FISHERIES SCIENCE 2003; **69**: 277–287

Effects of lunar phase and habitat depth on vertical migration patterns of the sergestid shrimp *Acetes intermedius*

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ABSTRACT: The effects of lunar phase and habitat depth on the vertical migration patterns of the sergestid shrimp *Acetes intermedius* were examined based on seven field observations in coastal waters off south-western Taiwan. The results indicate that the pattern of nocturnal vertical movement of *A. intermedius* depends on the lunar phase. The shrimp evaded moonlight during the ascending period and then the moon was used as a trigger for resuming an ascent towards the sea surface or descending towards the 10 m water layer. During the descending period, *A. intermedius* moved rapidly to the bottom or to a middle water depth at 50–80 m before sunrise. However, *A. intermedius* in waters of deep Kaoping Canyon can also perform a slow descending migration that coincides with photosynthetically active radiation of 4 μmol/s per m^2. Because the density of *A. intermedius* on the surface layer is affected by moonlight, the lunar phase is one of the factors affecting the catch rate of large-skimming nets during the night in waters off south-western Taiwan.

KEY WORDS: ***Acetes intermedius*, diel vertical migration, lunar phase, sergestid shrimp, Taiwan.**

INTRODUCTION

Diel vertical migration is commonly seen in several zooplanktons species, such as euphausiids and sergestids.[1–5] Many *Acetes* species perform vertical migration associated with diurnal cycles for varying purposes, including ontogenetic migration,[6] population maintenance in estuary habitats[5] and avoidance of visual predators.[7] Such behavior may be affected by multiple environmental factors and the regulating factors may vary among species. Furthermore, factors regulating the migration pattern of a species may also differ according to geographic locations.[8]

In summer, when the south-west monsoon prevails and river discharge is greatest, adult sergestid shrimp (*Acetes intermedius*) migrate from estuaries to coastal waters and perform a diel vertical migration off south-western Taiwan.[9] *Acetes intermedius* aggregate near the surface during the night and migrate to water layers deeper than 30 m during the day. There are seven rivers along the south-western coast of Taiwan, with two incised submarine canyons, where geographic environments change greatly. It is possible that the vertical migration pattern of *A. intermedius* may differ between coastal and deep canyon waters.

Light is generally agreed to be the most significant external factor initiating nocturnal vertical migration of zooplankton. However, the effect of lunar illumination on such a process has seldom been discussed. Lunar rhythmicity is commonly seen in marine organisms, particularly marine invertebrates.[10] Ho[11] indicated that catches made by large-skimming nets at night during the first to sixth and the 15th to 17th of the lunar month are apparently greater than catches during other periods. This implies that the lunar phase may be an important factor affecting the nocturnal vertical migration of *A. intermedius*. However, the results of the study of Ho were based mainly on statistical data from commercial fisheries and direct *in situ* studies on factors affecting diel vertical migration of *A. intermedius* have never been performed along the south-western coast of Taiwan.

In the present study, the vertical migration patterns of *A. intermedius* off Tungkang were examined using both *in situ* observations and data relating to fishing conditions in combination with the lunar phase. The objective of the present study was to clarify the effect of lunar phase and water

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Received 17 January 2002. Accepted 3 October 2002.

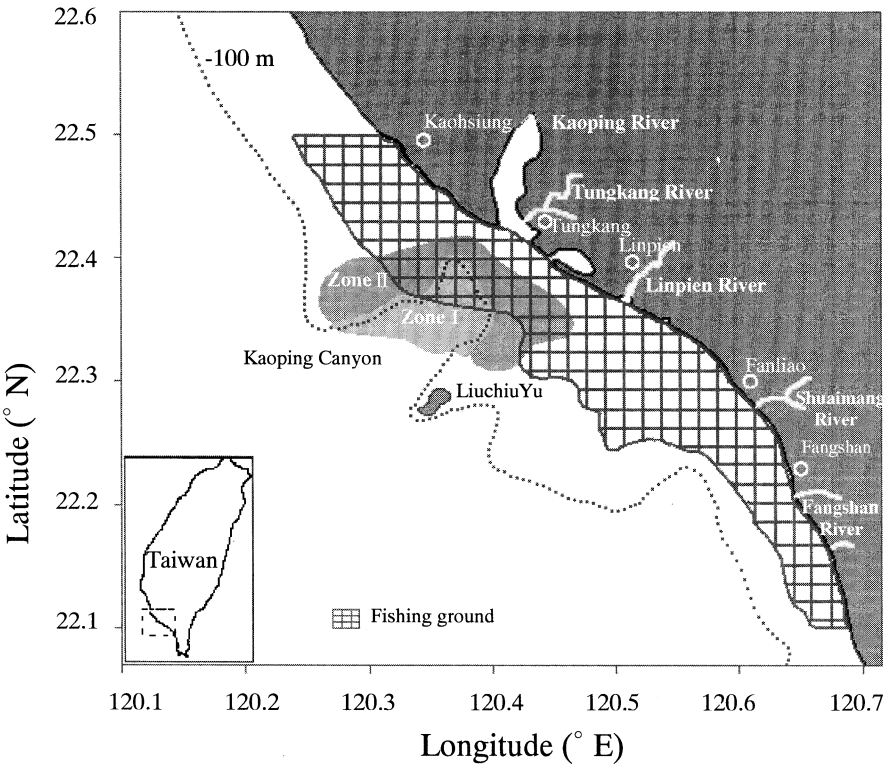

Fig. 1 Observation sites and fishing grounds for *Acetes intermedius* caught by large skimming nets in the waters of south-western Taiwan.

