Emergence Rhythms of Subtidal Small Invertebrates in the Subtropical Sea: Nocturnal Patterns and Variety in the Synchrony with Tidal and Lunar Cycles

Authors: Saigusa, Masayuki, and Oishi, Kazushi

Source: Zoological Science, 17(2) : 241-251

Published By: Zoological Society of Japan

URL: https://doi.org/10.2108/zsj.17.241

ZOOLOGICAL SCIENCE **17**: 241–251 (2000)

Emergence Rhythms of Subtidal Small Invertebrates in the Subtropical Sea: Nocturnal Patterns and Variety in the Synchrony with Tidal and Lunar Cycles

Masayuki Saigusa* and Kazushi Oishi

Department of Biology, Faculty of Science, Okayama University, Tsushima 2-1-1 (General Education Buildings), Okayama 700-8530, Japan

ABSTRACT—The subtidal zones near the shore are inhabited by many small invertebrates, including benthos and plankton. To characterize their emergence in the water column with regards to day/night, tidal, and lunar cycles, field investigations were carried out at the subtropical island (Iriomote-jima), Okinawa Prefecture. By use of two impeller pumps installed in both surface and bottom waters, invertebrates were sampled continuously for 23 days. Although most patterns were much the same between the surface and bottom waters, the abundance of animals was different between the two depths. A notable feature was that nocturnal patterns were very dominant. More than half of these patterns were not affected by the tidal cycle at all. In contrast, the pattern of *Ericthonius* sp. (Amphipoda) showed a clear synchrony with the nocturnal tide. Other patterns were weakly modified by the nocturnal tide (e.g. *Propallene longiceps*; Pantopoda). A pattern coincided with the lunar phase was only seen in *Vargula hilgendorfii* (Myodocopida). Most arthropods would hide in the bottom substrate, or would swarm under or near the lower pump in the daytime, and they would disperse in the water column at night. A variety in the synchrony with nocturnal tides strongly supports a notion that the tidal rhythm is only a variation of the day/night rhythm, rather than the hypothesis that both rhythms are present simultaneously in an animal. Statistical methods (autocorrelogram and periodogram) are used to demonstrate the tide-correlated component of the activity. However, these methods are not sufficient for this purpose; visual inspection of the pattern is very important.

INTRODUCTION

The tidal rhythm can be defined as a biological timing in synchrony with the tidal cycle. The tidal cycle recurs at intervals of 12.4 hr in the mean, so the period of some tidal rhythms is about 12.4 hr: a single-tidal interval. On the other hand, the period is often about 24.8 hr (a double-tidal interval), when the activity occurs either in the daytime or at night (e.g., Saigusa, 1982,1997a; Neumann, 1987), or when it is correlated with the fluctuations of the height of semidiurnal tides (e.g., Enright, 1972; Saigusa and Kawagoye, 1997). Since there is clear evidence that synchrony with the tidal cycle is changeable between the single-tidal interval (12.4 hr) and the double-tidal interval (24.8 hr) (see Saigusa and Akiyama, 1995), it is not reasonable to define a new term such as 'circalunidian' for the double-tidal interval (e.g., Palmer, 1995; Naylor, 1996).

Some opposing notions have been produced as to the timing systems of marine organisms. One of them is the case of explanation of the tidal rhythm coinciding with both day/night and tidal cycles. Intertidal and estuarine organisms are exposed to the day/night cycle as well, and they have developed the activity in synchrony with both cycles (see Neumann, 1981; Palmer, 1995). Some activities are controlled endogenously (Saigusa, 1997b). Accordingly, a hypothesis proposed was that the activity is organized by two kinds of different timing, i.e., circadian and circatidal rhythms (e.g., Naylor, 1958, 1996; Palmer and Round, 1967; Reid and Naylor, 1989; Palmer, 1995). An opposing notion is that the day/night cycle is one of the zeitgebers of the tidal rhythm (Saigusa, 1988, 1992, 1997a; Saigusa and Kawagoye, 1997).

A field research can test whether the circadian and circatidal rhythms are simultaneously present in an organism. In intertidal and estuarine environments, where the influences of the tidal cycle would appear most strongly, many animals show well-demarcated tidal rhythms (Neumann, 1981; Palmer, 1995; Saigusa, 1997b). In contrast, influences of the tidal cycle would decrease as the habitat is away from intertidal zones and estuaries. Then, the tidal rhythms would be weakened corresponding to decreased influences of the tides. Nevertheless, if both rhythms are simultaneously driven in an organism, the 'period' of the tidal rhythm should be maintained at about 12.4 hr or 24.8 hr even in such conditions. In contrast, if the period of the activity does not accurately correspond to that of the tidal cycle, we would have to consider an

* Corresponding author: Tel. +81-86-251-8500.
E-mail: saigusa@cc.okayama-u.ac.jp

alternative explanation.

Influences of the tidal cycle would be weaker in the subtidal zones near the shore than in intertidal and estuarine shores. The subtidal zone is inhabited by many kinds of small invertebrate comprising benthos and plankton (Biernbaum, 1979; Edgar, 1983; Ueda *et al.*, 1983; Lalli and Parsons, 1993). This study focused on the daily activity of the subtidal invertebrates, and temporal fluctuations of their emergence in the water column were surveyed. For the assessment of the emergence patterns, however, the sampling must have been carried out continuously for a long period, because such investigations do help to distinguish tidal rhythms from day/night rhythms in the field.

Another problem is related to nocturnal emergence in a variety of subtidal invertebrates. We have already examined daily emergence of subtidal small arthropods in the Inland Sea of Japan, and reported a wide variety of their emergence patterns, ranging from patterns synchronized only with the day/night cycle to patterns clearly synchronized with the tides (Oishi and Saigusa, 1999). It is not known, however, whether such a variety of the emergence pattern is common to the other locations.

To settle these questions, field investigations were carried out in the subtropical sea of Okinawa Prefecture, Japan. Among the many taxa collected, the emergence patterns of dominant taxa, mostly crustaceans, were examined with regard to the synchrony with day/night, tidal, and lunar cycles, and in relation to their abundance in surface and bottom waters.

