5, where lower salinity found in the river-based stations. Salinity consistently increased from river towards the mouths of rivers and the straits. Similar pattern was observed with pH values with a range of 5.9–8.2 and transparency with a range of 0.2–1.6 m. Dissolved oxygen (DO) ranged from 2.3 mg/l (Siak River) to 5.0 mg/l (Bengkalis Strait), however, there was no clear pattern of the DO distribution like salinity and pH. In several occasions, there were no DO values available e.g. May–June 2015 and June–Aug 2016. Meanwhile, the surface water temperatures were relatively constant (29.2–32.8 °C) (Table 3).

In general, mean water surface temperature at full and new moon were relatively lower compared to other phases with a very volatile value. It was also lower towards the open sea (Bengkalis Strait) and

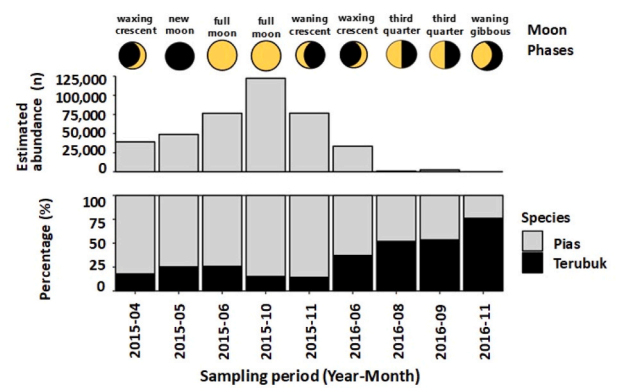


Fig. 3. Estimated abundance and proportion of *T. macrura* showing *pias* (male) and *terubuk* (female) based on the phase of the moon during the survey.

higher upstream, whereas a contrary pattern was found in salinity, pH and DO. Similar average values of salinity distribution among sub areas (Bengkalis Strait, Sei Pakning and Lalang Strait) indicated dominant in sea water mass entering the area, while the water mass in the Siak river and river mouth was dominated by warmer fresh water mass with low salinity, pH and DO delivered from upstream.

Sub area Bengkalis Strait had a relatively high-water transparency (0.9–1.6 m) compared to other areas. Sei Pakning/Padang Island and Lalang Strait revealed slightly lower water transparency (0.3–1.3 m), whereas the Siak river and river mouth revealed the lowest water transparency (0.1–1.0 m). The Moon phase did not seem to play a role for the water's transparency, instead, it was allegedly influenced by how far the distance of the stations were located from the sources of the flow of murky peat water mass.

Surface current circulation in the area study was suspected to be originated from the main Southeast Asian stream, infiltrated from Malacca Strait but not entirely driven by wind but rather influenced by mixed diurnal dominant tidal mechanism (Fig. 4). The tidal current flowed from the northwest to the southeast at high tide, and from the southeast to the northwest at low tide (Fig. 5). The tidal mass surges into the Bengkalis Strait from the northeast and south-southeast in the direction to the Malacca Strait. The Lalang Strait also contributes to the tidal mass. The water mass at the mouth of the Siak River was pushed by the high tide mass, allowing seawater to penetrate very far upstream of the Siak River.

The maximum current velocity was measured in April 2015, and the lowest was in August 2016, with an average current velocity of 0.3–3.5 m/s based on sub-areas. The average current velocity in the Bengkalis Strait ranged from 0.6 m/s (April) to 2.9 m/s (September); in Sei Pakning, it ranged from 0.6 m/s (August) to 3.5 m/s (June); in the Lalang Strait, it ranged from 0.8 m/s (April) to 1.6 m/s (June); near the mouth of the Siak River, it ranged from 0.3 (August) to 3.5 m/s (June).

At the greatest tide during maximum high tide on the full moon phase (June and October 2015) (Fig. 5c and f), high current velocities

Table 2

Estimated number of individual and density of *T. macrura* (*terubuk* and *pias*) acquired from hydro-acoustic surveys.

| Year | Month     | Moon phases     | Individuals (n) |                |         | Density (n/km <sup>2</sup> ) |                |       |
|------|-----------|-----------------|-----------------|----------------|---------|------------------------------|----------------|-------|
|      |           |                 | <i>Pias</i>     | <i>Terubuk</i> | Total   | <i>Pias</i>                  | <i>Terubuk</i> | Total |
| 2015 | April     | Waxing crescent | 31,258          | 6837           | 38,095  | 53                           | 12             | 64    |
|      | May       | New moon        | 36,478          | 12,383         | 48,861  | 62                           | 21             | 82    |
|      | June      | Full moon       | 56,749          | 19,723         | 76,471  | 96                           | 33             | 129   |
|      | October   | Full moon       | 103,634         | 18,641         | 122,274 | 175                          | 31             | 206   |
|      | November  | Waning crescent | 65,719          | 10,882         | 76,601  | 111                          | 18             | 129   |
| 2016 | June      | Waxing crescent | 21,033          | 12,416         | 33,449  | 35                           | 21             | 56    |
|      | August    | Third quarter   | 429             | 463            | 893     | 1                            | 1              | 2     |
|      | September | Third quarter   | 1145            | 1317           | 2462    | 2                            | 2              | 4     |
|      | November  | Waning gibbous  | 11              | 35             | 46      | 0                            | 0              | 0     |

**Table 3**  
Summary of mean value of oceanographic parameters in the Bengkalis waters during sampling period 2015 and 2016.

