Abundance and distribution of *Stolephorus baganensis* Hardenberg 1933 and *Thryssa kammalensis* (Bleeker 1849) larvae in relation to ontogeny and environmental factors in a Malaysian estuary

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Larval abundance and distribution of *Stolephorus baganensis* Hardenberg 1933 and *Thryssa kammalensis* (Bleeker 1849), two species of anchovies in the Selangor River estuary, were related to water parameters, planktonic biomass and individual developmental stages. Ontogenetic shifts in these relationships were observed for both species, suggesting that larval adaptiveness is crucial to the estuary's use as a nursery area. Both species are multiple spawners, spawning all year round but with peaks of intensity. In the case of *S. baganensis*, mass spawning occurred from April to July in clear and relatively deep coastal waters and was associated with an increase in dissolved oxygen and food availability. At approximately 10.0 mm SL, larvae moved towards shallower and more turbid waters where they remained until the juvenile stage. *T. kammalensis* spawning peaks were observed at approximately 3-month intervals without any strong association with the abiotic parameters considered. Their spawning ground was located in the shallow waters of the estuary. At approximately 10.0 mm SL, larvae moved upstream where they remained until the juvenile stage. This study does not fully support the match-mismatch hypothesis for tropical waters.

KEY WORDS: anchovy, ontogeny, distribution, water quality, estuary, Malaysia.
INTRODUCTION

Anchovies represent an important source of food and income in Southeast Asia. The alarming decline of the clupeoid fishery observed worldwide over the past few decades did not spare Asian countries (www.worldfishcenter.org), affecting all those depending directly or indirectly on this natural resource. Overfishing, destruction of nursery and/or spawning grounds, climate changes and pollution are responsible for this outcome (Brown 2000, Deket al. 2005). Although fishery policies are being readjusted to fit the new situation (Sainsbury et al. 2000, Salayo et al. 2006), proper management of fish stocks can only be carried out if a wide range of ecological data on the local species are available (Beckley & Lingen 1999).

The Klang Strait, on the west coast of peninsular Malaysia, is well known for its port and associated industries, its fishing ground, and also its mangroves and ecological parks. However, this prosperous area is also famous for the numerous conflicts that have arisen as a consequence of the multiple and incompatible uses of the environment (Leong et al. 2005). In order to have a better understanding of the ecology of this Strait and provide pertinent data to support the elaboration of an appropriate management plan, a vast multidisciplinary research program was initiated in 1996 at the University of Malaya (Kuala Lumpur, Malaysia). Among the topics considered was the life cycle of Stolephorus baganensis and Thryssa kammalensis, the two main anchovy species present in the area. The description and ontogeny of the larvae (Sarpedonti et al. 2000) were used as complementary data to discuss larval abundance and distribution in relation to body development. In addition, the match-mismatch hypothesis (Cushing 1990), based on the premise that fish cue their reproduction cycle on prey abundance in order to optimize the chances of survival newly of hatched larvae was discussed for these two tropical fish.