Table 1 Diel vertical migration of *Acetes intermedius* observed off Tungkang, Taiwan

Observation no.	Observation time and date	RDS (m)	RDW (m)	AP	Time: Sunrise	Sunset	Moonrise	Moonset
1	14.40 h, 25 Aug. 1998 to 12.30 h, 26 Aug. 1998	0–40	26–67	C	05.39 h 05.39	18.22 h 18.23	08.07 h	20.27 h
2	15.10 h, 24 Aug. 2000 to 02.00 h, 25 Aug. 2000	0–58	30–160	A	05.38 h	18.22 h	00.03 h	13.42 h
3	15.10 h, 11 Sep. 2000 to 04.00 h, 12 Sep. 2000	0–52	30–140	D	05.44 h	18.05 h	16.43 h	03.15 h
4	15.30 h, 17 Sep. 2000 to 01.30 h, 18 Sep. 2000	0–50	30–130	B	05.45 h	17.59 h	20.31 h	08.38 h
5	03.20 h, 21 Sep. 2000 to 13.40 h, 21 Sep. 2000	0–80	42–180	A	05.47 h	17.55 h	23.46 h	12.37 h
6	15.05 h, 30 Sep. 2000 to 12.00 h, 1 Oct. 2000	0–67	38–100	C	05.50 h 05.50 h	17.46 h 17.45 h	07.54 h	19.43 h
7	15.40 h, 14 Aug. 2001 to 02.00 h, 15 Aug. 2001	0–56	38–120	A	05.34 h	18.29 h	00.13 h	14.00 h

RDS, range of the depth of shrimp swarming; RDW, range of the depth of the water column; AP, ascending pattern (the ascending pattern refers to Fig. 2).

depth on the vertical migration patterns of *A. intermedius* in waters off south-western Taiwan.

MATERIALS AND METHODS

Two areas, separated by distinguishing geographic features and water depths (i.e. zones I and II were sampled. Zone I represented the area of the Kaoping Canyon with a water depth from 80 to 300 m and zone II was in the vicinity of Kaoping Canyon from 30 to 80 m (Fig. 1). In total, seven field observations on diel vertical migration have been performed throughout the present study (Table 1). An echo sounder (SUZUKI-ES-2200; Suzuki, Aichi, Japan) operating at a frequency of 200 kHz was

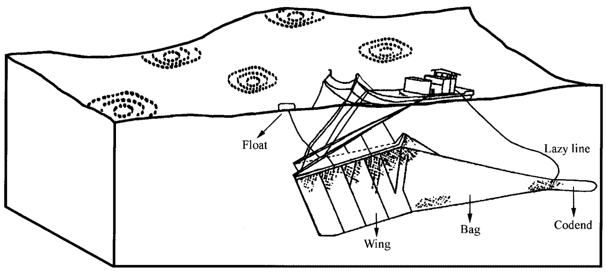

Fig. 2 Schematic sketch of the sergestid shrimp large skimming net in Taiwan.

used to locate schools of *A. intermedius. In situ* observation generally started at 15.00 h, after a test trawl was undertaken to ensure that the findings of the echo sounder were *A. intermedius.*

Measurements on salinity and temperature (using Data Sonde 4; Hydrolab, Austin, TX, USA), photosynthetically active radiation (PAR; using LI-193SA; LI-COR Lincoln, NE, USA) and chlorophyll-a (using Seabird Electronics (Washington, PA, USA) 5T and Wetlabs (Philomath, OR, USA) 9810002) were conducted every 1 h at the water depths of 0, 10, 20, 30, 40, 50 and 60 m.

Astronomical information during the period 1998–2000 in Tungkang area was obtained from the Central Weather Bureau of Taiwan. Offshore meteorological information was collected from the Fishery Broadcasting Station in Taiwan for the period 1999–2000.

Fisheries statistics used in the present study were obtained from the logbooks of Linyuang large skimming-net operators fishing along the coastal waters off south-western Taiwan (Fig. 1) during 1999–2000. The skimming net (Fig. 2) is commonly used for sergestid shrimp fishing in the Linyuang area. The fishing logbooks include fishing position, fishing time and the amount of catches. The skimming depth was approximately 12–15 m. The longest fishing time in one operating day was approximately 7 h from 19.30 to 02.30 h. A total of 212 operation days obtained from eight vessels was analyzed during the main fishing seasons in October 1999 and September 2000.

The density of shrimp was represented by catch per unit effort (CPUE; kg/h per boat). Fishing conditions (FC) for each lunar day were calculated based on the following equation:[11]

$$FC_{ij} = C_{ij}/\Sigma C_i \times 100\%$$

where FC_{ij} is the percentage of catch for the *j*th lunar day to the total catch made in the *i*th month, C_{ij} represents the catch (kg) for the *j*th lunar day in the *i*th month and ΣC_i is the summation of catch in the *i*th month.