| Parameters       | Location         | 2015 |      |      |      |      | 2016 |      |      |      |
|------------------|------------------|------|------|------|------|------|------|------|------|------|
|                  |                  | Apr  | May  | Jun  | Oct  | Nov  | Jun  | Aug  | Sep  | Nov  |
| Tem (°C)         | Bengkalis Strait | 30.8 | 30.6 | 30.4 | 30.1 | 30.3 | 31.3 | 31.2 | 30.8 | 31.5 |
|                  | Sei Pakning      | 31.1 | 30.0 | 30.3 | 29.2 | 29.7 | 31.7 | 30.8 | 30.3 | 29.8 |
|                  | Lalang Strait    | 31.1 | 31.4 | 31.3 | 29.5 | 29.8 | 32.0 | 31.6 | 31.1 | 30.8 |
|                  | Siak River Mouth | 31.3 | 30.8 | 30.4 | 29.5 | 31.7 | 32.5 | 32.3 | 30.5 | 30.9 |
|                  | Siak River       | 30.9 | 31.6 | 31.1 | 29.9 | 30.2 | 32.8 | 31.5 | 30.5 | 30.6 |
| Salinity         | Bengkalis Strait | 29.0 | 30.0 | 30.0 | 29.5 | 29.5 | 30.1 | 30.7 | 30.4 | 29.4 |
|                  | Sei Pakning      | 27.0 | 30.5 | 30.5 | 28.5 | 29.0 | 30.0 | 29.0 | 29.3 | 25.5 |
|                  | Lalang Strait    | 28.0 | 30.0 | 30.0 | 29.0 | 29.0 | 27.5 | 27.8 | 26.0 | 28.4 |
|                  | Siak River Mouth | 17.0 | 8.5  | 19.0 | 27.0 | 21.5 | 10.0 | 18.0 | 14.0 | 7.0  |
|                  | Siak River       | 9.5  | 7.5  | 15.5 | 25.0 | 6.6  | 7.0  | 5.0  | 10.0 | 7.0  |
| pH               | Bengkalis Strait | 6.5  | 7.5  | 7.4  | 8.1  | 7.9  | 8.0  | 8.0  | 7.7  | 7.9  |
|                  | Sei Pakning      | 6.8  | 6.4  | 6.6  | 8.0  | 8.1  | 8.0  | 7.9  | 7.7  | 7.5  |
|                  | Lalang Strait    | 6.6  | 6.1  | 6.6  | 7.7  | 8.0  | 7.5  | 7.8  | 7.6  | 7.8  |
|                  | Siak River Mouth | 6.2  | 5.9  | 7.3  | 7.7  | 7.7  | 6.5  | 7.2  | 6.6  | 6.4  |
|                  | Siak River       | 6.2  | 6.4  | 6.6  | 7.7  | 7.0  | 6.5  | 6.3  | 6.2  | 6.5  |
| DO (mg/l)        | Bengkalis Strait | 5.0  | N/A  | N/A  | 4.4  | 4.4  | N/A  | N/A  | 3.2  | 5.0  |
|                  | Sei Pakning      | 4.1  | N/A  | N/A  | 3.6  | 3.7  | N/A  | N/A  | 2.7  | 3.9  |
|                  | Lalang Strait    | 4.1  | N/A  | N/A  | 3.7  | 4.0  | N/A  | N/A  | 3.1  | 3.7  |
|                  | Siak River Mouth | 3.7  | N/A  | N/A  | 3.8  | 3.3  | N/A  | N/A  | 3.9  | 3.6  |
|                  | Siak River       | 3.0  | N/A  | N/A  | 4.4  | 2.4  | N/A  | N/A  | 4.6  | 2.3  |
| Transparency (m) | Bengkalis Strait | 1.4  | 1.3  | 1.0  | 1.1  | 0.9  | 1.5  | 1.3  | 1.6  | 1.6  |
|                  | Sei Pakning      | 1.1  | 1.0  | 0.5  | 0.5  | 0.3  | 1.3  | 1.0  | 0.8  | 1.0  |
|                  | Lalang Strait    | 0.6  | 0.6  | 0.6  | 0.5  | 0.3  | 0.9  | 0.6  | 0.7  | 1.1  |
|                  | Siak River Mouth | 1.0  | 0.5  | 0.6  | 0.4  | 0.5  | 0.2  | 0.4  | 0.3  | 1.0  |
|                  | Siak River       | 0.9  | 0.3  | 0.4  | 0.3  | 0.2  | 0.2  | 0.2  | 0.3  | 1.5  |

Note: N/A (no data/not available).

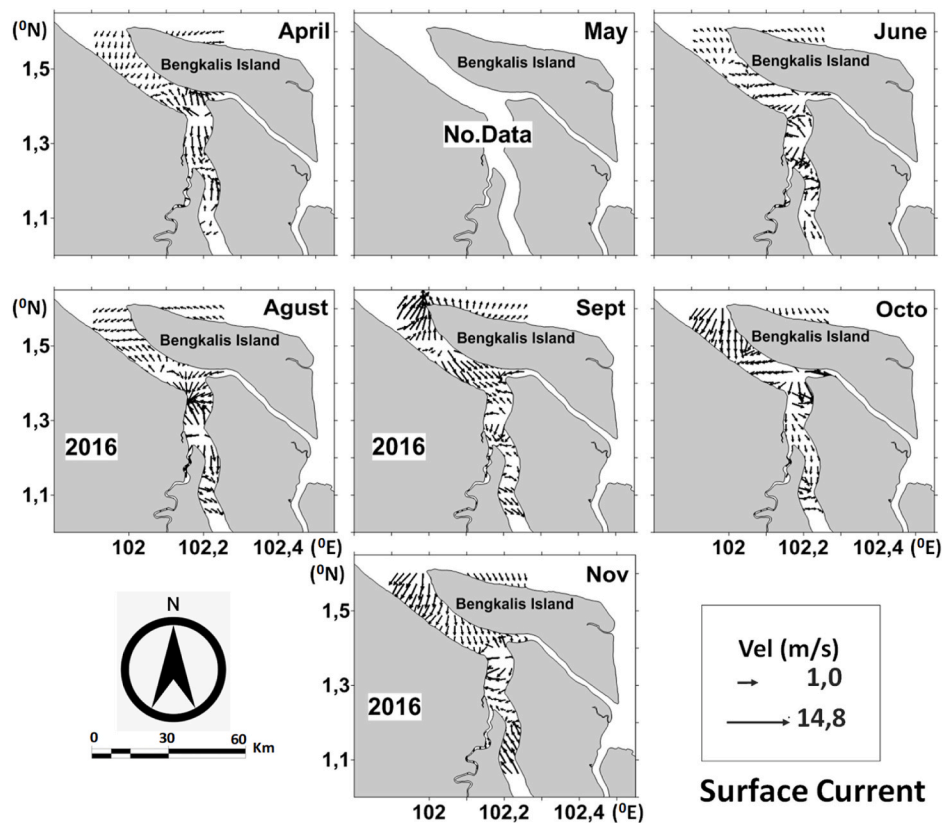


Fig. 4. Surface current's speed and direction within Bengkalis waters from 2015 to 2016.

