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Environmental Factors Associated with the Occurrence and Abundance of Larval Porgies, *Acanthopagrus latus* and *Acanthopagrus schlegeli*, in the Coastal Waters of Western Taiwan

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Abstract

In the coastal waters of western Taiwan, temperature, atmospheric pressure and wind speed were the main environmental variables associated with the occurrence of larval yellowfinned black porgy, *Acanthopagrus latus*, and black porgy, *A. schlegeli*. However larvae of *A. latus* and *A. schlegeli* differed significantly in their response to cloud cover, precipitation and current velocity. The latter environmental variables may be important causal factors for the temporal segregation of the larvae of these two sympatric species. Air temperature and atmospheric pressure were also correlated with the abundance of the larval porgies. Atmospheric pressure was positively correlated with the standard length of larval *A. latus* and *A. schlegeli*.

Key words: Sparidae; temperature; atmospheric pressure; wind speed; abundance; body length.

INTRODUCTION

The fishes of the subfamily Sparinae, commonly known as porgies, are important species for the commercial, recreational, and aquaculture fisheries in Taiwan (Jean *et al*., 1992), Japan (Fukuhara, 1987), and the Indo-West Pacific (Abu-Hakima, 1984). In the coastal waters of Taiwan, there are two genera and five species of sparinae (Jean *et al*., 1992). The genus *Acanthopagrus* includes four species: the black porgy, *A. schlegeli* (Bleeker), the yellowfinned black porgy, *A. latus* (Houttuyn), the black sea bream, *A. berda* (Forsskål) and the yellowfin sea bream, *A. australis* (Günther). The genus *Sparus* is represented by a single species, the silver sea bream, *S. sarba* Forsskål. *A. latus* and *A. schlegeli* are common and sympatric in the coastal waters, but their larvae occur at different times of the year: autumn and winter for *A. latus*, and winter and spring for *A. schlegeli* (Hung and Chiu, 1991).

The reproduction and growth of many species of porgies in the western Pacific have been studied: *A. australis* in Australia (Pollock, 1982; 1985), *A. schlegeli* in Japan (Fukuhara, 1987) and Taiwan (Lin *et al*., 1986; Lie *et al*., 1989), *A. latus* in Australia (Abu-Hakima, 1984), Japan (Akazaki and Tokito, 1982) and Taiwan (Tsay and Yu, 1981; Leu *et al*., 1991), and *S. sarba* in Japan (Mihelakakis and Kitajima, 1995) and Taiwan (Lin *et al.*, 1989; Leu, 1994). Most of these studies dealt with gonado-somatic indices (GSI) and the artificial breeding process, and were rarely concerned with the relationships between environmental conditions and the early life history of natural populations. Pollock *et al.* (1983) studied the seasonal occurrence of postlarvae of *A. australis*, and suggested that moon and tidal phases are two important factors affecting their abundance in the estuary of Moreton Bay, Australia. Liu (1978) did an ecological survey of juvenile *A. schlegeli* in Taiwan and found the optimal water temperature for larval survival ranged from 12 to 25°C. Environmental variables, oceanographic and meteorological, have been shown to play an important role in the occurrence, abundance, and growth of the larvae of many other species of fish (Frank and Leggett, 1982; Tzeng and Wang, 1992, 1993; Lee *et al.*, 1994, 1995).

We studied the relationships between environmental conditions and the occurrence, abundance, and body length of larval *A. latus* and *A. schlegeli* in the coastal waters of western Taiwan.

MATERIALS AND METHODS

The west coast of Taiwan is part of the continental shelf of the East China Sea. A coastal water area at Wan-kung south of the Da-du River, one of the main rivers in Taiwan, located on the central western part of the island, was selected as the study area (Figure 1). This area is a shellfish farm. We deployed a set-net modified from one that was used by local fishermen. The net, similar to a fyke net which is generally used in shallow waters (Hubert, 1992), was 13.4 m wide at the mouth and 18.5 m long, with 13.5 m sleeves and a 5.0 m conical body. The mesh sizes in its sleeves and conical body were 1.95 mm and 0.86 mm, respectively (Figure 2). Larval fish were collected monthly from October 1991 to September 1994. The period of one year, such as 1991/92, was from October 1991 to September 1992. Each sampling started one hour after the onset of day-time ebb tide and lasted for 30 minutes. The samples were fixed immediately in brackish water with 10% formalin. The larval fish were sorted in the laboratory and each was identified to the lowest possible taxon. Numbers of larval fish were counted and the standard lengths of larval *A. latus* and *A. schlegeli* were measured to the nearest 0.1 mm.