RESULTS

Ascending patterns of *A. intermedius* at different lunar phases

The upward migration patterns of *A. intermedius* were similar in both the Kaoping Canyon (zone I) and continental shelf waters (zone II). *Acetes intermedius* stayed at or near the bottom in coastal waters or below 30 m at the slope of Kaoping Canyon off Tungkang during daylight hours and gradually left the sea bottom, preparing for upward migration, at dusk (approximately 30–50 min before sunset). The seven diel vertical migration observations with different lunar phases can be divided into four patterns, as shown in Fig. 3.

Patteren A

When the moon did not appear during the evening (18.00–24.00 h), *A. intermedius* ascended directly towards the surface and scattered around at the surface after sunset. The upward migration of this species did not stop temporarily at the 10 m water layer. During their stay at the sea surface, shrimps jumped out of the water when the searchlight was shone slong the water surface (Fig. 3, plot A).

Pattern B

When the moon rose during the evening (18.00–24.00 h), *A. intermedius* ascended to the surface at sunset and stayed there for a few hours before further descending slowly to the 10 m water layer. The shrimp resumed their descent towards the 10 m depth immediately after the moon had risen. Hence, the duration for remaining at the sea surface depended on the difference between the time the moon rose and sunset. Approximately 2 h after the moon had risen, there were no shrimps jumping out of the water when the searchlight was shone on the sea surface (Fig. 3, plot B).

Pattern C

When the moon set during the evening (18.00–24.00), *A. intermedius* moved rapidly to the 10 m water layer and stayed there for a few hours before further ascending slowly. The shrimp normally resumed their ascent towards the surface immediately after the moon had set (Fig. 3, plot C).

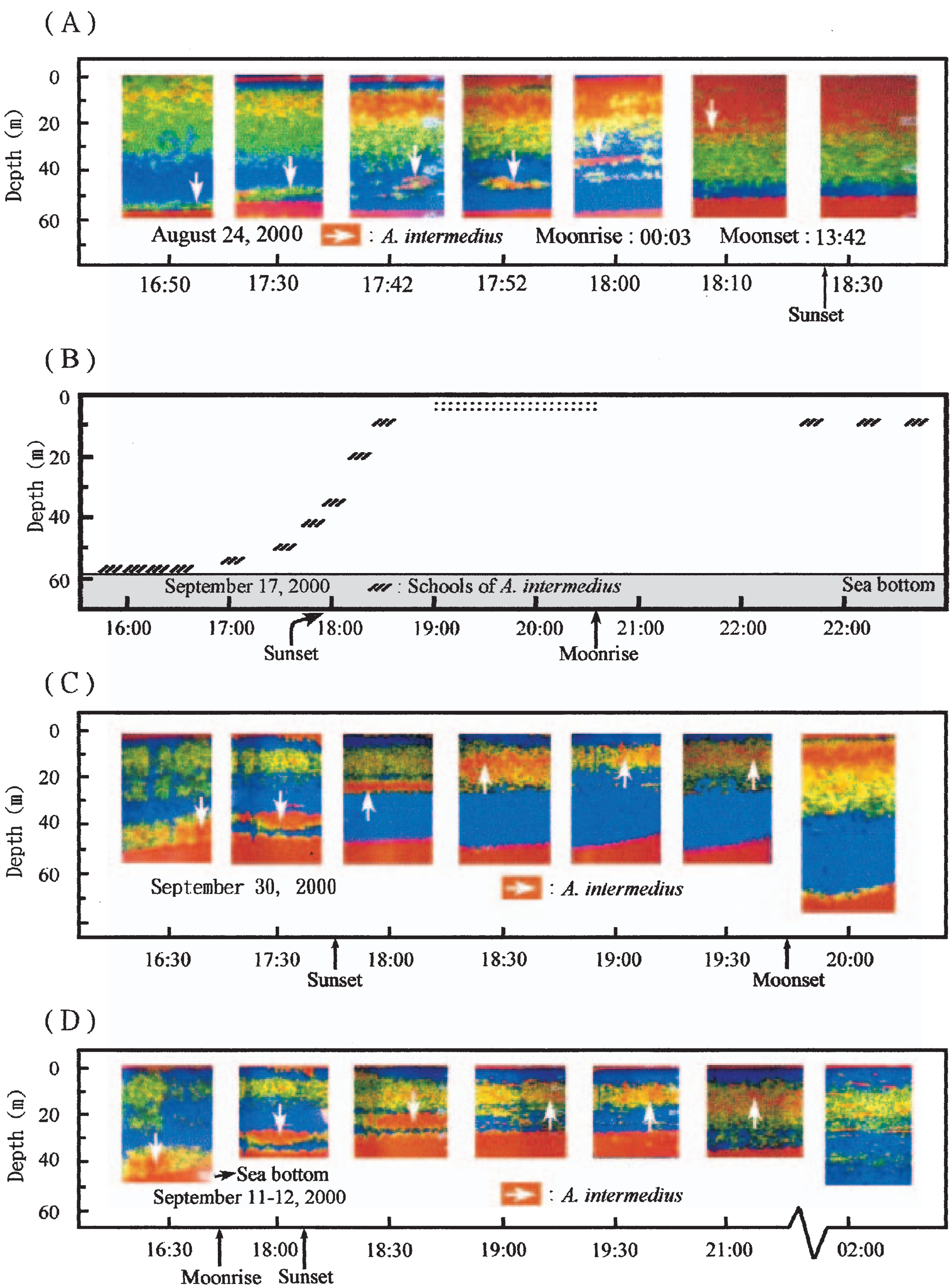

Fig. 3 Ascending patterns of nocturnal vertical movement of schools of *Acetes intermedius* observed with the color echo sounder off Tungkang, Taiwan.