occur due to the entry of a huge volume of water from the Siak River's mass flow as well as the push for expansion of due to the expanding the water mass from the Kampar River's estuary to the Lalang Strait. The

current speed fell in August, coinciding with the dry season's peak, and was distinguished by a weakening of the current in this downstream section of the Siak River due to a reduction in river water mass.

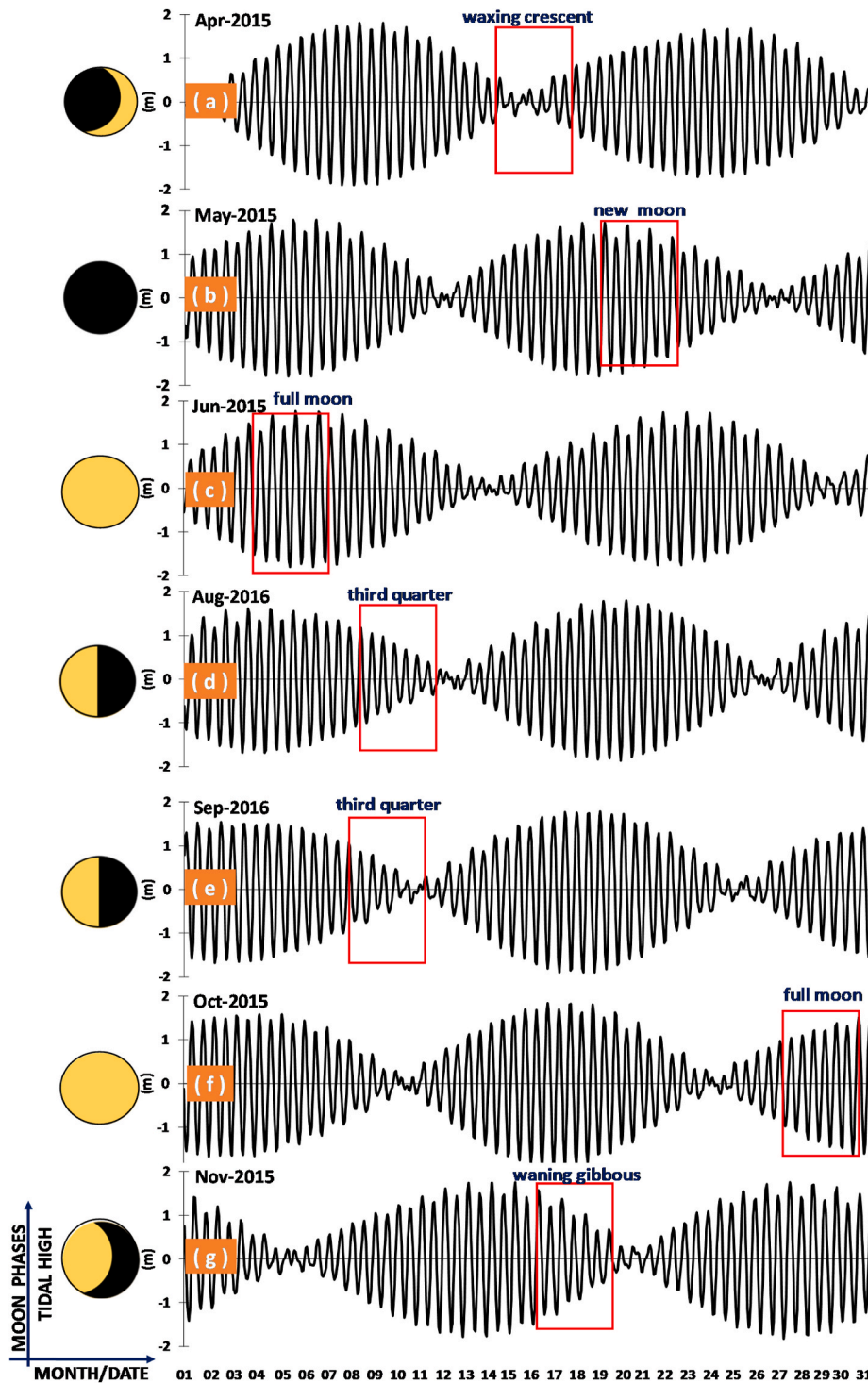


Fig. 5. Time series tides in Bengkalis waters associated with the moon phases on the survey period.

Furthermore, with the arrival of the rainy season in October and November, the volume of the Siak River’s water mass rose, causing the downstream flow to increase as well. Due to the lower current impulse from the Malacca Strait, as well as current seasonal fluctuations in of currents in these waters, the current velocity in the Bengkalis Strait and the Padang Strait become slower.