METHODS

Field trips

The study was realized at the mouth of the Selangor River (3°19'N – 101°15'E), on the west coast of peninsular Malaysia, which opens into the Malacca Strait via the
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Klang Strait (Fig. 1). This area is characterized by macro-tides of up to 5 and 1 m amplitude at spring and neap tides, respectively. Current velocities range from 0.05 m sec\(^{-1}\) to 0.35 m sec\(^{-1}\) at neap tide, and from about 0.15 m sec\(^{-1}\) to 1.00 m sec\(^{-1}\) at spring tide (Chong 1993). The weather is defined by a strong northeast monsoon prevailing from November to March, and by a milder southwest monsoon from May to September. The strongest rainfalls and winds are recorded during the inter-monsoon periods, in April and October. Samples were taken at nine stations established within a 5 km radius from the Selangor River mouth, and grouped into three zones according to the stations' depth and distance from the shore. Hence, stations 1 and 2, within the river and with a depth of 5 to 6 m, formed the first zone; the coastal stations 3, 4, 5 and 9, of about 3 m depth, formed the second zone and the seaward stations 6, 7 and 8, of about 10 to 12 m depth, constituted the third zone (Fig. 1). Field trips took place monthly, January 1997 to April 1998, in daytime and at flood/spring tides. At each station, dissolved oxygen (mg l\(^{-1}\)), pH, turbidity (NTU), salinity and temperature (ºC) were systematically measured throughout the water column, following a one-meter-interval sequence from the bottom to the surface, using a Grant-YSI sonde (model 3815). This series of values was then averaged to get a mean value representative of the overall water characteristics at each station and per abiotic factor. In the sequence, 12 liters of seawater were collected from the top 1 m surface layer and sieved through a 10 µm-mesh plankton net for future chlorophyll \(a\) determination. Lastly, ichthyoplankton and meso-zooplankton were sampled concomitantly using a bongo sampler composed of two conical nets of 363 µm and 180 µm mesh sizes, respectively. The oblique tows had a duration of about 4 min. The volumes of water passing through were estimated by two flowmeters placed at the mouth of each net. Two pseudo-replicates were taken per station. Collected plankton samples were immediately preserved in neutralized formalin 4%.

Samples treatment

Chlorophyll \(a\) concentrations were determined by spectrophotometry analysis following Strickland & Parson’s (1976) method. The zooplankton collected by the 180 µm mesh net was washed through a series of sieves and separated into the three size categories: 0.12-0.25 mm or ‘small-size’ group, 0.25-0.50 mm or ‘medium-size’ group and ≥ 0.50 mm or ‘big-size’ group. Each fraction was dried for 4 days at 80 ºC then weighed.

Fig. 1. — Location of the nine sampling stations in the study site, Selangor State, peninsular Malaysia.
for biomass estimation. Anchovy larvae of *Stolephorus baganensis* and *Thryssa kammalensis* were sorted, under a dissecting microscope, from the ichthyoplankton samples (363 µm mesh net) and separated into the five size-groups defined by Sarpedonti et al. (2000). In this classification, the size-groups were defined based on individual size at first observation of meristic characters, morphological changes and switches in the allometric growth of 10 body segments. Hence, size-group 0 (Sb0 and Tk0 for *S. baganensis* and *T. kammalensis*, respectively) corresponds to the first development of stage while size-group 4 corresponds to the last larval stage, when the larva turns into a juvenile.

**Data treatment**

Larval abundance (no. 100 m$^{-3}$), plankton biomass and chlorophyll $a$ concentration values were log transformed [log (x+1)] to homogenize the variance and normalize the distribution as required for parametric analysis (Sokal & Rohlf 1998). Variance homogeneity of the transformed data was checked using Cochran’s test, while normality of the distribution was assessed by plotting the within-cell residuals on the expected normal values. Water quality differences between zones were tested using Newman-Keuls multiple range test. Temporal and spatial variations in abundance of each larval size-group were tested by analysis of variance (1-way ANOVA). Correlations between larval size-groups abundance and water quality were assessed through canonical correspondence analysis (CCA; CANOCO package version 2.2; ter Braak 1988). Parameters of the final regression were given as (1) intra-set correlation, representing the correlation coefficients between environmental variables and ordination axes, and (2) canonical coefficients, defining the ordination axes as linear combinations of the environmental variables. However, as the latter can be unstable when the environmental variables themselves covary (ter Braak 1988), intra-set correlations were used in this study to interpret the derived relationships between species and environmental factors in the given area.