Pattern D

When the moon appeared all evening (18.00–24.00 h), *A. intermedius* moved slowly upward to a depth of 10 m and stayed there all night. There were no shrimps jumping out of the water during this time when the searchlight was shone on the sea surface (Fig. 3, plot D).

Descending patterns of *A. intermedius* in zones I and zone II

Acetes intermedius usually performs a diurnal vertical migration from the surface to the bottom or to a middle depth (50–80 m) at dawn. There were no shrimps jumping out of the water when the searchlight was shone on the sea surface approximately 2 h before sunrise. Thus, shrimps may have started their downward migration during this time and scattered at the subsurface layer. Approximately 30 min before sunrise, *A. intermedius* generally swarmed at a depth of 15–37 m and then moved downward to the bottom or to a deeper layer at approximately 50–80 m. During the course of the downward migration at dawn, the aggregation of *A. intermedius* became more apparent. After sunrise, swarms of *A. intermedius* stayed at or near the bottom in zone II and at the middle depth in zone I until dusk. A selected example is shown in Fig. 4.

However, shrimps swarming at a depth of 30 m at approximately 10.00 h and gradually descending to a deeper layer in zone I was also observed. This descending movement coincided with a PAR of 4 μmol/s per m^2 (Fig. 5).

Diel vertical migration of *A. intermedius*

According to our observations, the diel vertical migration of *A. intermedius* near Tungkang, south-western Taiwan, can be summarized as shown in Fig. 6. *Acetes intermedius* migrate from estuaries to deeper coastal waters with river plume. They usually descend rapidly to the bottom or the middle water layer (50–80 m) before sunrise, but some schools gradually descend to a deeper layer following the PAR of 4 μmol/s per m^2 in the Kaoping Canyon waters. Based on our observations and those of local fishermen, schools of *A. intermedius* are usually found on the bottom at a depth of approximately 30–60 m at dusk, the depth at which they are caught becomes shallower after 13.00 h[9] and shrimps may migrate to shallow coastal waters along the sea bottom after 13.00–14.00 h. The shrimp will gradually leave the sea bottom and ascend towards the sea surface at dusk. Apparently, the ascending pattern is affected by the lunar phase. Shrimps that have ascended to the surface layer will then be transported gradually to deeper coastal waters by the river discharge when fresh waters are transported through the surface layer.

Hydrography

Profiles of chlorophyll-a, salinity and temperature in the coastal and canyon stations are shown in Fig. 7. A high salinity and colder water mass was uplifted from deeper waters in Kaoping Canyon waters. The concentration of chlorophyll-a decreased in the surface layer in both areas and was relatively low in the coastal station compared with the canyon station.

The Tungkang coastal region was occupied by a warm water mass from May to October. During this period, temperature stratification in water column was obvious and was a result of weak vertical convection. However, in Kaoping Canyon waters, colder deeper waters overflowed due to an internal tidal wave coming from a remote source; thus, a thermocline was developed at a depth of 50–70 m.[12,13]

Zooplankton was more abundant in inshore waters (depth < 20 m) and at the upper head of the Kaoping Canyon than in coastal waters. Zooplankton were more concentrated at the upper 10 m depth than at the surface. Zooplankton density decreased with increasing depth.[14]

Relationship between lunar phase and fishing conditions

The relationship between lunar phase and fishing conditions in the coastal waters of south-western Taiwan were analyzed for the main fishing seasons in 1999 and 2000 (Fig. 8). The results showed that the catch of *A. intermedius* was poor during the last 6 days of the lunar month when the moon did not appear during the evening (18.00–24.00 h). In contrast, the catch was usually higher when the moon appeared during the evening (18.00–24.00 h) and a good harvest could only be achieved during rainy days.

DISCUSSION

Acetes sibogae inhabiting waters 1.3 km from the estuarine mouth in eastern Australia exhibit both nocturnal and tidal vertical movements.[7] Shrimps were more abundant in the surface water than in bottom area during flood tides and at night. Such movements have implications for population maintenance in estuarine waters.[5] However, vertical movements of *A. intermedius* in the nearby waters of Kaohsiung Harbor[15] and in the coastal waters of Tungkang, Taiwan, were not found to be related to local tidal movements. Nocturnal vertical movement performed by this species is to avoid predators and to allow for the safe feeding of the shrimp based on a number of reasons. First, during the south-west monsoon (May to October), schools of *A. intermedius* migrate from estuaries to