MATERIALS AND METHODS

Field studies were carried out from 17 April until 11 May, 1998, on the shore (Uehara) of a subtropical island (Iriomote-jima), Okinawa Prefecture (Fig. 1). This island (24°N and 124°E) is located on the route of Kuroshio originating from the east of the Philippines. During the experimental period, the water temperature was 24.5–28.0°C,

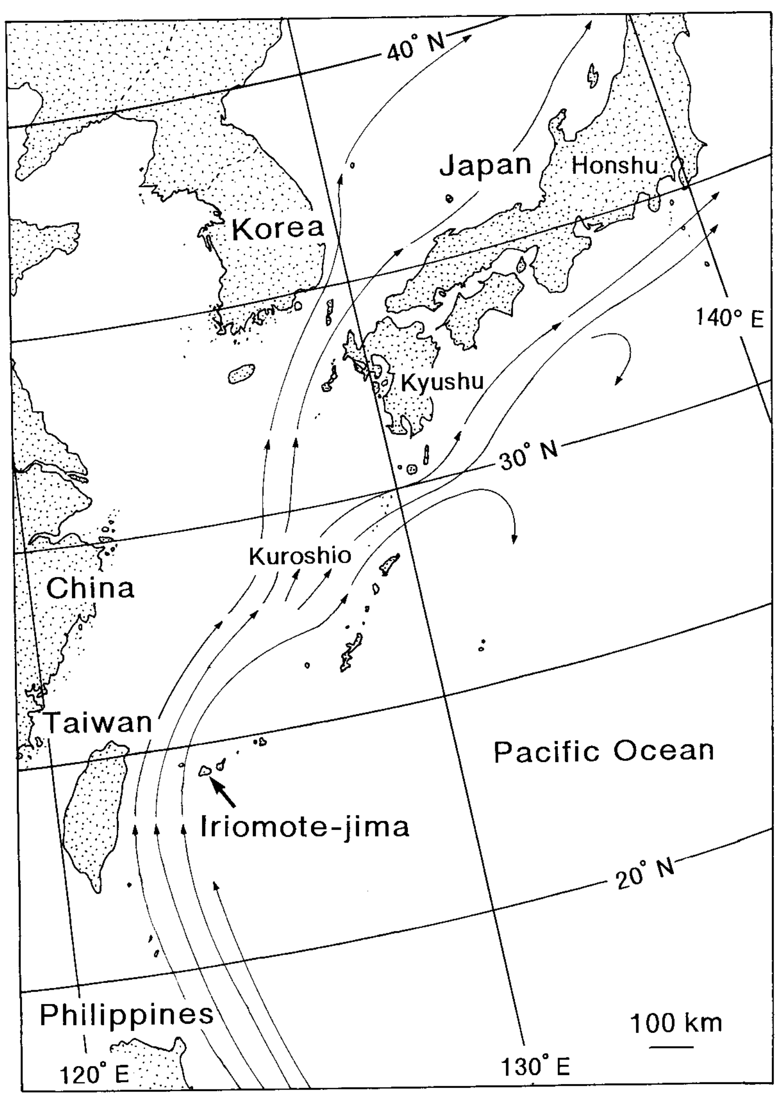

Fig. 1. Location of Iriomote-jima (*solid thick arrow*). This island is one of the Yaeyama Group in the Ryukyu Islands, and is largely surrounded by coral reefs and mangroves. The ocean current (Kuroshio) is also shown by solid arrows.

and the salinity was 30−32‰ at the sea surface. The tidal pattern is semidiurnal from April to May. The height of high tides is only moderately different between day and night, but differs 0.7 m between spring and neap tides. Afternoon low waters recede further than morning low waters.

Subtidal small invertebrates were collected by use of two impeller pumps (SX-150; Terada Pump Co. Ltd., Japan). One pump for sampling the bottom water was fixed at 50 cm above the seabed using a rope and stones, and another pump for sampling the surface water was floated at a depth of 50 cm by two vinyl chloride floats (diameter of 30 cm). Water was pumped at a flow rate of about 120 liters per one minute. The position of the floating pumps fluctuated vertically with the height of the tides. At spring tides, the surface pump was 2 m above the bottom at low tide, and 4 m above the bottom at high tide. At neap tides, it was 2.5−3 m above the bottom at low tide, and about 3.5 m above the bottom at high tide.

The two pumps ran continuously, and invertebrate samples were collected from a nylon net (15×23 cm; 300−500 μm in mesh size) every 30 min (3600 liters). The samples were separately fixed with 5% (v/v) formalin and stored. Sampling was carried out continuously from 17 April to 11 May 1998, except when the investigation was interrupted for 4 hr (0000−0400 hr) on 25 April because of a power failure.

After the sampling at Iriomote-jima, fixed specimens were transferred to Okayama, and invertebrates were identified under a stereomicroscope. Identification was made at the species level in accordance with two illustrated books recently published in Japan (Nishimura, 1995; Chihara and Murano, 1997), but it was sometimes very difficult to us. In such cases, the animals were classified to the genus or family level.

The specimens collected were counted after identification of species or groups, and the number collected every 30 min was plotted in relation to time of day, and tidal and lunar cycles. Differences of emergence patterns were analyzed by visual inspection. In addition, the period of each pattern was estimated by two kinds of statistical treatments: autocorrelogram (Chiba and Takahashi, 1991) and periodogram (Enright, 1965). Furthermore, two-way ANOVA was applied to test whether there was a significant difference of emergence between day and night, or between surface and bottom.

RESULTS

Nocturnal activity patterns

Table 1 shows the dominant taxa (24 groups) collected from 17 April until 11 May 1998. Almost all invertebrates collected by the pump method were small crustaceans, but *Propallene longiceps* (Pantopoda) and a small snail (species unknown) were also collected. In terms of the number of specimens, copepods were the most abundant taxon in both surface and bottom samples.

The results of ANOVA are summarized in Figure 2A (day and night) and Figure 2B (surface and bottom). A notable feature was that almost all these taxa showed very strong nocturnal activities except *Corycaeus* sp. (Poecilostomatoida) (F=1.02<3.96). While nocturnal activity of *Longipedia* sp. (Harpacticoida) and *Ericthonius* sp. (Amphipoda) was the strongest (F=94.92 for *Longipedia* sp.; F=107.72 for *Ericthonius* sp.), that of *Lucifer hanseni* (Decapoda) was significant at the 5% level (F=5.95; 3.96<F<6.97). Figure 2B shows the difference between surface and bottom waters. Clear difference was seen for two species of opossum shrimp (*Pseudanchialina inermis* and *Haplostylus indicus*; results of two lumped together): for these species, more than 10 times

Table 1. Small invertebrates collected from bottom and surface waters (only major taxa). Sampling period : 17 April -11 May 1998. Accuracy of counting is three digits. * : The taxa used for assessment of the emergence pattern.

