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Early life history of *Acanthopagrus latus* and *A. schlegeli* (Sparidae) on the western coast of Taiwan: temporal and spatial partitioning of recruitment

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Abstract. *Acanthopagrus latus* and *A. schlegeli* are phylogenetically closely related. The seasonal occurrence and distribution, age and length at recruitment, growth rate and hatching dates of their larvae were compared by collecting fortnightly specimens from four estuaries on the north-eastern and western coast of Taiwan between September 1997 and August 1998. Age and growth rate were determined from the daily growth increments in otoliths of the larvae. Occurrences of *A. latus* and *A. schlegeli* larvae on the western coast of Taiwan were temporally and spatially separated. Recruitment of the former progressed from north to south from November through March, whereas the latter progressed from south to north from December through May. Age and length of the larvae at estuarine arrival were greater in *A. latus*; these values increased southward for *A. latus* and northward for *A. schlegeli*. Age at recruitment was inversely correlated with growth rate which was positively correlated to water temperature. *A. latus* spawned mainly in autumn, whereas *A. schlegeli* spawned mainly in spring with a minor spawning peak in autumn. Coastal currents and the spawning behaviour of the adults may influence the geographic gradients of the seasonal occurrence and distribution of the larvae on the western coast of Taiwan.

Introduction

Acanthopagrus spp. are widely distributed in shallow coastal waters, lagoons and estuaries of the Indo–West Pacific (Springer 1982). Adults spawn in coastal waters and the larvae move to estuaries (Hu 1983). Four species of *Acanthopagrus* are recorded from Taiwan: *Acanthopagrus australis*, *A. berda*, *A. latus* and *A. schlegeli* (Jean *et al.* 1992). Yellow sea bream (*A. latus*) and black porgy (*A. schlegeli*) are comparatively abundant and economically important for recreation and aquaculture. In Taiwan, wild larvae and juveniles of these two species have been harvested in estuaries for restocking for many years. However, many aspects of their natural life history are poorly understood.

The otolith is a powerful proxy for describing the early life history of fish (Pannella 1971; Campana and Neilson 1985). Daily growth increments in otoliths are widely used to determine larval ages, to estimate their growth rates and hatching dates, as well as to separate different cohorts of a species with protracted spawning period (Tzeng 1990; Stevenson and Campana 1992; Tzeng *et al.* 1998; Wang and Tzeng 1999; Chang *et al.* 2000). Previous studies of the *Acanthopagrus* spp. in Taiwan have focused mainly on aquaculture (Tang and Twu 1979), artificial propagation (Hu 1983; Leu *et al.* 1991) and taxonomy (Lee 1983; Jean *et al.* 1992, 1995). Age and growth of *A. schlegeli* larvae have been studied for a particular estuary on the western coast of Taiwan (Huang and Chiu 1997*b*). Information on the seasonal occurrence, abundance and distribution of *A. latus* and *A. schlegeli* larvae on the western coast of Taiwan is fragmentary (Liu 1978; Huang *et al.* 1985; Hung and Chiu 1991; Tzeng and Wang 1992, 1993, 1997; Tzeng 1995; Huang and Chiu 1997*a*; Tzeng *et al.* 1997).

A. latus and *A. schlegeli* are similar phylogenetically, morphologically and in their habitat use. This raises the question of whether members of these two species compete for habitat use and food resources. If they do not, how have they evolved differences in habitat use in time and space? To elucidate this, the early life history of these species on the western coast of Taiwan was studied, including seasonal occurrence and distribution, age and length at recruitment, growth rates and hatching dates and the linkage between larval dispersal and coastal currents induced by the monsoon.

Materials and methods

Sampling design

Fish larvae and juveniles were collected while immigrating into four estuaries, Shuangchi Creek (SC), Gongshytyan Creek (GST), Tatu Creek (TT) and Tongkang River (TK) (Fig. 1). The west coast of

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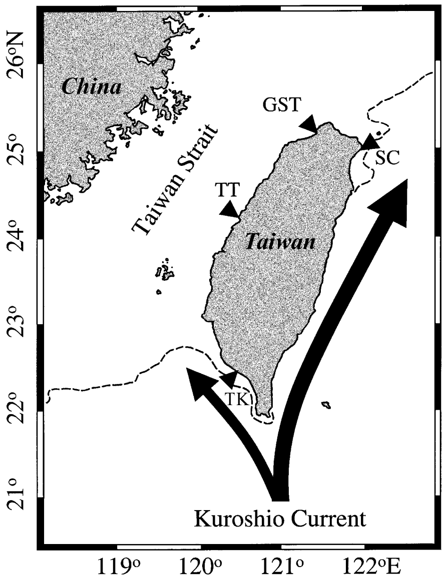

Fig. 1. Sampling sites of *A. latus* and *A. schlegeli* larvae in the estuaries of Shuangchi Creek (SC), Gongshytyan Creek (GST), Tatu Creek (TT) and Tongkang River (TK). Dashed line, 200 m depth contour.