Five oceanographic variables, including water temperature, salinity, pH, dissolved oxygen (DO), and current velocity, were monitored at the beginning, middle, and end of each sampling period. Water temperature and salinity were measured with a digital salinometer that was calibrated using a mercury thermometer and standard sea water. pH was measured with a pH-meter, and DO by a dissolved oxygen meter calibrated using Winkler's method. A flowmeter (Hydro-Bios) was mounted at the center of the net opening for calculating the current velocity and water volume passing through the net. Six meteorological variables were obtained from the Wu-chi Station of the Taiwan Weather Bureau (Figure 1). They were atmospheric pressure, air temperature, total cloud cover, wind speed, precipitation, and air visibility. For each of the meteorological variables, the mean of the last 30 days including the day of sampling was calculated.

The abundance of larval fish was expressed as the number of fish per $1000m^3$ water sieved (no./$1000m^3$). We treated the five oceanographic and six meteorological variables as a multivariate response by a random-effect multivariate analysis of variance (MANOVA) with the general linear model: five oceanographic and six meteorological variables = μ + year + ε (Dillon and Goldstein, 1984), where μ is the overall mean of the environmental variables; year is 0, 1, and 2 for the sampling year 1991/92, 1992/93, and 1993/94, respectively; and ε is random error of the model. Analysis of variance (ANOVA) was employed to test the change of a single environmental variable among sampling years when the MANOVA test

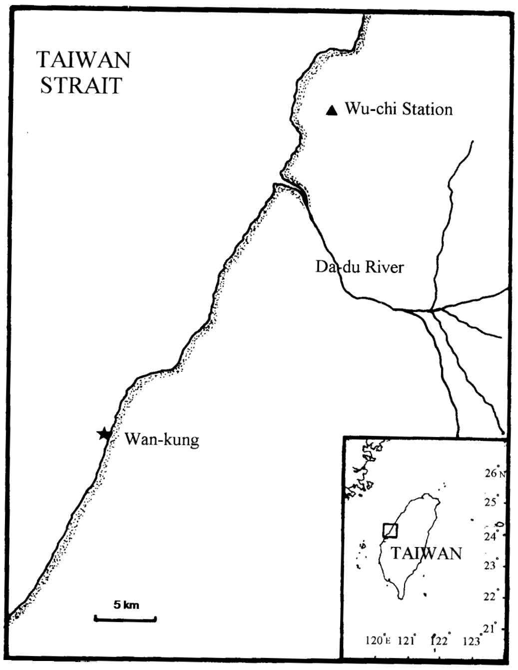

Figure 1. Locations of the sampling area (H) and the meteorological station (s).