### 3.3. Spawning migration process

*Pias* prefer warmer temperatures (31 °C) with low salinity, generally

located in the Siak river mouth, whereas *terubuk* prefers slightly colder water (29–30 °C) with higher salinity which was mainly associated with seawater mass (Fig. 6, Fig. 7). The pH water value was normally high (8.5–8.7) in August, September, and October, slightly lower (8.0–8.5) in April and November and considerably lower in May and June (7.5–8.0) (Fig. 8). The waters connecting to the Malacca Strait (Bengkalis Strait and Sei Pakning/Padang Island) had a greater DO distribution value concentration (4.5–5.5 mg/L) than the Siak River estuary (3.0–4.4 mg/L) (Fig. 9). *Terubuk* tends to be more prevalent in waters with a high DO distribution value concentration. However, there was no difference in

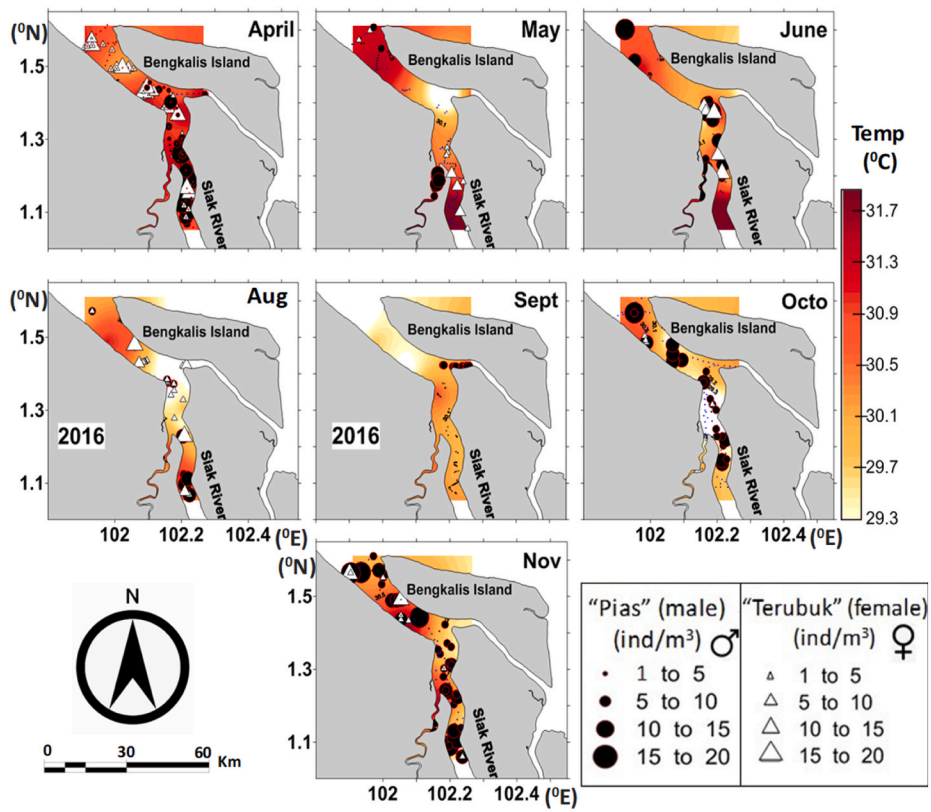


Fig. 6. Monthly surface temperature map overlaid with the abundance of *pias* and *terubuk*.

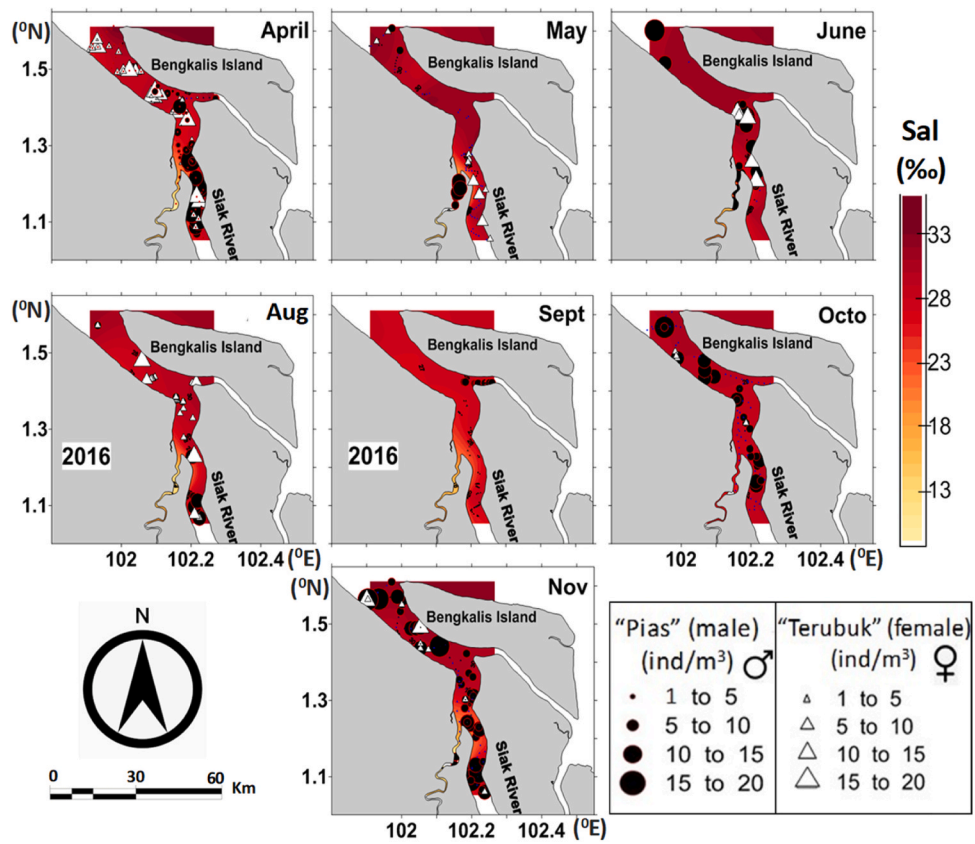


Fig. 7. Monthly salinity map overlaid with the abundance of *pias* and *terubuk*.