Taxa	Surface	Bottom
PYCNOGONIDA		
1. Pantopoda		
Propallene longiceps	429	454*
OSTRACODA		
2. Myodocopida		
Vargula hilgendorfii	2,430	5,940*
Xenoleberis yamadai	45	12
COPEPODA		
3. Calanoida		
Labidocera pavo	9,030	17,300*
Chiridius poppei	67,900	72,800*
Acartia fossae		
Paracalanus parvus s.l.	72,300	44,900*
Pontella sp.		
4. Harpacticoida		
Longipedia sp.	4,900	5,360*
Porcellidium sp.	72	83
5. Poecilostomatoida		
Corycaeus sp.	44	48
MALACOSTRACA		
6. Mysidacea		
Pseudanchialina inermis	126	1,340*
Haplostylus indicus		
7. Tanaidacea		
Anatanais normani	987	745*
Apseudes sp.		
8. Cumacea		
Nannastacus gibossus	1,030	450*
9. Isopoda		
Cymodoce japonica	245*	78
Limnoria lignorum	302	351*
Gnathia sp.	80	215*
10. Amphipoda		
Pontogeneia rostrata	399	359*
Ericthonius sp.	4,330	1,910*
Urothoe sp.	57	93
11. Decapoda		
Acetes japonicus	66	8
Lucifer hanseni	24	488*
Zoea (shrimps)	2,980	3,740*
Zoea (crabs)	2,210	718*
Megalopa	95	80
12. GASTROPODA		
snail (single species)	8,590	5,630*

as many specimens were collected at the bottom water as were those collected at the surface water (F=48.54). Most other taxa did not show such a large difference between the two depths.

Emergence patterns synchronized with the day/night cycle

Characteristics of each emergence pattern were determined by visual inspection when more than 200 specimens were collected. Among the 24 dominant taxa summarized in Table 1, 18 groups fulfilled this condition. The patterns were not conspicuously different between surface and bottom waters in any group. So this study compared the patterns obtained from the sampling of bottom water except *Cymodoce japonica* (see the asterisk in Table 1).

Visual inspections of each emergence pattern indicated that patterns of 11 groups (61%) appear to be only synchronized with the day/night cycle (Table 2). For example,

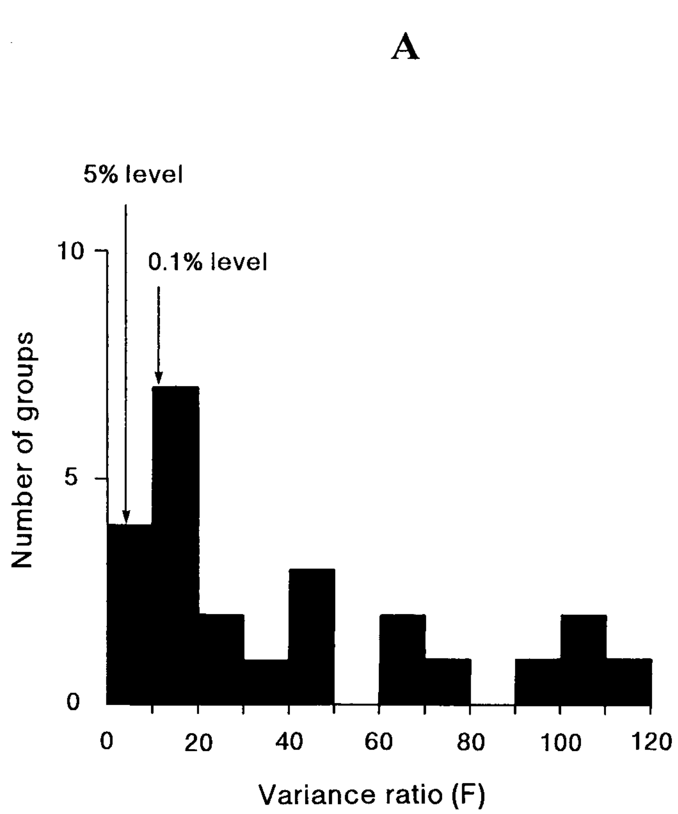

Fig. 2. Results of ANOVA test for the dominant 24 groups collected at Iriomote-jima. A: Difference of abundance between day and night. B: Difference of abundance between surface and bottom. The horizontal axis indicates the “variance ratio (F)” of ANOVA. Significant levels at 5% (3.96), 1% (6.97), and 0.1% (11.68) are shown by the vertical arrows, respectively. For the groups tested, see Table 1.

Table 2. Classification of nocturnal patterns in relation to synchrony with tidal and lunar cycles. Each pattern was obtained from the bottom water except *Cymodoce japonica* (see the asterisk inTable 1).

Day/night cycle alone	Tidal cycle		Lunar cycle	
	Weak	Very clear		
Chiridius poppei	*Propallene longiceps*	*Ericthonius* sp.	*Vargula hilgendorfii*	
Acartia fossae+*Paracalanus parvus* s.l.+*Pontella* sp.	*Labidocera pavo*			
Longipedia sp.	*Limnoria lignorum*			
Pseudanchialina inermis+*Haplostylus indicus*	*Lucifer hanseni*			
Anatanais normani+*Apseudes* sp.	Zoea (shrimps)			
Nannastacus gibossus				
Cymodoce japonica				
Gnathia sp.				
Pontogeneia rostrata				
Zoea (crabs)				
Gastropod				
11	5	1	1	18 (Total)