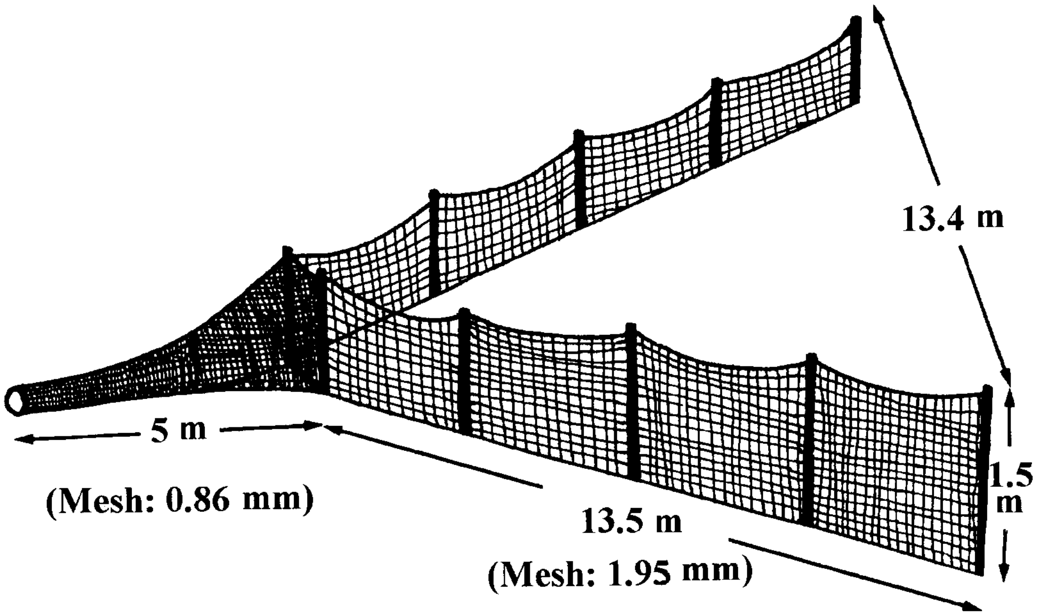

Figure 2. Schematic diagram of the set-net used for larval fish sampling.

Table 1. Oceanographic and meteorological variables (mean ± SE) during the years of this study.

	1991/92	1992/93	1993/94	*p*
Water temperature (°C)	24.8±1.8	25.3±1.7	26.1±1.7	0.877
Salinity (‰)	28.7±0.5	29.3±1.1	31.5±0.4	0.030*
Dissolved oxygen (mg/l)	6.31±0.31	6.88±0.29	7.42±0.18	0.021*
pH-value	7.39±0.12	7.99±0.08	7.71±0.14	0.004*
Current velocity (m/sec)	0.36±0.02	0.36±0.02	0.39±0.02	0.466
Atmospheric pressure (mb)	1009.4±1.7	1010.4±1.5	1009.7±1.6	0.907
Air temperature (°C)	23.0±1.4	23.4±1.5	23.6±1.4	0.957
Total cloud cover (%)	64.2±3.4	54.2±4.3	60.8±3.1	0.159
Wind speed (m/sec)	4.77±0.42	4.85±0.38	4.87±0.47	0.984
Precipitation (mm)	13.3±3.3	13.3±6.0	17.5±7.8	0.851
Air visibility (km)	12.4±0.5	13.2±0.7	12.8±0.6	0.659

* ANOVA, $p < 0.05$.

was significantly different for all environmental variables. The size variation of larval fish was represented by the coefficient of variation (SD/$\overline{X}$, where SD is standard deviation; $\overline{X}$ is the mean of sample) in standard length. Principal component analysis (PCA), modified from Dillon and Goldstein (1984) and Lee *et al.* (1995), was used to relate the occurrence of the larval *A. latus* and *A. schlegeli* to environmental variables. All data were standardized using the formula described by Johnson and Wichern (1988).

The assemblage of all larval fishes was evaluated by the species richness, abundance, and Simpson's species diversity and evenness indices (Pielou, 1966). Canonical correlation (Dillon and Goldstein, 1984) was used to study the relationships between biotic factors and abiotic factors. The biotic factors were the variables of the larval fish assemblage and the abundance of the larval *A. latus* and *A. schlegeli*; the abiotic factors were the oceanographic and meteorological variables. The relationships between the sizes (standard length) of the larval porgies and environmental variables were evaluated using Spearman's rank correlation (Siegel, 1956).

RESULTS

Yearly comparison

There were significant differences in environmental conditions between the three years (MANOVA, Wilk's $\lambda = 0.194$; $df = 22, 44$; $F = 2.65$; $p = 0.003$) (Table 1). Comparison of single variables indicated that salinity, DO, and pH were significantly different between years, but the other environmental variables were not (ANOVA, Table 1). Atmospheric pressure and wind speed, which are high during the winter, were negatively correlated with air and water temperatures (Figure 3).