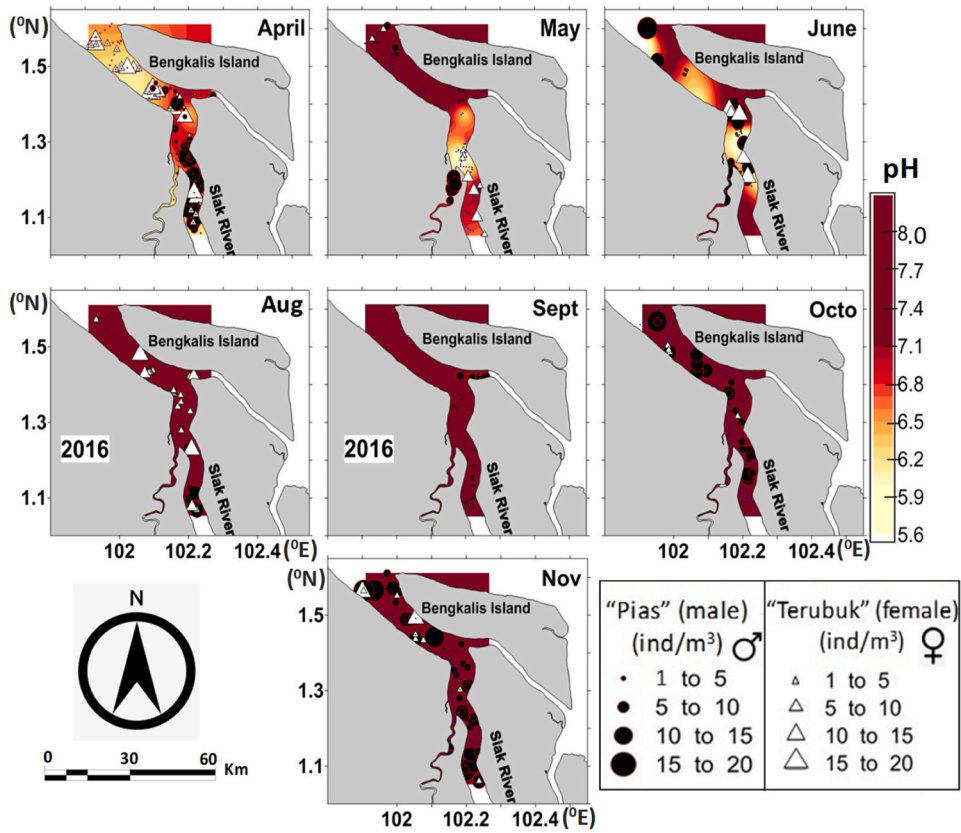


Fig. 8. Monthly pH map overlaid with the abundance of *pias* and *terubuk*.

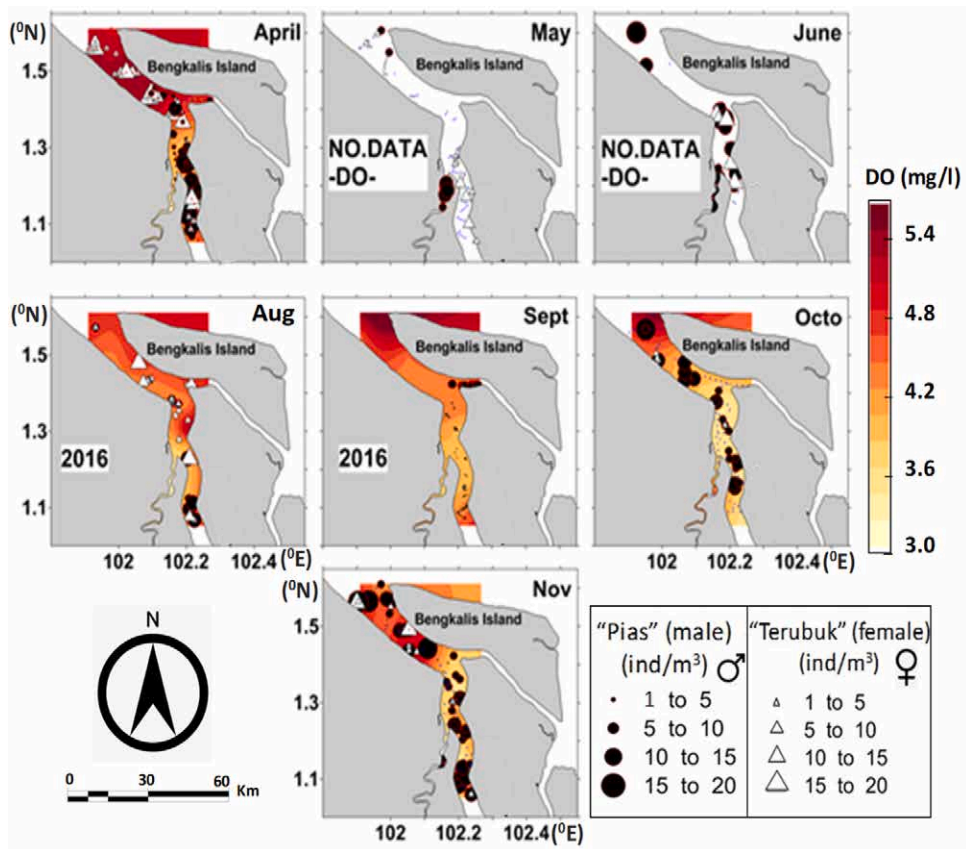


Fig. 9. Monthly dissolved oxygen map overlaid with the abundance of *pias* and *terubuk*.



preference for certain pH values between *pias* and *terubuk*.

The first sign of spawning migration was detected in April (waxing crescent) (Fig. 10) marked by the movements of large schoolings of *pias* and *terubuk* in their spawning habitat, with both entering from the Malacca Strait and spreading into the Bengkalis Strait, Padang Island/ Sei Pakning, Lalang Strait and the Siak river mouth. *Pias* were predominantly found from the upper layer (5–10 m depth) to the intermediate layer (20–30 m depth), whereas in the bottom layer (30–35 m depth) the number of each sex was roughly balanced. This period was touted as the first stage of the spawning process.

The later stage of the spawning process was visible during the new moon (May) and full moon (June) phases in zones C and D, as evidenced by the presence of schooling *pias* and *terubuk* in the same swimming

layer at a depth of 5–20 m. The largest spawning schooling was observed near the mouth of the Siak River in zone D, with a small fraction also occurring in zone C. The spawning continued in August (third quarter), albeit at a lower intensity, as seen by the separation of *pias* and *terubuk*. The surface layer (5–10 m) was dominated by *pias*, while the middle and bottom layers of the waters body were dominated by *terubuk*. During this month, we could observe the *terubuk* schools migrating back to sea waters, with only a tiny fraction of *pias* discovered in the Bengkalis Strait at the time.