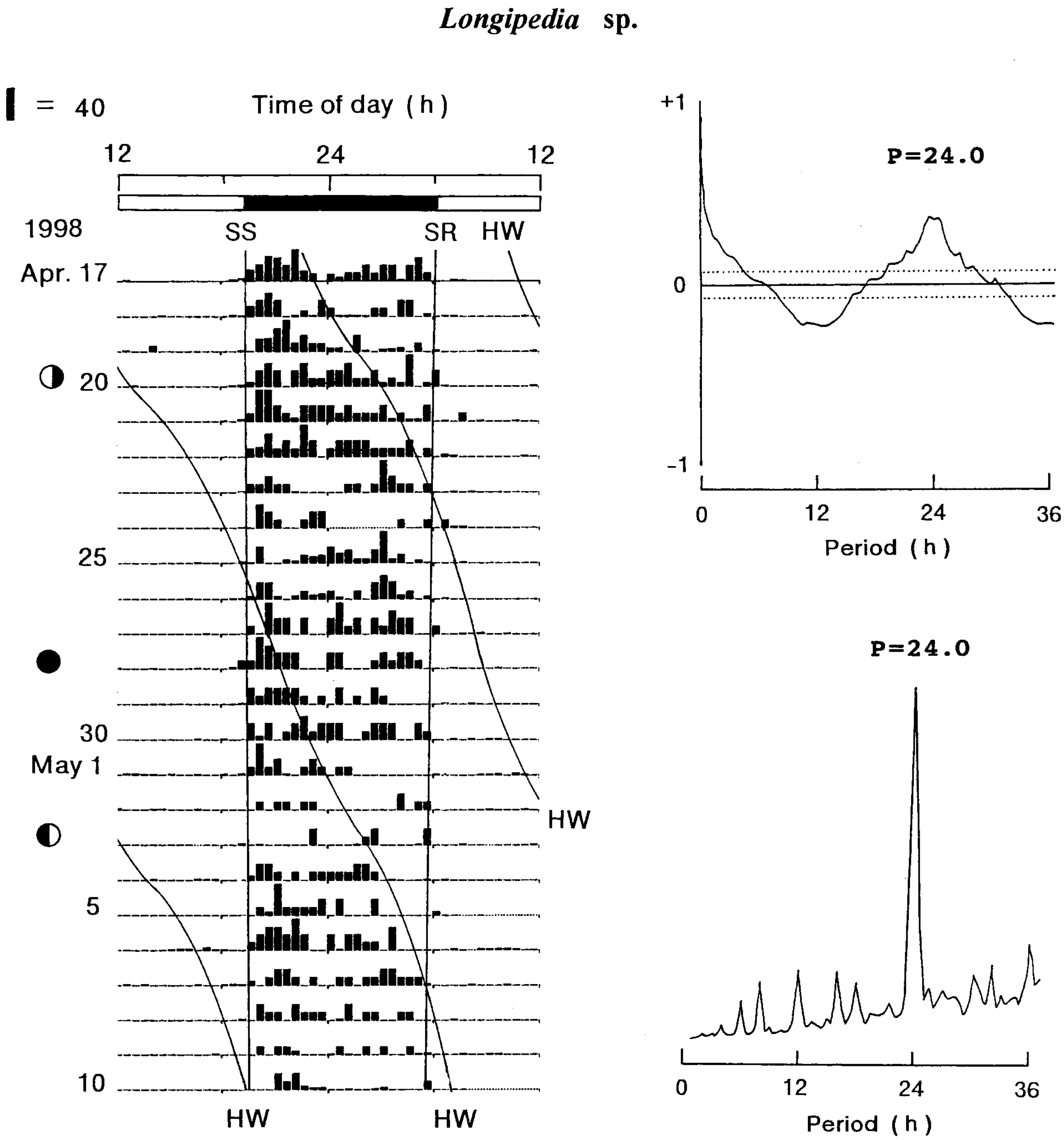

Fig. 3. The emergence pattern with no influence of the nocturnal tide (*Longipedia* sp.; Harpacticoida). Collection from bottom water. SS and SR are the times of sunset and sunrise (solid horizontal bar indicates the period of darkness). HW indicates the times of high tide. Vertical bars represent the number of specimens collected every 30 min.●: new moon; ◐ and ◑ : the first and last quarters of the moon, respectively. The results of the period analysis are shown in the upper right (autocorrelogram) and in the lower right (periodogram). P indicates the period (hrs) in each pattern. Dotted line on the autocorrelogram indicates the 95% confidence limit.

Figure 3 shows the emergence pattern of *Longipedia* sp. (Harpacticoida). This species emerged just after sunset, and emergence lasted throughout the night. Emergence seemed to be more vigorous in the first half of the night than the second half, but there was no clear peak of emergence during the night. The autocorrelogram showed large amplitude with a period of 24.0 hr; the periodogram also showed a sharp peak at 24.0 hr.

Emergence patterns synchronized with not only day/night cycle but also tidal cycle

Some nocturnal patterns (5 groups; 28%) were weakly modified by the tide. Figure 4 shows the emergence pattern of *Propallene longiceps* (Pantopoda). This arthropod appeared in the water column after sunset. For 3–5 days before the half moon (17–19 April and 24–28 April), a peak of emergence was seen during the first half of the night, but emergence was spread throughout the night thereafter. This