Taiwan is separated from China by the Taiwan Strait which has a wide and shallow continental shelf suitable as a spawning and nursery area for coastal fishes. In contrast, on the east coast the continental shelf is narrow except in the north-east and is influenced by the Kuroshio current. The direction of coastal currents on the western coast that transport larvae to the estuary changes with the seasonal monsoon (Chu 1963). Water temperatures on the western coast decrease when the NE monsoon prevails in autumn and winter and increase when the SW monsoon prevails in spring and summer.

An anchored net was set against the tidal current in the estuaries to collect fish larvae and juveniles during the night-time flood tide around the new and full moons between September 1997 and August 1998. The mesh size of the net ranged from 0.8 to 1.8 mm. *A. latus* and *A. schlegeli* larvae were found abundantly from October through May, which is the commercial fishing season for collecting the larvae for restocking. Larval abundance was estimated roughly by the number of fish caught per hour. Surface water temperature was also measured to 0.1°C on a microprocessor conductivity meter (Model LF196, Wissenschaftlich-Technische Werkstätten) during sampling.

Specimen preparation and measurement

Both *Acanthopagrus* species were sorted and separated from the other larvae collected by the net. They were identified in fresh samples according to the melanophore distribution patterns as described by Okiyama (1988). The larvae were then preserved in 95% alcohol for length measurement and otolith analysis. Larval total length was measured to the nearest 0.1 mm at a magnification of 10X by a profile projector. Larval shrinkage due to alcohol preservation was not adjusted for. The shrinkage of total length was estimated as ~4.7 ± 1.7% ($n = 39$).

Sagittal otoliths of the larvae were extracted, air-dried, embedded in resin, ground, polished and etched. Preparation of otoliths for age determination followed Chang *et al.* (2000). Growth increments in the larval otoliths were clearly discernible by microscope under reflected light and no sub-daily increments were found (Fig. 2). The increments in otoliths of *A. schlegeli* larvae have been validated as deposited daily (Huang and Chiu 1997*b*). The increments in otoliths of *A. latus* were assumed to be deposited daily because they are related species. Daily growth increments in the magnified (300–600X) photographs of otoliths were counted independently by two people. The daily age of the larvae was the average of the daily growth increments from these two independent counts if the difference in counts between readers was <5%; otherwise, the otolith was excluded from the age estimation. Larval hatching dates were back-calculated from their daily age and capture dates. The increment widths on the maximum otolith radius of the larvae were measured to evaluate the growth rate of an individual on the assumption that otolith and somatic growth are coupled. Increment widths were measured by digital caliper on the magnified (300–600×) photographs.

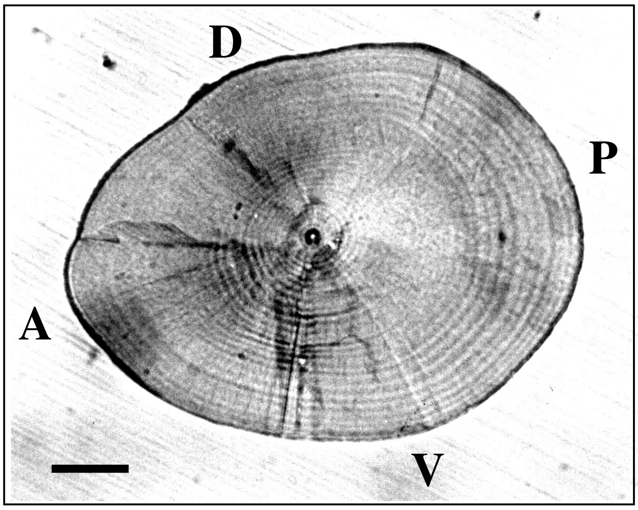

Fig. 2. Daily growth increments in the sagittal otolith of a 12.3 mm TL *A. schlegeli* larva. A, anterior; P, posterior; D, dorsal; V, ventral. Scale bar, 100 µm.