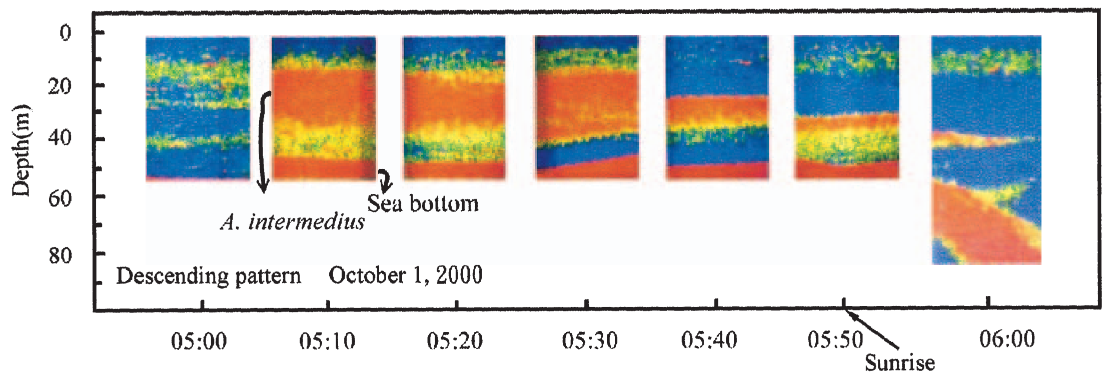

Fig. 4 Descending movement of schools of *Acetes intermedius* observed with the color echo sounder off Tungkang (zone II), Taiwan. The right-hand plot was observed in the final stage of the same cruise operating in the Kaoping Canyon (zone II).

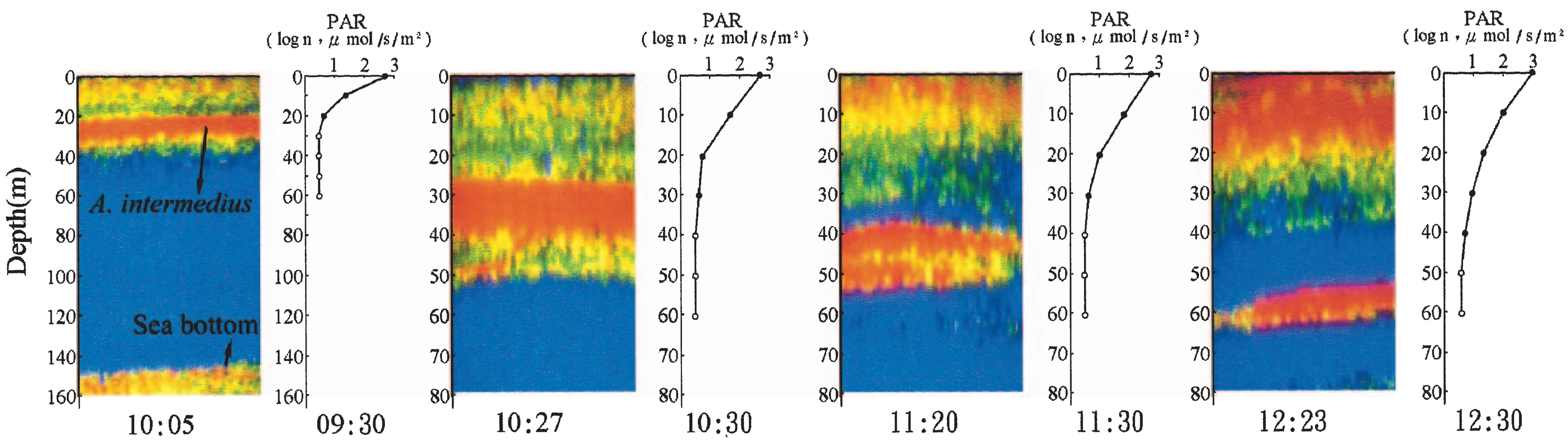

Fig. 5 Examples showing the swarming layer of *Acetes intermedius* and profiles of photosynthetically active radiation (PAR) in the waters of Kaoping Canyon. (❍), a PAR of 4 μmol/s per m², possibly reflecting the preferable PAR of *Acetes intermedius*.