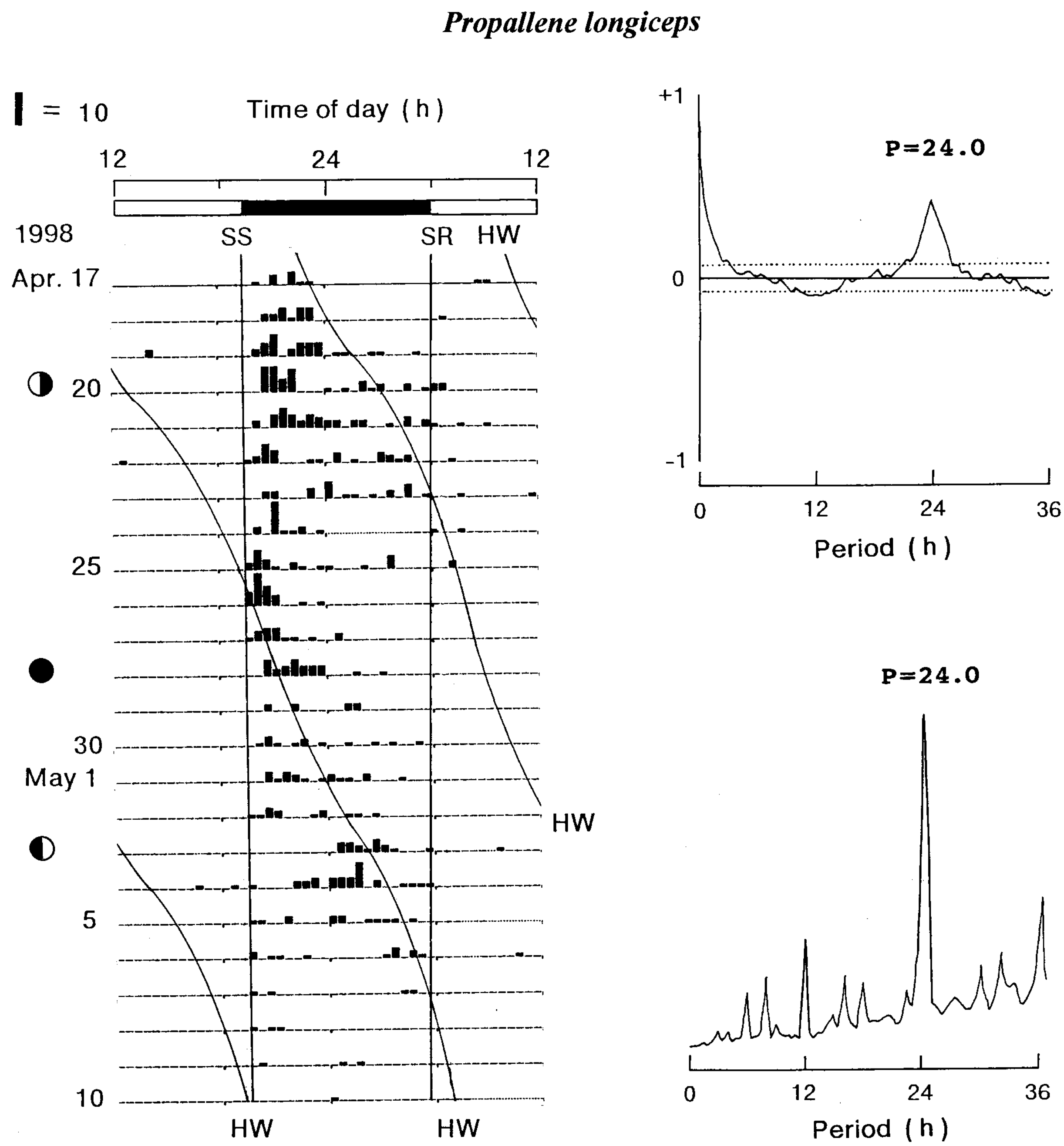

Fig. 4. The emergence pattern that is very weakly modified by the nocturnal tide (*Propallene longiceps*; Pantopoda). Collection from bottom water. Symbols are the same as in Fig. 3.

pattern seems to be very weakly affected by the tide, but this characteristic was not clearly demonstrated in either the autocorrelogram or the periodogram.

The emergence pattern of *Labidocera pavo* (Calanoida) was more clearly affected by the nocturnal tide (Fig. 5). Most calanoids are plankton; so they were expected to be abundant in the water column by day, too. But this species emerged only at night. Emergence seemed to be more vigorous just after sunset and close to dawn than the midnight, in the first half of the investigation (17–26 April). No clear influence of the tidal cycle was discernible in this period. But in the second half of the investigation (26 April to 10 May), the emergence was clearly modified by the nocturnal tide. The period of the pattern was 24.3 hr in the autocorrelogram and 24.2 hr in the periodogram.

Figure 6 shows the pattern of *Ericthonius* sp. (Amphipoda). The nocturnal pattern of this species was also clear. Furthermore it showed a very clear correlation between the emergence and the nocturnal tide. From 17 April to 25 April, most individuals appeared at the rising tide at night. From 25 April to 30 April, emergence split into two peaks: after sunset and before sunrise. Emergence then occurred at rising

Labidocera pavo

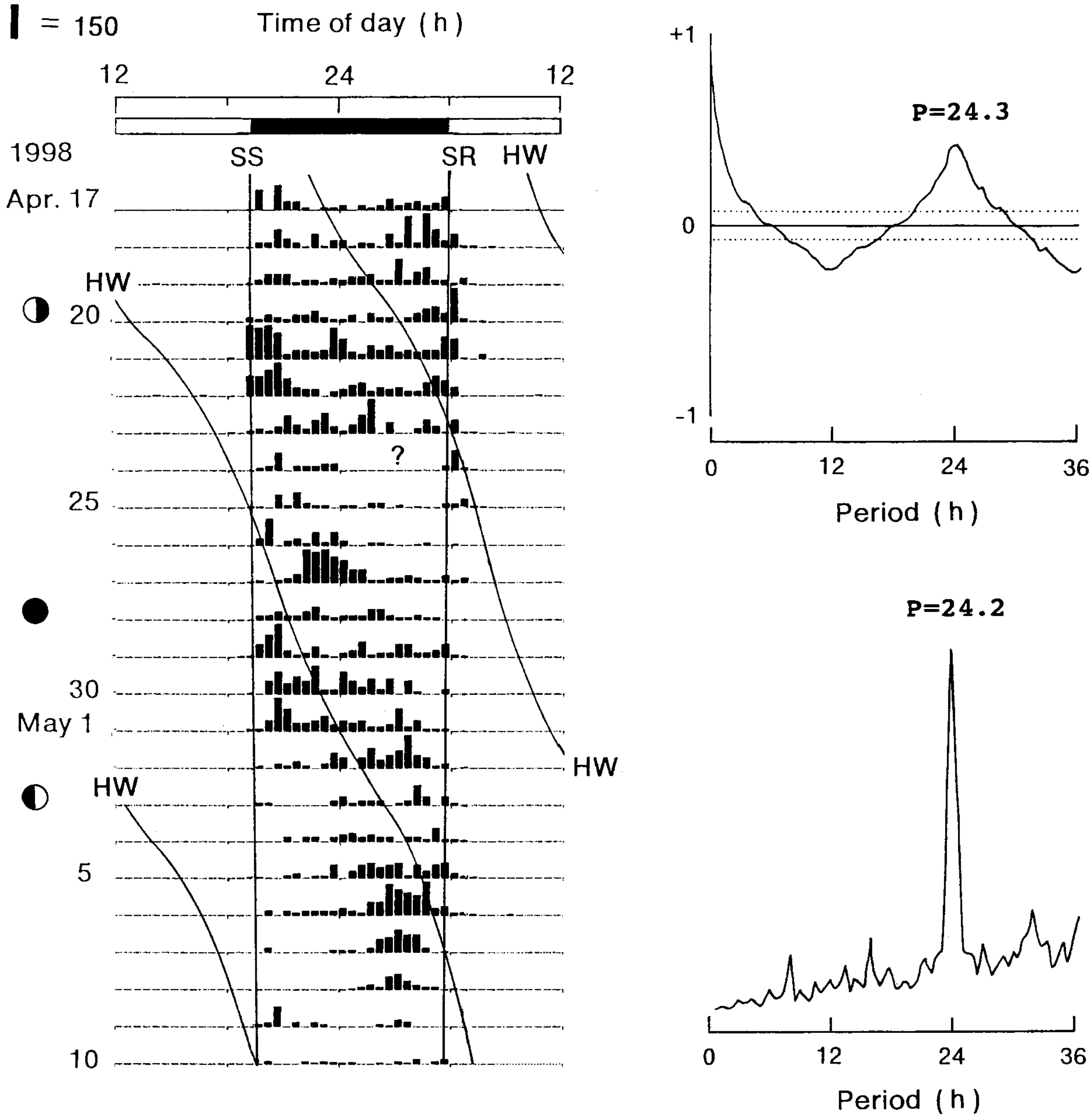

Fig. 5. The emergence pattern that is weakly modified by the nocturnal tide (*Labidocera pavo*; Calanoida). Collection from bottom water. Symbols are the same as in Fig. 3.

tide at night from 1 May to 10 May. The period of this pattern was estimated to be 24.5 hr on the autocorrelogram and 24.2 hr on the periodogram.