Data analysis

Significant differences in age and length between species and among estuaries and sampling dates were determined by one-way analysis of variance (ANOVA) and Tukey multiple-comparison test (Winer 1971).

Results

Spatial distribution

The *A. latus* larvae were most abundant at GST (32.2 ± 33.14 fish h^{-1}), followed by TT (4.8 ± 6.3 fish h^{-1}) and SC (0.3 fish h^{-1}). In contrast, *A. schlegeli* larvae were most abundant at TT (58.1 ± 57.9 fish h^{-1}), followed by TK (30.0 ± 30.5 fish h^{-1}) and GST (26.8 ± 43.5 fish h^{-1}). The larvae of *A. latus* were not caught in TK and *A. schlegeli* not in SC (Fig. 3). The density distribution of the larvae indicates that *A. latus* may originate from the north and disperse southward. In contrast, *A. schlegeli* may originate from the south and disperse northward.

Geographic gradient in seasonal occurrence of larvae and water temperature

The geographic gradient in seasonal occurrence was opposite for these two species (Fig. 4). Larvae of *A. latus*

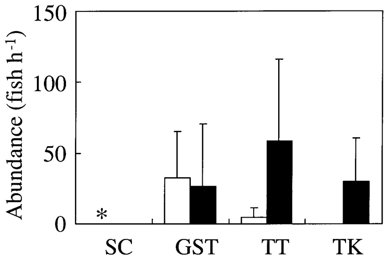

Fig. 3. Abundance of (□) *A. latus* and (■) *A. schlegeli* larvae in four estuaries, Shuangchi Creek (SC), Gongshytyan Creek (GST), Tatu Creek (TT) and Tongkang River (TK). Vertical lines, s.d. *Small number of *A. latus*.

occurred earlier in the north (GST) than in the central west (TT) in the period between November and February. In contrast, larvae of *A. schlegeli* occurred first in the south (TK), then in the central west (TT) and later in the north (GST) in the period from December through May.

The peak abundance of *A. latus* larvae occurred at water temperatures of 20.5–20.9°C in GST and 18.3°C in TT, whereas for *A. schlegeli* larvae, water temperatures were 24.0–30.0°C in TK, 24.0–25.6°C in TT and 26.3°C in GST (Fig. 4). Thus, the water temperature at peak larval occurrence was higher for *A. schlegeli* than for *A. latus*, but the temperature at peak occurrence of each species was similar among areas and shifted with the season. That is, the occurrence of larvae in the estuaries followed the seasonal changes in water temperature. *A. latus* larvae occurred early in the north and later in the south, following the seasonal decrease in temperatures during autumn. In contrast, *A. schlegeli* larvae occurred early in the south and later in the north, following the seasonal increase in temperatures during spring (February–April), although a minor group of *A. schlegeli* larvae (TK in December and TT in January), like *A. latus*, occurred in autumn following the seasonal decrease in temperatures.

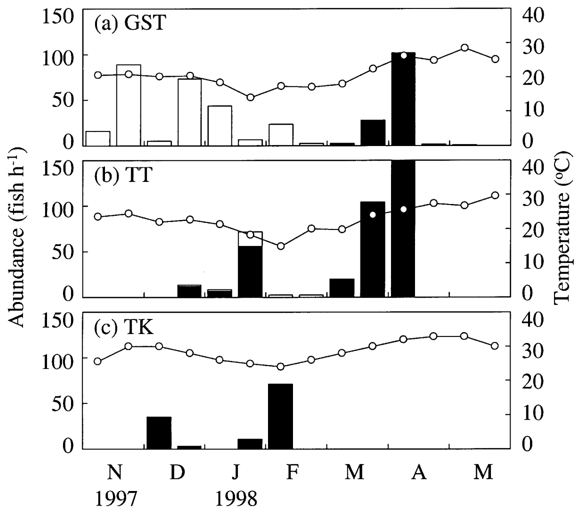

Fig. 4. Seasonal occurrence of (□) *A. latus* and (■) *A. schlegeli* larvae in *(a)* Gongshytyan Creek (GST), *(b)* Tatu Creek (TT) and *(c)* Tongkang River (TK) estuaries, November 1997 through May 1998. ○, water temperature.