As the CCA indicated a correlation between the youngest larvae and zooplankton abundance, further analysis were conducted to better investigate the match and mismatch between larval abundance and the monthly variations in biomass of their favorite zooplankton group-size. Hence, the number of standard deviations from the annual mean abundance of larval size-groups 0 and 1 were plotted with those of their likely food items. The data were treated as follows: (1) the mean monthly population densities of newly-hatched larvae were log (x+1) transformed; (2) the ‘annual’ mean and standard deviation (i.e. for the 16 months of the survey) of the monthly log-transformed densities were calculated; (3) the annual mean was then subtracted from the monthly means and the differences were divided by the ‘annual’ standard deviation. The resulting values gave the deviations (from the annual mean) in terms of number of standard deviations. Hence, a negative value indicated a larval density lower than the annual mean stock density, whereas a positive value indicated a larval density stock above the average. Zooplankton biomass and chlorophyll $a$ abundance were treated similarly, and the three parameters were plotted together in the same graph.

**RESULTS**

**Water quality**

Water temperature was constant over time ($P > 0.05$), averaging 30.5 °C ± 1.0, but differed spatially with zone 1 presenting lower values ($P < 0.05$)
than zones 2 and 3. Mean pH was 8.0 ± 0.5 and constant \( (P > 0.05) \) over time and space. Monthly salinity fluctuated between 26 and 34; the minimum values were recorded throughout the estuary during the two annual rainy seasons; spatially, salinity increased in the seaward direction. Dissolved oxygen averaged 6.0 mg l\(^{-1}\); minimum values of 4.5 to 5.0 mg l\(^{-1}\) were recorded in February-March 1997 and December-January 1998 at all stations while maximum concentrations of about 6.5 mg l\(^{-1}\) were recorded in August 1997. The lowest values were generally encountered in zone 1. Monthly turbidity values remained constant \( (P > 0.05) \) and approximated 50 NTU except in zone 1 where values from 100 NTU to 250 NTU were recorded from January to May of 1997 and 1998.

**Plankton and chlorophyll a**

Chlorophyll \( a \) concentrations averaged 3.2 mg m\(^{-3}\) from January to March 1997, then increased to 14.0 mg m\(^{-3}\) in October 1997. In November and December, concentrations dropped to 2.5 mg m\(^{-3}\) before increasing again in January 1998. The highest monthly concentrations were generally recorded in zone 2. Higher biomasses of total zooplankton were registered in March and April 1997 and again in March 1998, with values around 23.0 g 100 m\(^{-3}\); minimum values of about 9.0 g 100 m\(^{-3}\) were noted in May and June 1997 and from December 1997 to February 1998. The three size categories presented monthly variations similar to those for the total zooplankton and were characterized by high monthly standard deviations reflecting a patchy distribution of the organisms within the estuary. The spatial distribution between zones did not show any clear pattern throughout the study period.

**Larval abundance**

*Stolephorus baganensis*

*S. baganensis* larvae were found in all months (Fig. 2) with abundances ranging between 142.0 100 m\(^{-3}\) (April 1997) and 2.0 100 m\(^{-3}\) (September 1997). Despite these large variations, and probably because of patchy larval distribution, abundances were significantly different \( (P < 0.05) \) only in April and July 1997, indicating, in both cases, an increase of the larval population.

Larvae < 10.0 mm standard length (SL) (i.e. size-groups 0, 1 and 2) presented similar patterns of temporal abundance characterized by higher values \( (P < 0.05) \) from January to July 1997. Larvae from 10.0 to 18.0 mm SL (i.e. size-group 3) were significantly more abundant \( (P < 0.05) \) from January to April 1997 and from December to February 1998. No significantly differences were observed in the temporal abundance of larvae > 18.0 mm SL (i.e. size-group 4).