A pattern synchronized with the lunar cycle

Figure 7 indicates the emergence pattern of *Vargula hilgendorfii* (Myodocopida). Emergence of this species also occurred at night, but most of the specimens emerged in the second half of the night. The peak of emergence occurred between 0300 hr and 0500 hr every night. In addition, the number of individuals collected per night showed two peaks at around the last and first quarters of the moon, indicating a semilunar rhythm of emergence. The amplitude of the autocorrelogram was small, but the peak was significant at 24.0 hr. The periodogram also indicated a peak of at 24.0 hr.

DISCUSSION

Subtropical arthropods inhabiting a shallow subtidal zone were continuously collected near one month in the subtropical sea. The emergence patterns of the dominant 18 groups were examined in relation to synchrony with day/night, tidal, and lunar cycles. In most taxa, the abundance of animals was different between surface and bottom waters, but their emer-

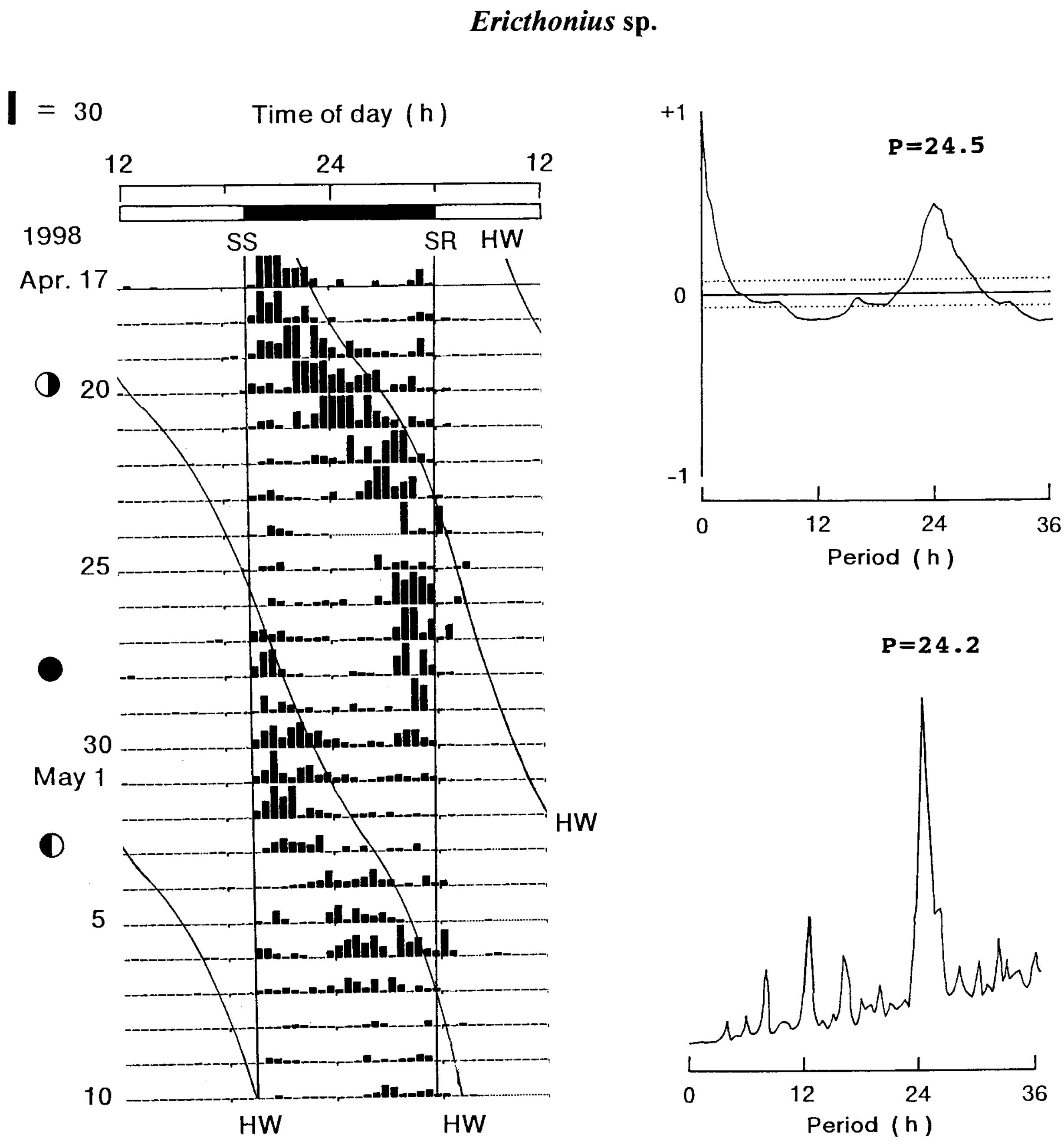

Fig. 6. The emergence pattern that is clearly modified by the nocturnal tide (*Ericthonius* sp.; Amphipoda). Collection from bottom water. Symbols are the same as in Fig. 3.

gence pattern was not largely different between the two depths. All the taxa, except *Corycaeus* sp. (Poecilostomatoida), showed very clear nocturnal patterns. As shown in Table 2, some patterns (11 groups: 61%) were not affected by the tidal cycle at all, but other patterns (6 groups: 33%) showed a variety in the synchrony with the nocturnal tide. This characteristic was common to the other sea we had been investigated (Oishi and Saigusa, 1999). These results raise the following three issues on biological rhythms research.