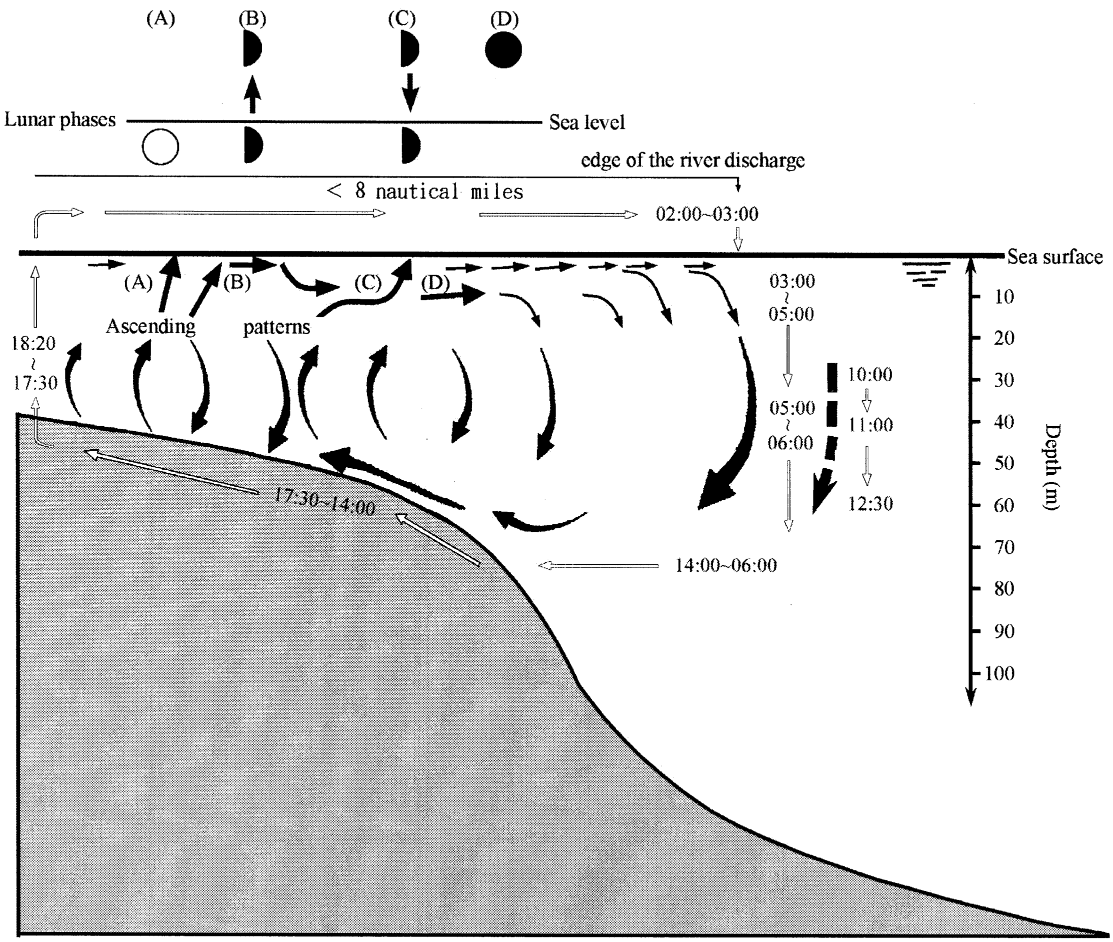

Fig. 6 Schematic presentation of the route of diel vertical migration of *A. intermedius* near Tungkang, south-western Taiwan. *Acetes intermedius* are distributed up to 8 nautical miles out. This distance coincides with the river discharge. Ascending patterns (A) (B) (C) and (D) refer to Fig. 3. The time of sunrise and sunset during July and October is 05.00–06.00 and 17.30–18.50 h, respectively.

deeper coastal waters and perform a diel vertical migration off south-western Taiwan. Similar swarming and horizontal migration of *Acetes japonicus* occurs in the near-shore waters of Japan when the prevailing wind is blowing landward.[16] Populations of *A. intermedius* could be maintained in coastal waters through the net landward movement of tidal current flow during the summer off south-western Taiwan.[17] Second, feeding activity of *Acetes* is more active during the night, when they take phytoplankton, zooplankton, amorphous materials and mud.[6,18] In south-western Taiwan, zooplanktons are more abundant at a depth of 0–10 m and decline with increasing water depth.[14] However, *A. intermedius* is also a prey of many fish and big shrimp in the important coastal fishing grounds of south-western Taiwan.[9] *Acetes intermedius* may bear more predation pressure than *A. sibogae*. Hence, the nocturnal vertical migration of *A. intermedius* and active feeding at night on the surface layer can reduce mortality caused by visual predators. Third, during the ascending period, the pattern of nocturnal vertical movement depends on the lunar phase. This suggests that the ascent strategy of *A. intermedius* is to evade moonlight and the moon is used as a trigger for resuming movement towards the surface or towards the 10 m water layer. This evidence supports the hypothesis that the nocturnal vertical movement performed by *A. intermedius* may be related to predator avoidance.

During the descending period, *A. intermedius* descended to the bottom or a middle water depth at 50–80 m before sunrise to reduce predation risk during the day. Based on these observations, the diel vertical migration performed by *A. intermedius* allows them to avoid visual predators.

Schools of *A. intermedius* in the waters of Kaoping Canyon also perform a slow downward migration coinciding with the PAR of 4 μmol/s per m^2.