Within the estuary, newly hatched larvae (i.e. size-groups 0 and 1) were significantly \( (P < 0.05) \) more abundant at station 8, the deepest and most offshore station. Size-group 2 larvae were homogeneously distributed in the
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estuary, with no significant differences among stations ($P > 0.05$). Size-group 3 larvae were more numerous on the coastline, with station 6 presenting a significantly higher mean abundance ($P < 0.05$) than the more offshore stations. This trend was maintained for the bigger larvae (size-group 4), which were almost absent from the three deeper stations of zone 3. In terms of relative abundance, size-group 1 was significantly ($P < 0.05$) more abundant than the other groups. The highest / lowest / mean monthly abundances were 42.3 / 0.0 / 5.5 100 m$^{-3}$, 74.6 / 0.3 / 17.7 100 m$^{-3}$, 43.4 / 0.0 / 9.5 100 m$^{-3}$, 22.3 / 0.0 / 6.5 100 m$^{-3}$ and 27.7 / 0.0 / 7.0 100 m$^{-3}$ for size-groups 0, 1, 2, 3 and 4, respectively.

*Thryssa kammalensis*

*T. kammalensis* larvae presented significant peaks of abundance in April, July, September, December 1997, and March 1998 (Fig. 3). The maximum (159.5 100 m$^{-3}$) and minimum (1.4 100 m$^{-3}$) mean abundances were recorded in April and August 1997, respectively. Size-group 0 larvae were very few throughout the study period, not exceeding a monthly abundance of 2.0 100 m$^{-3}$ (November 1997). Size-group 1 presented significant peaks of abundance in April, July, September and December 1997. In contrast, size-group 2 larvae were more abundant from January to April 1997 and in March and April 1998. Larvae of size-group 3 were dominant and significantly ($P < 0.05$) more abundant in January and March 1998. Size-group 4

![Fig. 2. — Percentage abundance of the five size-groups of *Stolephorus baganensis* larvae within the study area from January 1997 to April 1998. Right column values indicate the total abundance of fish larvae.](image-url)
was absent in all months, except for a few specimens collected in July 1997 and in March and April 1998.

In terms of spatial distribution, newly hatched larvae were absent from station 8, the most offshore station, and found mainly along the coastline with significantly higher abundances at stations 5 and 9. Size-group 2 larvae were homogeneously distributed in zones 1 and 2. Larvae of size-groups 3 and 4 were not sufficiently abundant to show a spatial pattern of distribution. The highest / lowest / mean monthly abundances were 4.5 / 0.0 / 0.9 $100 \text{ m}^{-3}$, 111.9 / 0.1 / 23.3 $100 \text{ m}^{-3}$, 45.8 / 0.0 / 14.2 $100 \text{ m}^{-3}$, 81.8 / 0.0 / 9.7 $100 \text{ m}^{-3}$ and 4.8 / 0.0 / 0.5 $100 \text{ m}^{-3}$ for size-groups 0, 1, 2, 3 and 4, respectively.

**Canonical correspondence analysis**

The first two ordination axes from the CCA explained 59.9% of the total variability in larval abundance with 32.2% referring to the first canonical axis and 27.7% to the second canonical axis. Components of the first two axes are given in Table 1. The first axis was primarily related to temperature and turbidity in the positive direction (to the right) and ‘medium-size’ zooplankton in the negative direction (to the left). The second axis was related to chlorophyll $a$, temperature, ‘medium’- and ‘big-size’ zooplankton in the positive direction, and ‘small-size’ zooplankton and salinity in the negative direction.

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Fig. 3. — Percentage abundance of the five size-groups of Thryssa kammalensis larvae within the study area from January 1997 to April 1998. Right column values indicate the total abundance of fish larvae.
The CCA results indicate that newly hatched *S. baganensis* were more abundant in waters with high levels of dissolved oxygen and ‘medium-size’ zooplankton, whereas the bigger larvae of size-group 2 showed a higher correlation with large-size zooplankton biomass (Fig. 4). Size-groups 3 and 4 did not show a particular food preference but were more abundant in cooler,