The tidal rhythm as a variation of the day/night rhythm

In the marine environment, most activity rhythms in synchrony with both day/night and tidal cycles have been accounted for by a hypothesis that an organism possesses two kinds of rhythm with different periods (see Naylor, 1958, 1996; Palmer and Round, 1967; Reid and Naylor, 1989; Palmer, 1995). If it is true, day/night and tidal rhythms could be separated in experimental conditions. For example, administration of a day/night cycle should cause a phase- shift of the circadian rhythm without affecting the phase of the tidal rhythm. The larval release activity of some crabs (*Sesarma haematocheir* and *S. erythrodactylum*) is synchronized with the nocturnal high tide, so the period of the rhythm is a double-tidal interval (e.g., see Saigusa, 1982). The 24-hr light/dark

Vargula hilgendorfii

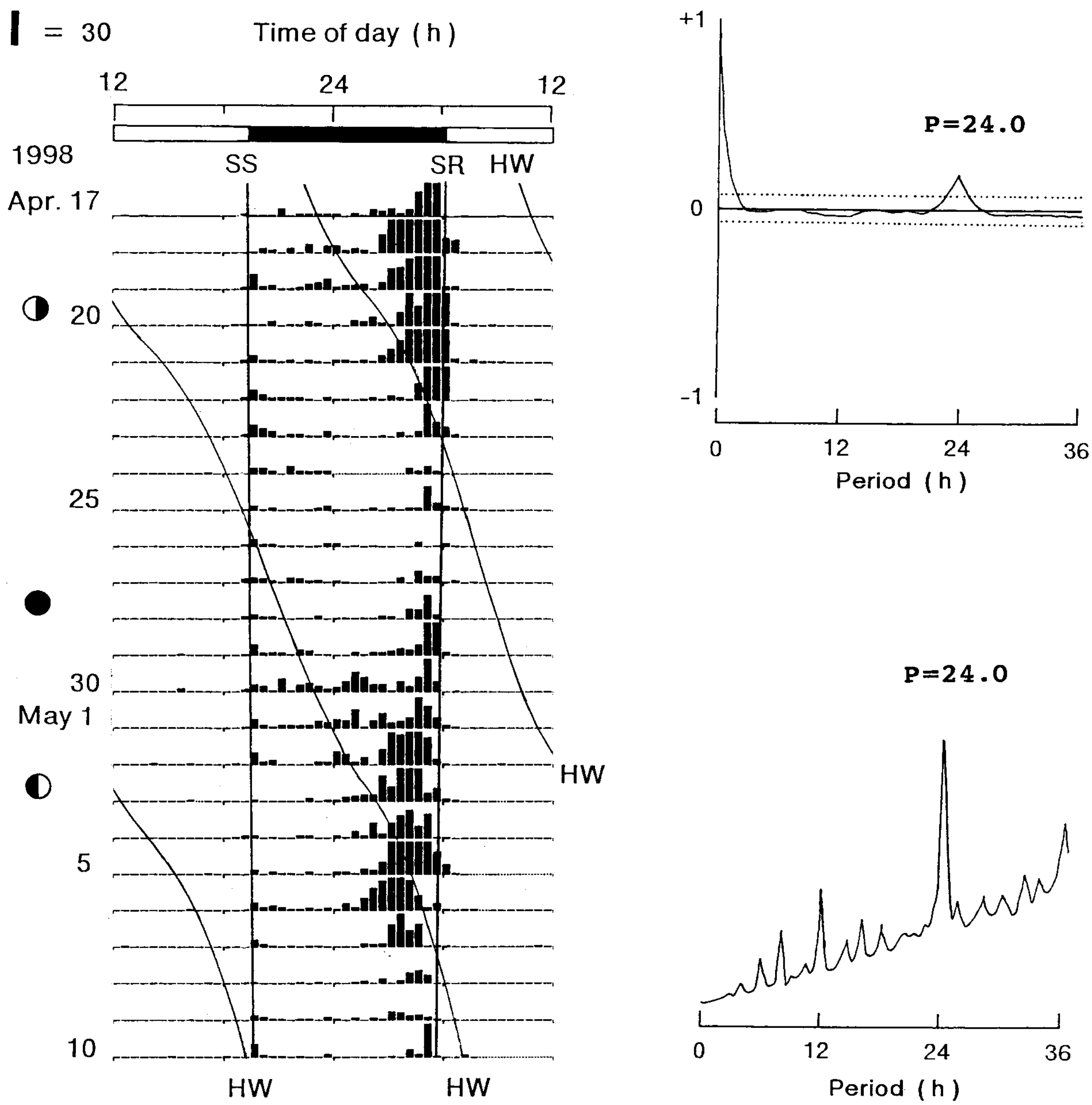

Fig. 7. The emergence pattern in synchrony with the lunar cycle (*Vargula hilgendorfii*; Myodocopida). Collection from bottom water. Symbols are the same as in Fig. 3.

(LD) cycles caused a phase-shift of the tidal rhythm (Saigusa, 1988, 1997a). A notable feature was that the magnitude of the phase-shift clearly 'corresponded' to that of the phase-shift in the LD cycle. Furthermore, the larval release activity of the semi- terrestrial crab, *Sesarma pictum*, is synchronized with both of the semi-diurnal tides. So the period of the rhythm is a single-tidal interval. The circatidal rhythm of this crab was also phase- shifted by 24-hr LD cycles; in addition, the magnitude of the phase-shift also corresponded clearly to that of the phase-shift in the LD cycle (Saigusa, 1992). These results did not support the assumption that an organism possesses two rhythmic systems with different periods. They strongly supported a notion that a 24-hr LD cycle is only one of the zeitgebers of the tidal rhythm (Saigusa, 1988, 1992, 1997b; Saigusa and Kawagoye, 1997).

Let us assume again that an animal simultaneously possesses day/night and tidal rhythms. Then the pattern of *Longipedia* sp. (Fig. 3) is regarded to consist of a day/night rhythm alone. In *Ericthonius* sp. (Fig. 6), the activity coincided well with nocturnal high tides, at least for the first half of the data. So the pattern of *Ericthonius* sp. (Fig. 6) would be regarded to consist of both day/night and tidal rhythms.

On the other hand, some patterns, e.g. *Propallene longiceps* (Fig. 4) and *Labidocera pavo* (Fig. 5), were intermediate between these extremes, and their period was between 24.0 hr and 24.5 hr. To explain these patterns in terms of two different rhythms, we could assume that the tidal rhythm is 'weakened' in the subtidal environment. Yet, even if the tidal rhythm is weakened in accordance with decreased tidal influences, it should be still synchronized with the tidal cycle. Then, the period of the tidal rhythm should be the same as that of the tidal cycle. However, Figures 4 and 5 clearly demonstrates that the period of the activity is very close to 24.0 hr. These results would show that the original assumption (i.e., simultaneous presence of two different rhythms) is not correct. Furthermore, the emergence patterns (Figs. 3–6) varied continuously from the synchrony with the day/night cycle alone to the synchrony with the tidal cycle as well. These characteristics were also discernible in the Seto Inland Sea (Oishi and Saigusa, 1999). These results would favor the notion that the tidal rhythm is only a variation of the day/night rhythm.

There remains a possibility that the patterns weakly modified by the tidal cycle (Figs. 4 and 5) may be caused by any interaction between day/night and tidal rhythms with a double-tidal interval. If so, such an interaction should cause a 'beat', because the period of both rhythms is very close to each other. However, the emergence pattern of *Vargula hilgendorfii* (Fig. 7) did not support a clear relationship between the manifestation of the semilunar rhythm and the presence of the tide-correlated activity.