Most of the larval *A. latus* occurred in autumn and winter (October to December), while most of the larval *A. schlegeli* occurred in winter and spring (January to April) (Table 2). The total abundance of the larval *A. latus* was 1.69, 24.58, and 0.18 /1000m^3 and their percentage of the total catch was 0.11, 0.75, and 0.01% in 1991/92, 1992/93 and 1993/94, respectively (Table 2). The mean standard length of *A. latus* was significantly different between years (ANOVA, n = 89, $p = 0.000$) , but the coefficient of variation in standard length were not (n = 6, $p = 0.199$). The abun-

Table 2. Yearly comparisons of the occurrence, abundance, standard length (mean ±SE) and coefficient of variation of standard length (CVL) of larval *A. schlegeli* and *A. latus*, and of the species richness, all larval fish abundance, Simpson's species diversity index, and Simpson's evenness index of all larval fish assemblages in the coastal waters of western Taiwan.

	1991/92	1992/93	1993/94	*p*
Acanthopagrus latus				
months of occurrence	Oct.-Dec.	Dec.-Jan.	Oct., Dec.	-
abundance (/1000m^3)	1.69	24.58	0.18	-
percentage (%)	0.11	0.75	0.01	-
standard length (mm)	12.9±0.3	11.3±0.2	11.8±1.1	0.000*
CVL (%)	7.5±1.4	10.1±0.5	12.6	0.199
Acanthopagrus schlegeli				
months of occurrence	Feb.-Apr.	Jan.-May	Nov., Jan.-Apr.	-
abundance (/1000m^3)	153.4	112.9	68.0	-
percentage (%)	9.91	3.45	2.85	-
standard length (mm)	7.80±0.11	9.32±0.09	9.28±.010	0.006*
CVL (%)	8.76±1.49	12.61±2.19	8.15±1.15	0.153
Larval fish assemblage[a] of all species				
species richness	13.3±1.9	16.0±2.1	21.2±3.1	0.080
abundance (/1000m^3)	129±49	273±156	199±74	0.623
diversity index	1.18±0.19	1.43±0.10	1.46±0.18	0.658
evenness index	0.46±0.07	0.54±0.04	0.49±0.04	0.781

* ANOVA, $p < 0.05$.
[a] the values are the monthly means.

dance of the larval *A. schlegeli* was 153.4, 112.9, and 68.0 /1000m^3, and the percentage in total catch was 9.91, 3.45, and 2.85% in 1991/92, 1992/93, and 1993/94, respectively. The mean standard length of *A. schlegeli* was significantly different between years (ANOVA, n = 417, p = 0.006), but the coefficient of variation in standard length was not statistically different (n = 13, p = 0.153).

The monthly means of the species richness, abundance of all larval fishes, Simpson's species diversity index, and Simpson's evenness index ranged from 16.0 - 21.2 species/sample, 129 - 273 /1000m^3, 1.18 - 1.46, and 0.46 - 0.54, respectively (Table 2). The highest species richness and the highest diversity index were in 1993/94; the highest abundance of all larval fish and the highest evenness index were in 1992/93.

Environmental factors associated with the occurrence of larval porgies

Current velocity and precipitation during the occurrence periods were significantly different between the two species of larval porgies ($p < 0.05$) (Table 3).

Eigenvalues of the first and second principal components were 5.35 and 2.40, explaining 41.2 and 18.4% of the total sample variance (Figure 4). These two components explained 59.6% (the total cumulative percentage) of the total variance. In the first principal component, the eigenvectors of the occurrences of the larval *A. latus* and *A. schlegeli*, air temperature, water temperature, and visibility in air were 0.153, 0.244, -0.410, -0.378, and -0.344 respectively, suggesting a negative correlation between the occurrence of the two species of