Furthermore, schooling *pias* were sighted re-entering the Siak River estuary during a full moon (October). The majority were detected in the surface 5–10 m layer, with a tiny portion in the middle layer (10–25 m). In November (waning gibbous), most *pias* were already back in the

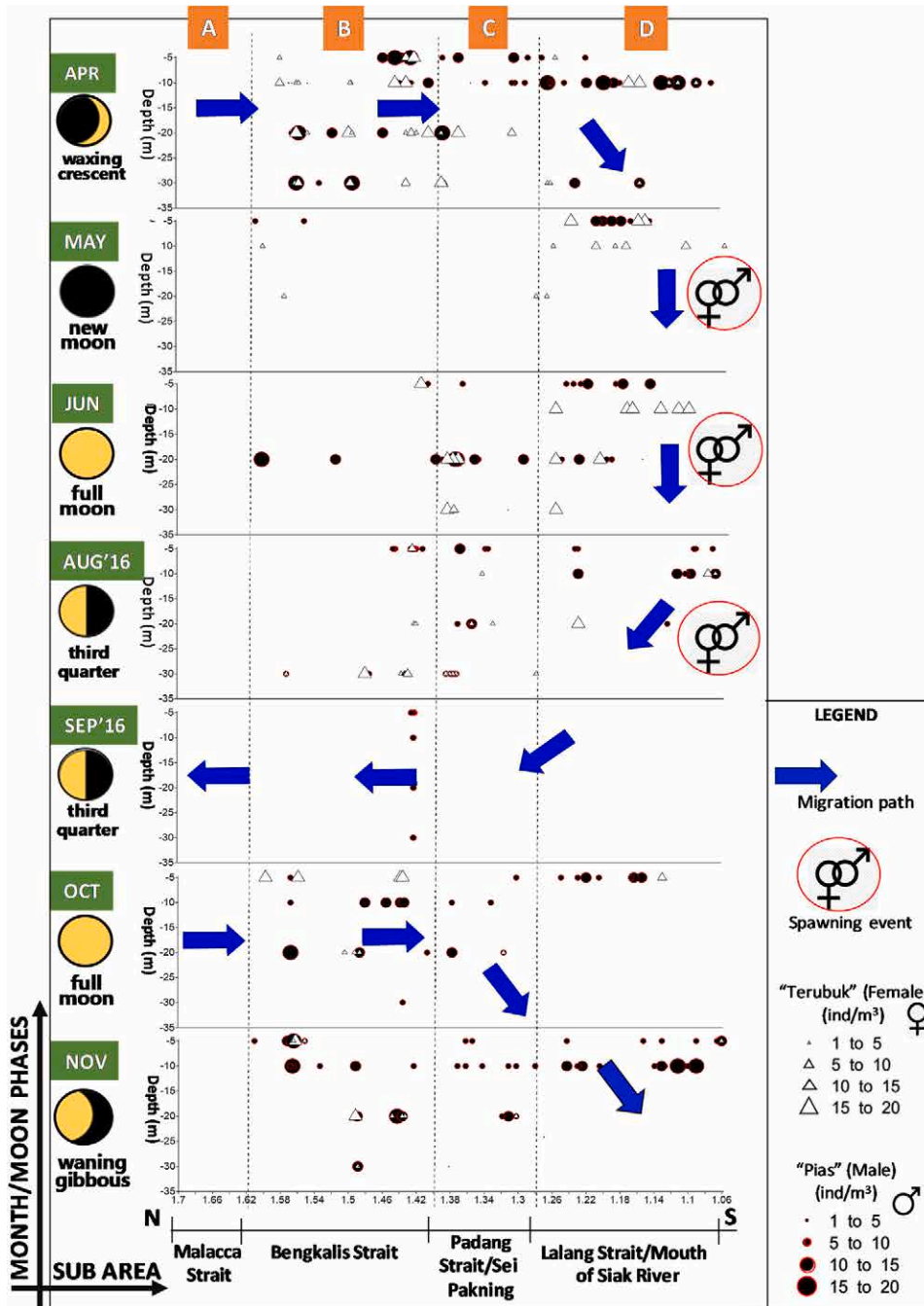


Fig. 10. Spawning migration pattern and timing (Note: A = sub area Malacca Strait; B = sub area Bengkalis Strait; C = sub area Padang Strait/Sei Pakning; and D = sub area Lalang Strait/Mouth of Siak River).

Lalang Strait/Siak River Estuary. However, no *terubuk* were found. *Pias* dominated practically all portions of the seas in all sub-areas. Still, *terubuk* were only found in a fair distribution at the surface and the middle of the water column in the Bengkalis Strait.

### 3.4. Models' performance

There was no significant association ( $r < 0.5$ ) among all model's covariates. The occurrence of low variance inflation factors (VIF) values (less than 3) for all variables also corroborated this evidence. The optimum scenario for obtaining the lowest deviance (37.590) and highest  $R^2$  (20.3%) was to add all variables to model. However, if we used AIC component, the best model (AIC = 1073.246) was obtained by leaving out DO and salinity parameters (Table 4). Moon phase and temperature played a key part in determining the abundance of *terubuk* compared to *Pias* (Table 5). With temperature, *Pias*, and DO all being positively associated to the amount of *terubuk*, however, pH was the inverse influence. On the other hand, salinity seemed to have little impact on the model (Fig. 11).