Spatial and temporal variations in age and length of the larvae at recruitment

Mean ages and lengths of *A. latus* larvae (33.7 ± 4.6 days, 14.1 ± 1.3 mm TL) were greater than for *A. schlegeli* larvae (23.8 ± 7.2 days, 10.5 ± 1.7 mm TL) ($P < 0.001$). The mean ages of *A. schlegeli* larvae did not differ significantly between GST (27.6 ± 7.4 days) and TT (26.9 ± 5.5 days), but were older in both those estuaries than in TK (17.9 ± 3.6 days) ($P < 0.001$). *A. latus* larvae were larger in TT (14.1 ± 1.2 mm) than in GST (13.1 ± 1.0 mm) ($P < 0.001$). Similarly, mean lengths of *A. schlegeli* larvae were greatest in GST (11.6 ± 1.4 mm), intermediate in TT (10.9 ± 1.3 mm) and smallest in TK (9.1 ± 1.2 mm) ($P < 0.001$). The geographic gradients in mean ages and lengths of *A. latus* increased from north to south but *A. schlegeli* increased from south to north, again suggesting that the dispersal direction of the larvae differs between species.

The mean ages and lengths of *A. latus* and *A. schlegeli* larvae at recruitment also differed significantly among sampling dates ($P < 0.005$), perhaps because the growth history and recruitment process of the larvae differed among cohorts. At recruitment, the larvae were less variable in size (lower CV) than in age (Table 1).

Temporal changes in growth rate

Mean increment widths in otoliths of *A. latus* larvae collected from GST in November increased from ~2 μm to 11 μm at 29 days after hatching, whereas those collected in December and February only increased to ~6 μm 36 days after hatching (Fig. 5*a*). The age of *A. latus* larvae at recruitment was thus inversely correlated to a growth rate that was faster in November than in December and February. The monthly difference in growth rate and age at recruitment of *A. latus* larvae may be due to the higher water temperatures in November than in December and February (Fig. 4*a*).

A similar phenomenon was also found in *A. schlegeli* larvae collected in GST, TT and TK (Figs 5*b*–*d*). The larvae in GST grew more quickly and had a smaller age at recruitment in April and May than in March. In TT the larva collected in December had grown faster and was younger than the larva collected in January, and the one collected in April had grown faster and was younger than the one in March. Larvae in TK grew faster and were younger at recruitment in December than in January and February. The

Table 1. **Mean age and length of *A. latus* and *A. schlegeli* larvae at recruitment in the Gongshytyan Creek (GST), Tatu Creek (TT) and Tongkang River (TK) estuaries**

n, sample size. –, problems with specimen preservation

Site	Sampling month	*n*	Age (days) Mean ± s.d.	CV	*n*	Total length (mm) Mean ± s.d.	CV
A. latus							
GST	Nov. 1997	24	30.7±3.1	10.1	132	13.0±1.2	9.0
	Dec.	35	33.7±4.6	13.7	113	12.9±1.1	8.2
	Jan. 1998	24	31.8±2.9	9.3	109	13.4±0.8	6.0
	Feb.	22	38.8±2.6	6.6	53	13.1±0.8	6.2
	Subtotal	105	33.7±4.6	13.5	407	13.1±1.0	7.9
TT	Dec. 1997	–	–	–	2	12.1±1.5	12.3
	Jan. 1998	–	–	–	17	14.4±1.0	6.9
	Feb.	–	–	–	6	14.2±1.2	8.8
	Subtotal	–	–	–	25	14.1±1.2	8.6
Overall		105	33.7±4.6	13.5	432	14.1±1.3	8.1
A. schlegeli							
GST	Mar. 1998	29	33.9±4.4	12.8	47	12.8±1.5	12.0
	Apr.	29	21.8±4.2	19.4	154	11.2±1.1	10.2
	May	2	20.5±0.7	3.4	2	10.8±0.6	5.2
	Subtotal	60	27.6±7.4	27.0	203	11.6±1.4	12.0
TT	Dec. 1997	2	21.5±3.5	16.4	3	10.1±0.4	4.0
	Jan. 1998	28	28.8±2.5	8.6	58	11.8±1.2	10.6
	Mar.	18	29.8±4.7	15.7	43	10.8±1.2	10.7
	Apr.	11	18.1±2.5	13.9	41	10.0±0.7	7.1
	Subtotal	59	26.9±5.5	20.6	145	10.9±1.3	12.0
TK	Dec. 1997	27	14.2±1.2	8.3	67	8.6±1.4	16.2
	Jan. 1998	18	22.3±1.3	5.7	21	10.4±0.8	7.3
	Feb.	24	18.9±2.0	10.8	134	9.2±1.0	10.4
	Subtotal	69	17.9±3.6	20.3	222	9.1±1.2	13.1
Overall		188	23.8±7.2	30.3	570	10.5±1.7	16.2