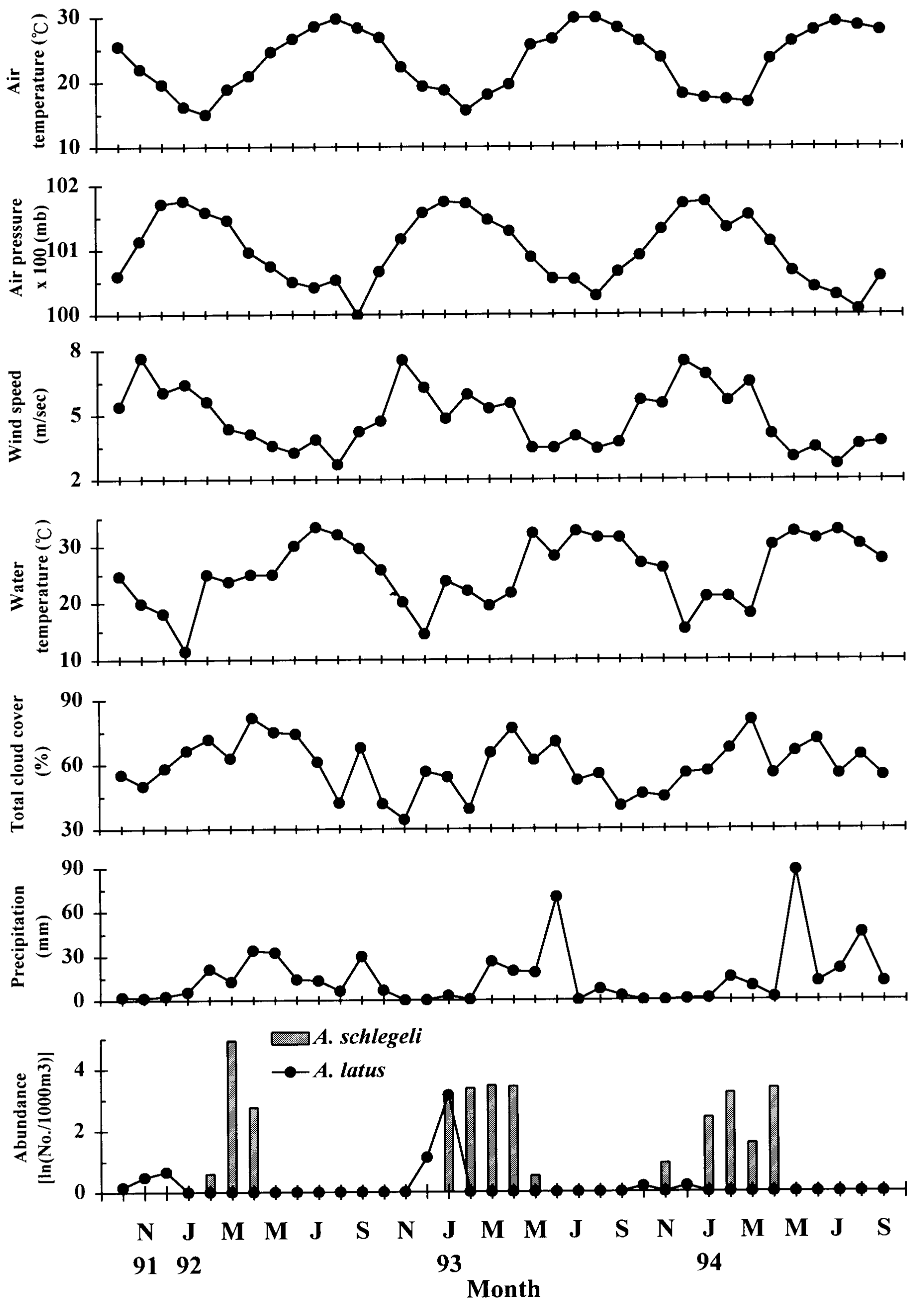

Figure 3. Temporal variations of environmental variables and the abundance of the two larval porgies (*A. schlegeli* and *A. latus*) in the coastal waters of western Taiwan.