## 4. Discussion

*T. macrura* has an unusual life cycle because, like a protandrous hermaphrodite fish, it undergoes sex changes at a specific age and lives for only two to three years (Blaber et al., 1999). The mature female (*terubuk*) migration pattern is closely tied to its life cycle, with the juvenile stage of the fish traveling to the nursery ground in the coastal waters of the Malacca Strait until it matures into an adult male (*pias*) at the age of 6 months (Blaber et al., 1999). *Pias* will travel to the Siak River estuary (Bengkalis Strait, Sei Pakning, Lalang Strait, and Siak River estuary) in the new moon and full moon phases with *terubuk* for the spawning process, then return to the Malacca Strait regularly throughout the year. A similar trend was reported by Blaber et al. (2003), with the spawning season lasting from April to November. There was a shift in sex composition between 2015 and 2016, with *pias* being the dominant component in 2015 and *terubuk* being the dominant component in 2016. El-Nino in 2016 could be a factor influencing a shift in sex composition in 2015 and 2016. El-Nino caused the low intensity of rainfall, so that the estuary waters received low freshwater supply. As a result of their preference habitat in high salinity, *Terubuk* were found abundantly in 2016. However, using total sample data, *pias* was more dominant than *terubuk*. The high percentage of *pias* (74–89%) compared to *terubuk* (10–26%) in the study area (Table 2, Fig. 3) was in line with the finding of Suwarso et al. (2017), who also found that the sex ratio between the two was 3:1 in total weight (kg) and 4:1 in number of individuals (n) at the same period (2014–2016). Compared to *terubuk*, the considerable quantity of *pias* may indicate that the location of these waters, in addition to serving as a spawning ground, also serves as a nursery ground for juveniles (immature males). As a result, migration is vital for spawning events and the growth and sex change process.

Intriguingly, we discovered that the presence of *terubuk* and *pias* was

**Table 4**

Summary of indicators as calculated using six model scenarios, from the highest to the lowest deviance.

| No | Model Scenario  | Deviance      | AIC             | R <sup>2</sup> |
|----|---|---------------|-----------------|----------------|
| 1  | Terubuk ~1  |               | 1084.187        | 0.000          |
| 2  | Terubuk ~ Pias  | 603.470       | 1080.378        | 0.040          |
| 3  | Terubuk ~ Pias + MoonPhase                                    | 1405.180      | 1077.869        | 0.132          |
| 4  | Terubuk ~ Pias + MoonPhase + s(Temp)                          | 749.760       | 1073.259        | 0.181          |
| 5  | Terubuk ~ Pias + MoonPhase + s(Temp) + s(pH)                  | 133.230       | <b>1073.246</b> | 0.189          |
| 6  | Terubuk ~ Pias + MoonPhase + s(Temp) + s(pH) + s(DO)          | 163.930       | 1073.824        | 0.200          |
| 7  | Terubuk ~ Pias + MoonPhase + s(Temp) + s(pH) + s(DO) + s(Sal) | <b>37.590</b> | 1075.710        | <b>0.203</b>   |

**Table 5**

Analysis of deviance table for the GAM model fitted to the abundance *terubuk* in relation with oceanographic parameters.

| Parameters | df    | F     | P     | Sig. |
|------------|-------|-------|-------|------|
| Pias       | 1.000 | 6.357 | 0.129 |      |
| MoonPhase  | 6.000 | 3.240 | 0.005 | *    |
| s(Temp)    | 1.646 | 3.428 | 0.034 | *    |
| s(pH)      | 1.318 | 1.241 | 0.215 |      |
| s(DO)      | 1.000 | 1.156 | 0.284 |      |
| s(Sal)     | 1.102 | 0.024 | 0.910 |      |

Note: df = degrees of freedom, F = F-value, P = P-value, s(x) = smoother function of the corresponding independent variable.

detected not only during the new moon and full moon but also during every moon phase outside of spawning time, namely waxing crescent, waning crescent, and waning gibbous phases between April–November. However, with smaller populations (Fig. 10), small-scale migration to spawning environments occurs outside of the spawning season. One essential item to note was that no *terubuk* was found in the third quarter (September), leaving just a tiny number of *pias*. Therefore, it concluded that the spawning season occurred where the fish (male and female adults) were heading back toward Malacca Strait. Even though the Bengkalis strait was within the vicinity of the Malacca Strait, the spawning season did not align with the seasonal upwelling in the Malacca Strait. Stronger monsoon winds induced upwelling and higher chlorophyll-a concentration during November–February than that boreal summer monsoon April–October (Mandal et al., 2021). The spawning events concentrated in several areas, namely Sei Pakning and Padang Island Strait, marked by the high proportion of adult fishes caught (Adiwanarta et al., 2021) between May–June. Due to its protected strait and mud substrate, *T. macrura* made the estuary waters surrounding Bengkalis a spawning habitat (Ahmad et al., 1995). Referring to the pattern of schooling migration (Fig. 10), we discovered that most spawning events occurred in the Lalang Strait, while a smaller portion happened in Sei Pakning/Padang Island Strait. It was presumably because Lalang Strait has the deepest contour (>40 m) and mainly consisted of the sand substrate (>90%), compared to Sei Pakning (~50%) (Fig. 12). Such features were understandably ideal for spawning. A Clearer water and low predation aid to increase the hatching rate and larval life.

The two spawning sites which are located close to the mouth of the Siak River estuary have a strategic position, because they make it easier for spawning and for larvae to travel to the fresh water mass as their initial source of life support. *T. macrura* larvae were discovered in freshwaters of the Siak River following the tidal surge, according to Blaber et al. (1999). The larvae were discovered in an area with a high concentration of phytoplankton species *Trichodesmium* sp. and zooplankton species *Tintinnopsis* sp. and *Nauplius* sp (Seygita et al., 2021). *Clupeidae* is known as plankton feeders because they ingest both phytoplankton and zooplankton (Andriani et al., 2017), while studying larvae feeding patterns showed similar results (Ara et al., 2011).