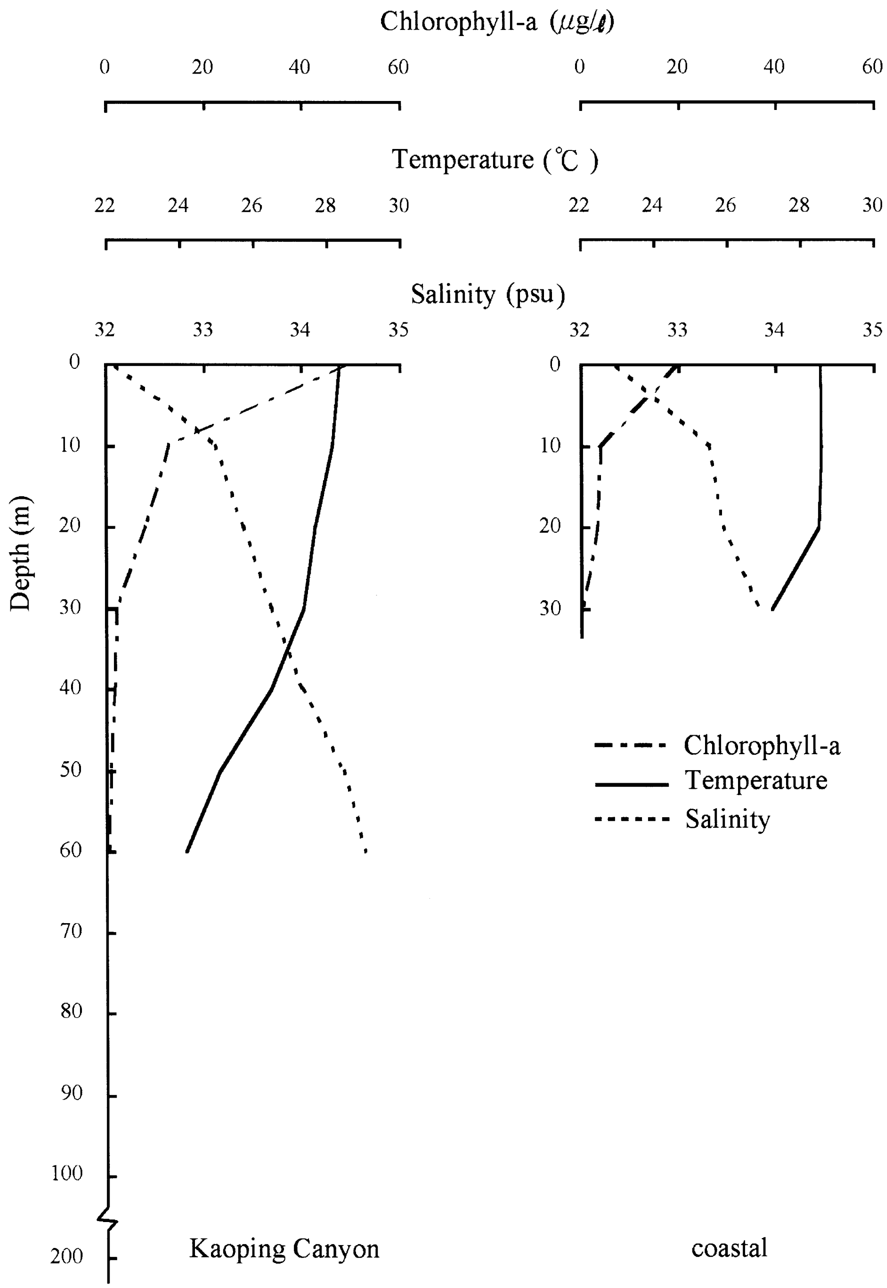

Fig. 7 Profiles of chlorophyll-a, temperature and salinity at the Kaoping Canyon (zone I) and coastal (zone II) stations.

The shrimp seem to prefer a water layer with an optimal lighting environment. Similar observations have been reported by Chiou *et al.*[9] Hence, predator avoidance is possibly the primary reason why *A. intermedius* perform a diel vertical migration. Nevertheless, shrimp schools would undertake migration searching for an optimal lighting environment because no predators exist in the deeper waters.

Zone I in the present study is highly stratified, with a pronounced temperature gradient, but colder, deeper waters from the canyon were uplifted and spread over the nearby seabed.[13,14] Cold water in deep layers attracts organisms to undergo descending movements in order to conserve energy[19,20] due to the reduction in metabolic rate. Hence, apart from the avoidance of predation, conservation of energy in low-temperature waters is also a cause for the retreat of *A. intermedius* to deeper, cooler water layers (50–80 m) before sunrise. It is beneficial for the subsequent maintenance and coastal-ward migrating at dusk. This