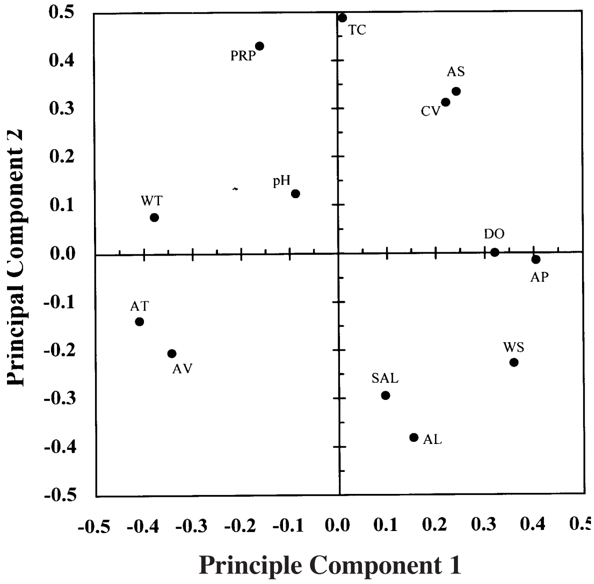

Figure 4. Principal component analysis on the occurrence of the two species of porgy larvae and environmental variables. AS, abundance of larval *A. schlegeli*; AL, abundance of larval *A. latus*; WT, water temperature; SAL, salinity; DO, dissolved oxygen; CV, current velocity; AP, atmospheric pressure; AT, air temperature; TC, total cloud cover; WS, wind speed; PRP, precipitation; AV, visibility in air.

porgies and the three environmental variables (Figure 4). The correlations implied that the occurrences of the larval fish of the two species of porgies were in the months of low temperature. The eigenvectors of the occurrences of the larval *A. latus* and *A. schlegeli*, atmospheric pressure, wind speed, and dissolved oxygen were 0.153, 0.244, 0.405, 0.359, and 0.321 respectively, suggesting that the occurrence of the larval porgies was positively correlated with these three environmental variables. Both species occurred in moths with high wind speed, atmospheric pressure, and dissolved oxygen and low temperatures.

In the second principal component, eigenvectors were -0.382, 0.334, 0.488, 0.431, and 0.312 for the occurrences of the larval *A. latus* and *A. schlegeli*, total cloud cover, precipitation, and current velocity (Figure 4). In other words, these three environmental variables were positively correlated with the occurrence of the larval *A. schlegeli*, but negatively correlated with the occurrence of the larval *A. latus*. The most negative dominant environmental variable in the second principal component was salinity and its eigenvector was -0.295. Salinity was thus positively correlated with the occurrence of the larval *A. latus* but negatively correlated with that of the larval *A. schlegeli*.

Correlations between the abundance of porgies and environmental variables

A canonical correlation between biotic and abiotic factors indicated that the abundance of the larval fish of the two species of porgies as well as other biotic factors were influenced by multiple abiotic factors (Figure 5). The first two canonical correlations between 11 abiotic and six biotic factors were significant (r_1 = 0.932, df = 66, p = 0.000; r2 = 0.867, df = 50, p = 0.008). The first, second, and both canonical variates explained 56.0, 25.8, and 81.8% of the total sample variance, respectively. Abundance of larval *A. schlegeli* was the negative and positive dominant loading factors for the first and second biotic canonical variates, respectively. This implied that the abundance of larval *A. schlegeli* and *A. latus* was negatively correlated