growth rates of *A. schlegeli* larvae were positively, and ages at recruitment negatively, correlated with water temperature (Fig. 4). Growth rates were faster in *A. schlegeli* than in *A. latus*.

Hatching date

A. latus and *A. schlegeli* differed in hatching dates (Fig. 6). *A. latus* hatched between late September and early January with a peak in October in GST (Fig. 6*a*). *A. schlegeli* hatched from late November to January, with peaks in early December and late January in TK (Fig. 6*c*), from late November to March with peaks in December and March in TT (Fig. 6*b*), and from February to April with peaks in February and March in GST (Fig. 6*a*). The hatching dates of *A. latus* and *A. schlegeli* were separated either temporally, if they occurred in the same estuary, or spatially if they occurred in the same season.

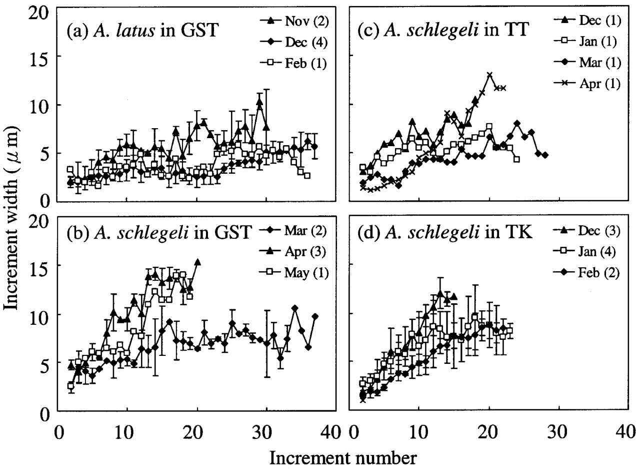

Fig. 5. Increment widths in otoliths of *(a) A. latus* and *(b–d) A. schlegeli* larvae. In parenthesis, sample size. Vertical lines, s.d.

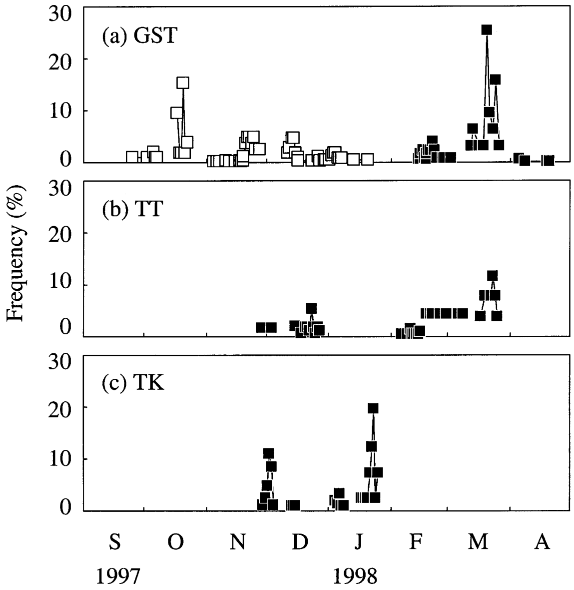

Fig. 6. Distribution of hatching dates of (□) *A. latus* and (■) *A. schlegeli* larvae in *(a)* Gongshytyan Creek (GST), *(b)* Tatu Creek (TT) and *(c)* Tongkang River (TK) estuaries.

Discussion

Effect of physical processes on the larval distribution

Along the west coast of Taiwan there were opposite gradients in the seasonal occurrence and distribution of *A. latus* and *A. schlegeli* larvae. *A. latus* larvae occurred progressively from north to south between late autumn and late spring, whereas *A. schlegeli* larvae occurred progressively from south to north between winter and spring.