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<tr>
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<th>Axis 1</th>
<th>Axis 2</th>
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<td><strong>Summary statistics for first two axes</strong></td>
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<td>Eigenvalues</td>
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<td>Fraction of species environmental variations explained</td>
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<td>27.70</td>
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<td>Species-environment correlations (R)</td>
<td>0.992</td>
<td>0.883</td>
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| Canonical coefficients for standardized variables |        |        |
| Oxygen (O₂)                                      | -0.27  | 0.22   |
| Turbidity (Turb)                                 | 0.23   | 0.05   |
| Temperature (Temp)                               | 0.46   | -0.02  |
| pH                                                | -0.07  | -0.08  |
| Salinity (Sal)                                   | 0.33   | -0.01  |
| Chlorophyll a (Chl a)                            | 0.07   | 0.14   |
| Big-sized zooplankton (Zpk big)                  | -0.47  | 0.10   |
| Medium-sized zooplankton (Zpk med)               | 0.14   | 0.11   |
| Small-sized zooplankton (Zpk small)              | 0.05   | -0.19  |

| Intra-set correlation of environmental variables |        |        |
| Dissolved oxygen (O₂)                           | -0.121 | 0.396  |
| Turbidity (Turb)                                 | 0.605  | 0.328  |
| Temperature (Temp)                               | 0.595  | 0.544  |
| pH                                                | -0.081 | -0.068 |
| Salinity (Sal)                                   | 0.313  | -0.260 |
| Chlorophyll a (Chl a)                            | 0.423  | 0.555  |
| Big-sized zooplankton (Zpk big)                  | 0.232  | 0.476  |
| Medium-sized zooplankton (Zpk med)               | -0.242 | 0.544  |
| Small-sized zooplankton (Zpk small)              | 0.262  | -0.498 |
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Less turbid and high pH waters, i.e. the deeper, more offshore waters. The younger larvae of *T. kammalensis* showed a higher correlation with the shallow, warmer and more turbid conditions along the coast (Fig. 4). In contrast, the larger but less abundant size-group 3 larvae were found in the cooler, less turbid waters of the most offshore stations.

**Match-mismatch hypothesis**

Matches of size-group 1 *S. baganensis* larvae abundances with medium-size zooplankton were observed from March to July 1997 and from November 1997 to February 1998. Mismatches were noted in September 1997 and March 1998, when plankton was abundant but larval abundance was well below the annual abundance (Fig. 5A).

The larval abundance pattern of *T. kammalensis* matched the planktonic abundance in all months except (1) December 1997, when larvae were relatively abundant but chlorophyll *a* and ‘small-size’ zooplankton levels were both well below the average, and (2) March and April of 1998 when plankton abundance was high but larval abundance remained below the annual mean (Fig. 5B).
DISCUSSION

Tropical clupeiform species are known to spawn practically all year round. Their peaks of activity can sometimes be correlated to a given protracted environmental window (LUTHER 1990, BARLETTA-BERGAN et al. 2002), indicating a spawning season selected to ensure the success of the early life stages. In the other cases, spawning occurs randomly over time so that there are always some batches of larvae that encounter environmental conditions favorable to individual survival (PALOMERA 1992). The observation of a single period of abundance of newly hatched S. baganensis larvae over a 16-months period, as indicated by the CCA and match-mismatch hypothesis study, and its association with high dissolved oxygen concentrations and zooplankton biomasses, suggest that this species follows the first spawning strategy mentioned above. On the other hand, and based on the same data source, the reiterated spawning peaks of T. kammalensis size-group 1 larvae on a 2- to 3-month basis regardless of climatic conditions and without any clear relationship with the abiotic factors considered indicate that this species follows the second spawning strategy. The match-mismatch hypothesis tested on S. baganensis did not implicitly reject the theory as the only mismatch occurred...
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in March 1998, when mature and spent females of this species were found in the estuary (Sarpedonti 2005). Therefore, the larval data alone, without a complementary study on the adult gonadal maturation pattern, could be deceptive. In the present case, it is likely that the young larvae died or drifted away following a storm or strong winds frequently recorded during the monsoon season (Cury & Roy 1989). In the case of T. kammalensis, the presence of a larval peak in December 1997, when plankton is at its lowest, tends to reject Cushing’s (1990) hypothesis. A longer-term study, complemented by better knowledge of fish feeding behavior (e.g. Cuttitta et al. 2006) and gonadal maturation stages, would be necessary to validate this rejection.