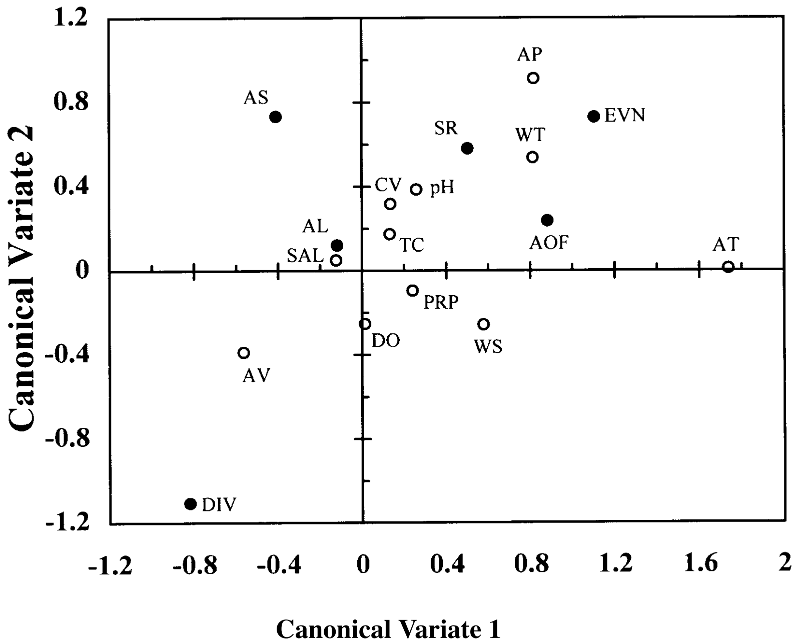

Figure 5. Ordination of biotic (•) and abiotic (○) factors by the first two canonical variates. AS, abundance of larval *A. schlegeli*; AL, abundance of larval *A. latus*; EVN, Simpson's evenness index; DIV, Simpson's species diversity index; AOF, abundance of all larval fish; SR, species richness; WT, water temperature; SAL, salinity; DO, dissolved oxygen; CV, current velocity; AP, atmospheric pressure; AT, air temperature; TC, total cloud cover; WS, wind speed; PRP, precipitation; AV, visibility in air.

with air temperature in the first canonical variate and positively with atmospheric pressure in the second canonical variate (Figure 5).

Correlation of the sizes of larval porgies to environmental variables

The standard length of the larval *A. schlegeli* was positively and significantly correlated with atmospheric pressure and wind speed, but negatively and significantly correlated with air temperature, pH, and water temperature ($p < 0.05$, Spearman's rank correlation). Atmospheric pressure was the only significant environmental variable that positively correlated with the standard length of the larval *A. latus* ($p < 0.05$, Spearman's rank correlation).

DISCUSSION

Nonspecies-specific environmental requirements

The occurrence of larval fish is naturally closely related with the reproductive season. The timing of reproduction in annual spawning species in the temperate region is controlled by an endogenous cycle that in turn is entrained by environmental cues (Scott, 1979; Bye, 1990; Scott and Pankhurst, 1992). One of the most important annual environmental cues is temperature (Bye, 1990). Several species in the family Sparidae that spawn in the low temperature months have been well-studied: *A. latus* (Abu-Hakima, 1984), New Zealand snapper *Pagrus auratus* (Bloch and Schneider) (Scott and Pankhurst, 1992), and gilthead sea-bream *Sparus aurata* (Linnaeus) (Zohar and Gordin, 1979). The spawning season of Japanese *P. auratus* starts earlier in the warmer southern seas (Scott and Pankhurst, 1992), and by keeping the temperature below the lower limit for ovulation, the spawning season of *P. auratus* can be delayed (Bye, 1987; Micale and Pardichizzi, 1988). This implies that although low temperature is the cue for spawning of porgies, temperature that is too low is not suitable for spawning. In addition to temperature, photoperiod has been cited as an additional factor controlling spawning success (Abu-Hakima, 1984; Zohar and Gordin, 1979; Bye, 1987; Micale and Pardichizzi, 1988).

The occurrence of the larval *A. latus* and *A. schlegeli* were negatively correlated with water temperature and air temperature, and positively correlated with atmospheric pressure and wind speed (Figure 4). Moreover, their abundance was also correlated with air temperature and atmospheric pressure (Figure 5). Apparently, the occurrence and abundance of the larval porgies were strongly influenced not only by temperature but also by atmospheric pressure and/or wind speed, suggesting that the latter two variables are also the important environmental factors for the occurrence of the larval porgies. Atmospheric pressure was also a significant factor that affected the size (standard length) of the larval porgies in the coastal waters.

In central western Taiwan, atmospheric pressure which is high in winter was negatively correlated with air temperature (Figure 3). Lee *et al.* (1990) and Lee *et al.* (1994) stated that high atmospheric pressure was associated with increased abundance of larval anchovy, and similar results were found for larval *A. latus* and *A. schlegeli* in this study (Figure 5). Optimal conditions for the survival of fish larvae occur when the wind is strong enough to deepen the mixed water into the nutricline and then followed by a calm period (Wroblewski *et al.*, 1989). For anchovies increased speed of the southeasterly wind increased the intensity of upwelling of the coastal water in the dry season (Takahashi and Kishi, 1984), resulting in nutrient enrichment of coastal waters, that in turn increased anchovy production (Cheng *et al.*, 1989; Lee *et al.*, 1994). In general, the moderately strong winds and high atmospheric pressure during the low temperature months are the environmental conditions correlated with the occurrence and abundance of the larval fish of the two species of porgies in this study (Figures. 3, 4, and 5).