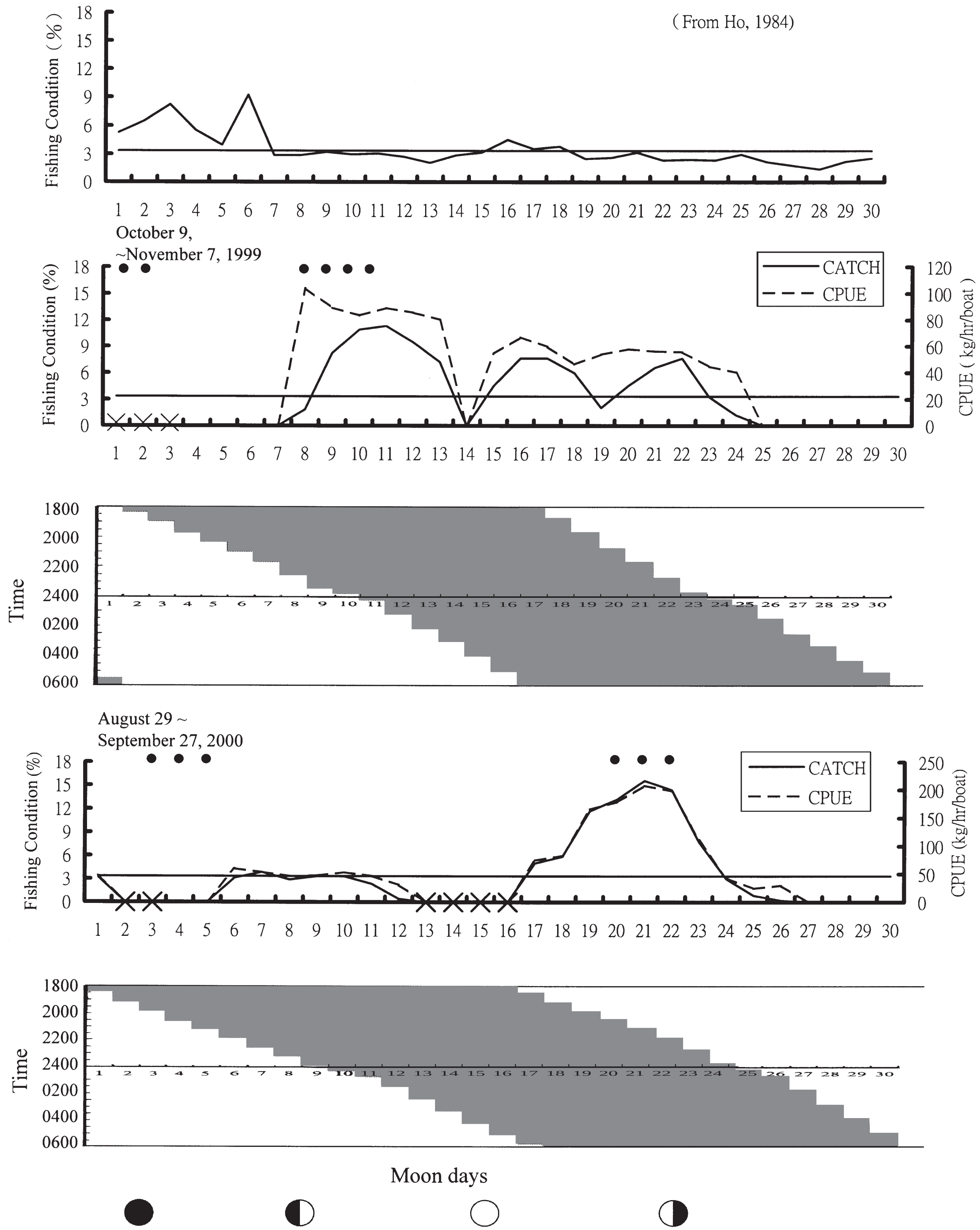

Fig. 8 Relationship between fishing conditions and lunar phase in the coastal waters of south-western Taiwan. Shaded areas represent the time the moon appeared off Tungkang, Taiwan. (Ñ), fishermen stop their operation when the weather is bad (mean wind speed ≥ 15.1 m/s); (•), rainy weather. The horizontal line in the first, second and fourth plots indicates the average daily catch as a percentage of monthly total catch (3.33%).

may be one of the reasons why *A. intermedius* prefer to aggregate on the slope of Kaoping Canyon,[9] where the water is colder.

Forward[1] and Ansell *et al.*[6] proposed that a change in water temperature could affect the speed of diel vertical migration. However, the present study found that the speed of vertical migration of *A. intermedius* depends primarily on the depth of the habitat. In order to avoid predation, *A. intermedius* tried to reach dark and safe places as soon as possible before sunrise. The ascending speed of this species in deeper waters is approximately twofold faster than in shallower waters observed in the present study. For example, *A. intermedius* at the offshore station (depth 67 m) ascended at a mean speed of 63.3 cm/min, whereas at the inshore area (depth 26 m), the speed of ascension was only 17.8 cm/min.

Acetes intermedius mainly gathered near the sea surface (0–10 m depth) at night and can be caught by a large skimming net that operates at depths between 12 and 15 m. Based on our results and the results of the study of Ho,[11] it is obvious that the fishing conditions in the last week of the lunar month are worse than on other lunar days and a good harvest can only be obtained during rainy days.

The catch of the large skimming net was greatly influenced by the density of shrimp (CPUE). From the results of the present study, the density of *A. intermedius* is mainly influenced by two factors: (i) the lunar phase; and (ii) rainfall. *Acetes intermedius* ascended directly and scattered near the surface after sunset when the moon was absent. In contrast, *A. intermedius* would swarm and stay at the 10 m water layer when the moon appeared. In addition, no dense patch of *A. intermedius* could be found by fishermen during the last week of the lunar month.

Observations of a large surface swarm of this species during the day have been made after heavy rainfall in the waters of Kaohsing Harbor, Taiwan.[15] Ho[11] suggested that the annual catch of *A. intermedius* by large skimming net increased with an increase in total annual precipitation. We also found that mild wind and rainy weather were essential conditions for a good catch of *A. intermedius*. Hence, rainfall is a cue for *A. intermedius* to aggregate largely at the sea surface during the night. Uen[15] suggested that massive swarms of *A. intermedius* after heavy rainfall were prespawning aggregations because large amounts of sexually matured shrimps were found 1 week after heavy rainfall. Prespawning aggregation has also been reported for other *Acetes* species.[16] However, the salinity of coastal waters is too great to be suitable for spawning for *A. intermedius*.[21] *Acetes intermedius* do respond to rainfall, possibly reflecting an endogenous stimulations that triggers the shrimp to swarm at the surface water in costal waters off south-western Taiwan.

ACKNOWLEDGMENTS

This study was funded by the Council of Agriculture, Executive Yuan, ROC. We are most grateful to Dr Sin-Che Lee of the Institute of Zoology Academia Sinica, and to Dr Chiee-Young Chen (National Kaohsiung Institute of Marine Technology), Dr Yih-Yia Liao and Dr Shyh-Bin Wang (National Taiwan Ocean University) for valuable suggestions. We also thank our colleagues Chi-Ming Wang and Mr Pyng-Chyuan Shieh (National Kaohsiung Institute of Marine Technology) for their assistance with the field survey.

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