The morphological differences between the larvae of the two species throughout their development, as described by Sarpedonti et al. (2000), were viewed as potential factors controlling the spawning patterns. Hence, it is suggested that the “opportunist” spawning strategy of T. kammalensis reflects a more advanced anatomical stage of the individuals at hatching (compared to S. baganensis) that endow the larvae with higher resistance and adaptability to withstand environmental variability. A similar pattern of long-lasting spawning activity followed by a period of inactivity has been reported for anchovy species inhabiting Indian waters (Luther 1990). On the other hand, S. baganensis would choose the most favorable environmental conditions to spawn in order to counterbalance the individual anatomical precariousness at hatching. Such time-targeted spawning has been reported for most Caribbean reef fish species and is related to temperature and plankton abundance (Munro et al. 1973).

The results of this study indicate that, although living in the same estuary, S. baganensis and T. kammalensis follow different patterns of distribution. Territorial occupation specificity is generally associated with distinct spawning grounds and uneven ontogenetic abilities to adapt to environmental conditions (Leis et al. 2005, Pinder et al. 2005). This segregation usually favors population survival through decreased competition between species and individuals at different developmental stages (Lambert & Ware 1984). The aggregation of S. baganensis young larvae in the more offshore stations and their association with low turbidity was related to the negative allometric growth rate of the eyes in individuals < 10mm SL (Sarpedonti et al. 2000). The small yolk-sac of S. baganensis larvae, along with the rapid depletion of its reserves (Sarpedonti et al. 2000), were associated with the presence in time and space of larvae in areas rich in zooplankton. The migration of S. baganensis larvae of about 10 mm SL to shallower, more turbid coastal waters occurs approximately when the eye diameter switches to positive allometric growth (Sarpedonti et al. 2000), marking the establishment of faster eye development and visual improvement. The importance of eye ontogeny on the distribution of individuals throughout the larval cycle has already been demonstrated in various studies on other species, such as the stone loach (Kováč et al. 1999). As they grow, S. baganensis larvae increase their chances of survival through biological development while the individuals spread along the coast. These ecological/biological aspects, sustained by the weaker biotic/abiotic associations shown by the CCA, reflect a greater capacity of the individual to withstand environmental heterogeneity. The biggest
larvae (and small juveniles occasionally captured in the net) were associated with a salinity rise, indicating a migration back to the sea where juveniles and adults remain (Sarpedonti 2005). The dispersion of *S. baganensis* larvae during the larval period is schematized in Fig. 6A.

The presence of newly hatched *T. kammalensis* larvae in the shoreline stations of zone 2 and their positive association with plankton biomass and water turbidity were related to the positive allometric growth of the eyes at hatching (Sarpedonti et al. 2000), which equips the larvae with suitable vision to evolve in that environment. The use of a spawning ground closer to the shore, compared to that of *S. baganensis*, minimizes the risks of mortality by dispersion and predation (Johannes 1978). This, along with the higher body developmental stage and bigger yolk-sac of *T. kammalensis* larvae at hatching, probably provide young *T. kammalensis* individuals with higher chances of survival than young *S. baganensis* larvae. Such associations between developmental stages and mortality rates were reported by Fiksen & Folkvord (1999). At about 10.0 mm SL *T. kammalensis* larvae gather at the river mouth and then enter the river where they remain until the juvenile stage. Similar migration was observed for this species in the Matang mangrove rivers system (Sasekumar et al. 1994). This residence period upstream is generally viewed as a behavior enhancing larval survival chances (Blaber 1997). The use of Kuala Selangor estuary by *T. kammalensis* larvae is schematized in Fig. 6B.
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