Based on the known length-age relationship of cultured larvae of *A. schlegeli* (Lie *et al.*, 1989), the ages of the larval *A. schlegeli* collected in this study were estimated to be 25-35 days. These ages were similar to those of the planktonic postlarvae of *A. australis* entering the estuary of Moreton Bay (Pollock *et al.*, 1983). The environmental conditions during the period from hatching to being caught in our samples were important in affecting the occurrence, abundance, and size of the larval porgies.

Species-specific environmental requirements

From the results of the second principal component of PCA, cloud cover, precipitation, and current velocity were positively correlated with the occurrence of the larval *A. schlegeli* but negatively correlated with the occurrence of the larval *A. latus* (Figure 4). In fact, precipitation and current velocity were significantly different between the months of the occurrence of the two species of porgies (Table 3). In other words, larval *A. schlegeli* occurred during periods of high cloud cover, precipitation and current velocity, while larval *A. latus* occurred when cloud cover, precipitation and current velocity were low.

Cloud coverage, precipitation and current velocity are closely related to one another (Level *et al.*, 1987; Lee *et al.*, 1994). Moreover, cloud cover is closely negatively correlated with sunshine duration and solar radiation. High precipitation induces high current velocity and carries a large quantity of nutrients from terrestrial water runoff into coastal waters. The high nutrient contents compounded with low

Table 3. Comparison of the environmental conditions (mean ± SE) between the periods of the occurrence of the larval *A. latus* and *A. schlegeli*.

	A. latus	*A. schlegeli*	*p*
Water temperature (°C)	20.5±4.8	23.8±4.0	0.118
Salinity (‰)	30.7±1.6	30.4±2.7	0.788
Dissolved oxygen (mg/l)	7.17±1.07	7.25±0.72	0.838
pH-value	7.44±0.59	7.83±0.50	0.136
Current velocity (m/sec)	0.35±0.03	0.41±0.07	0.049*
Atmospheric pressure (mb)	1013.4±4.6	1013.9±2.8	0.742
Air temperature (°C)	21.4±3.4	19.3±3.3	0.200
Total cloud cover (%)	53.7±4.2	63.0±13.0	0.086
Wind speed (m/sec)	6.19±1.04	5.22±0.99	0.054
Precipitation (mm)	1.5±1.2	12.6±11.0	0.017*
Air visibility (km)	12.0±1.5	11.2±7.0	0.102

* *t*-test, $p < 0.05$.

solar radiation favor photosynthesis (Paul, 1976). An increase in cloud cover causes an increase in phytoplankton and zooplankton production (Cheng *et al.*, 1989; Lee *et al.*, 1995).

In addition to the difference in abiotic factors, the characteristics of larval fish assemblages were also different among years (Table 2). The abundance and species richness during the period of occurrence of larval *A. schlegeli* were 333.3 larvae/1000m^3 and 16.5 species/sample, respectively, which were higher and larger than the 30.0 larvae/1000m^3 and 12.4 species/sample during the period of occurrence of larval *A. latus*. These data indicate that the larval production of other species of fish was high during the period of occurrence of larval *A. schlegeli* as compared with that of the larval *A. latus*. Apparently, larval *A. schlegeli* occur during more favorable environmental conditions than larval *A. latus*. They occupy different temporal niches.

In conclusion, high atmospheric pressure and strong winds during the months of low temperature are the environmental conditions correlated with the occurrence and increased abundance of larval *A. latus* and *A. schlegeli*. On the other hand, cloud cover, precipitation, and current velocity are the environmental conditions correlated with the temporal separation of the occurrence of the larvae of the two porgies. Temporal separation of the spawning of these two sympatric species allows for maximization of resource utilization and survival of their progeny.

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