According to the study, spawning allegedly happened all year round and reached its peak in July–September (Thamrin et al., 2021). The hypothesis supported by Muchlizar et al. (2017) based on hydroacoustic length frequency distribution analysis and Efizon et al. (2012) through monitoring of daily landing activity, wherein the proportion of *pias* and *terubuk* was close to equal (1:1) at that particular period. The balanced proportion between male and female fishes is essential to support the continuity of the spawning process (Effendi, 2002). We also discovered that spawning habitats had higher average salinity and pH distribution values during the peak spawning season (new/full moon), as shown in Table 3, namely at a salinity of 28.5–30.5 and pH 6.1–8.1. Meanwhile, the temperature ranged from 29.2 to 31.4 °C, with a DO of 3.6–4.4 mg/L and a transparency of 0.5–1.3 m. These results were similar to previous findings from Blaber et al. (1999) and still relevant with study by Thamrin et al. (2021). Since *T. macrura* spent most of their life in the

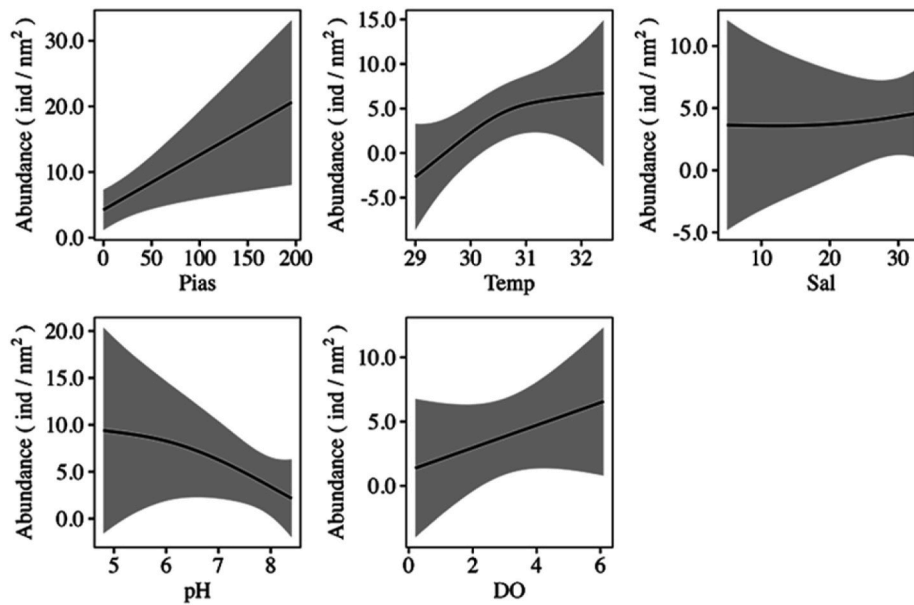


Fig. 11. Smoothing curves of predicted values for each covariate.

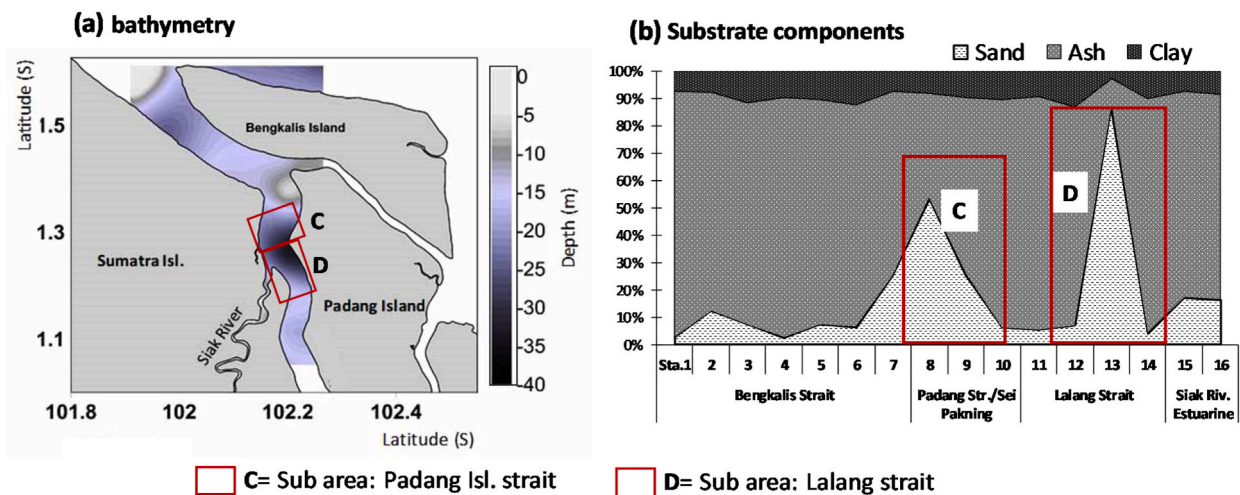


Fig. 12. Bathymetric structure (a) and bottom substrate profiles (b) in the spawning area. Sub area C (Padang island Strait) and sub area D (Lalang Strait) has the deepest contour and mostly consisted of sand substrate.

seawater environment and rarely penetrated deep into the estuary (Blaber et al., 2003), they only migrate when the conditions are met. In which this happened along with the infiltration of seawater mass with high pH during high tide (new/full moon).

The time, duration, and area of the peak spawning event in this study could be considered for developing or enhancing the laws governing the prohibition of capture and the zoning of spatial use in protected areas. The total ban of the bottom gillnet usage and restrictions on the dimensions of the nets' height will allow mature fishes to escape, which are often found in swimming layers >15 m. If this policy is applied, *T. macrura* will be able to reach the spawning ground safely, allowing the recruiting process to take place and produce a new generation.

**5. Conclusion**

Spawning migration of *T. macrura* from Malacca Strait to Siak River estuary occurred from April to November and reached its peak between May and July during the new moon or full moon phase. The spawning hotspot was identified in the deepest water column within Sei Pakning

and Lalang Strait which is dominated by the sand substrate. The emigration and sexual transfer happened at the end of the spawning event. There was a strong relationship between abundance and some oceanographic parameters, with temperature and phase of the moon being the most integral factors. The high salinity and pH at spawning areas during high tides in the new moon and full moon phases could be the driving force for spawning migration.

**Declaration of competing interest**

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

**Data availability**

Data will be made available on request.

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