The opposite distribution patterns of the larvae of these two species coincides with the coastal currents on the western coast of Taiwan. In autumn and winter, the north-eastern monsoon prevails and induces a southward flow of the cold China Coastal Current from the East China Sea into Taiwan Strait, causing a decline in water temperatures on the western coast of Taiwan (Chu 1963). *A. latus* spawns in autumn and thus the larvae drift southward with the coastal current toward the western coast of Taiwan. However, a branch of the warm Kuroshio Current stops the cold China Coastal Current in the middle of Taiwan Strait (Fan 1982), which limits the southward transport of *A. latus* larvae. In contrast, in spring and summer the south-western monsoon prevails and induces a warm coastal current flow northward into the Taiwan Strait from the South China Sea, causing water temperatures to increase from south to north along the western coast (Chu 1963). Thus, *A. schlegeli* larvae are dispersed northward with the current to the northern Taiwan Strait. In contrast with the China Coastal Current, the South China Sea monsoon current can reach the northern part of Taiwan Strait. This allows *A. schlegeli* to disperse to the north-western coast whereas *A. latus* can only disperse to the central western coast of Taiwan.

Variability of age and length of the larvae at recruitment

The recruitment of larvae to the estuaries may depend on size rather than age (Houde 1987). Our study supports this conclusion because the coefficient of variation of mean ages was larger than those of mean lengths for both *A. latus* and *A. schlegeli* larvae. Age at recruitment was inversely correlated to larval growth rate, as was found for other fishes (Tzeng 1990; Rutherford and Houde 1995; Wang and Tzeng 1999). Thus, the faster growing larvae arrived at the estuary at a younger age. In addition, the geographic gradient in the mean age of *A. schlegeli* larvae at recruitment, which was younger in the southern estuary (TK) than in the northern estuary (GST), corresponds to the geographic gradient in temperature which is higher in the south than in the north. Water temperature evidently plays an important role in determining the age and length of the larvae at recruitment.

Spawning and hatching date

A. latus and *A. schlegeli* hatched respectively at ~60 h and 41–50 h after fertilization at temperatures of 17.5–20°C (Lin and Yen 1980; Liu and Hu 1980; W. Y. Tzeng 1982; Leu *et al.* 1991), i.e. the larvae hatch about 2–3 days after spawning. The back-calculated hatching dates of *A. latus* larvae in GST lasted from late September to early January and were consistent with the October–December spawning period that was estimated from the gonadosomatic index (GSI) of mature fish in the Pescadores Islands of central western Taiwan (Liu and Hu 1980). Similarly, the hatching dates of *A. schlegeli* (from late November to January in TK, late November to March in TT, and February to April in GST) were also consistent with the January–March spawning period that was estimated from GSI of mature fish in central western Taiwan (Lin and Yen 1980).

Effect of spawning behaviour on larval distribution

The hatching date distributions, and thus the spawning dates, of both *A. latus* and *A. schlegeli* were extended and did not overlap among estuaries but shifted with the season. The spawning behaviour of adult fish is the basis of the geographical gradients in seasonal occurrence and distribution of the larvae. Temperature is one of the principal factors determining the seasonal maturation and spawning of fish (Crecco and Savoy 1985; Rutherford and Houde 1995). The onset of spawning of sparids depends on the occurrence of optimal temperature (Crossland 1980; Kojima 1981; Hu 1983; Scott and Pankhurst 1992; Francis 1994). Water temperatures increase from south to north on the western coast of Taiwan in spring causing the timing of spawning and larval hatching of *A. schlegeli* to shift with season and latitude. This phenomenon was also found in white croaker, *Argyrosomus argentatus* in the Taiwan Strait (Tzeng and Liu 1972). On the other hand, *A. latus* spawned in autumn (October) and a minor spawning period occurred in late autumn (November–December) for *A. schlegeli*, following the seasonal decrease in water temperature. The seasonal occurrence of *A. latus* larvae was consequently shifted from north to south, while *A. schlegeli* larvae were shifted from south to north. The seasonal occurrence and geographic distribution of larvae was highly correlated with adult spawning behaviour.

In conclusion, *A. latus* and *A. schlegeli* larvae on the western coast of Taiwan were opposite in terms of the geographic gradient in seasonal occurrence and distribution, mean age and length at recruitment, growth rate and hatching date. The monsoon-induced coastal current, water temperature, spawning behaviour and larval growth rate all have the potential to influence the variability of the geographic gradient in seasonal occurrence and distribution of larvae of these two species.

Acknowledgments

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