Since the tidal rhythm is regarded as a variation of the day/night rhythm, the difference between day/night rhythms and tidal rhythms is only a matter of definition. Our definition as to the day/night and tidal rhythm is as follows. The rhythmic patterns that are synchronized with day/night cycle (e.g., Fig. 3) alone in appearance could be called a day/night rhythm. On the other hand, the activity pattern that is correlated with the tidal cycle, even if they are weakly modified by the tidal cycle as shown in Figures 4 and 5, could be called a tidal rhythm.

Effectiveness of statistical treatments to assess the period of the rhythmic patterns

This study indicates a variety of emergence patterns of subtropical invertebrates ranging from synchrony with day/night cycle alone (Fig. 3) to clear synchrony with the tidal cycle (Fig. 6), and the lunar cycle (Fig. 7). The influence of the tidal cycle was assessed by the two statistical methods: autocorrelogram and periodogram. These methods, however, did not respond to the pattern very weakly modified by the tidal cycle. In *Propallene longiceps* (Fig. 4), the period the pattern was 24.0 hr on both methods. In addition, the period of the rhythm was often different between these methods, though slightly (e.g., see Fig. 7). The periodogram seems to respond more strongly to the day/night component of the pattern than the tide-correlated component (e.g., Fig. 6).

These statistical treatments are generally useful for biological rhythm research (Enright, 1965; Chiba and Takahashi, 1991). Application of these methods can effectively detect the presence of the period near 24.0 hr. However, it is very difficult to determine the period more exactly than this estimation, indicating that the period must be finally determined 'tentatively'. Hence, field investigations for a long time and visual inspection of each emergence pattern are essential to assess the period of the rhythmic patterns affected by both day/night and tidal cycles, especially for the patterns of many subtidal small invertebrates.

Nocturnal emergence in subtropical arthropods

A question is the formation of clear nocturnal patterns (Fig. 2A) in the subtropical invertebrates. One possible explanation is that all the invertebrates are strong swimmers and could easily avoid the suction pumps in the daytime. This pump is, however, powerful, often sucking in fishes and squids if the cage does not cover it. Thus, almost all invertebrates that swim near the pump should be sucked even in the daytime.

As indicated in Figures 3–7, very few specimens were collected in the daytime even by the pump placed near the bottom. It is reasonable to speculate that very few specimens swim in the water column in the daytime. Where are they seen in the daytime?

Several investigators have demonstrated that planktonic animals aggregate in the daytime. For example, the tropical copepod *Oithona oculata* swarms near the surface of the water in a continuous linear band (Hamner and Carleton, 1979). Swarming was also observed for *Labidocera pavo* at 0.5–1 m above the bottom with a disc shape of 10–20 cm in diameter (Ueda *et al*., 1983). A number of other temperate species are also known to aggregate, although the sites of swarming seem to be different depending on the species and time of day (Anraku, 1975; Ueda *et al*., 1983; Hirota, 1990).

In the opossum shrimp *Neomysis americana*, the normal habitat is on the bottom or immediately above it (Herman, 1963). Benthic animals inhabit the bottom substrate with a variety of life styles (e.g., Biernbaum, 1979; Fish and Mills, 1979). Some cling to the underside of stones, ropes, and seaweed (Brawley and Fei, 1987; unpublished our data).

We speculate that most subtropical invertebrates reported here swarm under or near the lower pump, or reside in the bottom substrate in the daytime; they would disperse in the water column at night. This would be responsible for the nocturnal emergence patterns. Difference of abundance between surface and bottom waters at night (Fig. 2B) shows that each species has a preferred layer in the water column for swimming or dispersing at night.

ACKNOWLEDGMENTS

Y. Katsube, A. Ikumoto, and H. Yamada helped us with daytime sampling. We thank the staff at the Tropical Biosphere Research Center (Iriomote Laboratory), of the University of Ryukyus for use of their facilities for this research. This work was supported by a Grant-in-Aid for Scientific Research (C)(2) to M. S. (No. 10836014: Natural History) from the Ministry of Education, Science, Sports and Culture, Japan, and by a Narishige Zoological Award to M. S. in 1997.

REFERENCES

Anraku M (1975) Microdistribution of marine copepods in a small inlet. Mar Biol 30: 79–87

Biernbaum CK (1979) Influence of sedimentary factors on the distribution of benthic amphipods of Fishers Island Sound, Conneticut. J Exp Mar Biol Ecol 38: 201–223

Brawley SH, Fei XG (1987) Studies of mesoherbivory in aquaria and in an unbarricaded mariculture farm on the Chinese coast. J Phycol 23: 614–623

Chiba Y, Takahashi K (eds) (1991) Chronobiology Handbook. Asakura-shoten, Tokyo (in Japanese).

Chihara M, Murano M (eds) (1997) An Illustrated Guide to Marine Plankton in Japan. Tokai University Press, Tokyo (in Japanese)

Edgar GJ (1983) The ecology of south-east Tasmanian phytal animal communities. I. Spatial organization on a local scale. J Exp Mar Biol Ecol 70: 129–157

Enright JT (1965) The search for rhythmicity in biological time-series. J Theor Biol 8: 426–468

Enright JT (1972) A virtuoso isopod. Circa-lunar rhythms and their tidal fine structure. J Comp Physiol 77: 141–162

Fish JD, Mills A (1979) The reproductive biology of *Corophium voltator* and *C. arenarium* (Crustacea: Amphipoda). J Mar Biol Ass UK 59: 355–368

Hamner WM, Carleton JH (1979) Copepod swarms: Attributes and role in coral reef ecosystems. Limnol Oceanogr 24: 1–14

Herman SS (1963) Vertical migration of the opossum shrimp, *Neomysis americana* Smith. Limnol Oceanogr 8: 228–238

Hirota R (1990) Microdistribution of the marine copepod *Oithona davisae* in the shallow waters of Ariake-kai mud flats, Japan. Mar Biol 105: 307–312

Lalli CM, Parsons TR (1993) Biological Oceanography: An Introduction. Butterworth-Heinemann Ltd, Oxford

Naylor, E (1958) Tidal and diurnal rhythms of locomotory activity in *Carcinus maenas* (L.). J Exp Biol 35: 602–610

Naylor E (1996) Crab clockwork: the case for interactive circatidal and circadian oscillators controlling rhythmic locomotor activity of *Carcinus maenas*. Chronobiol International 13: 153–161

Neumann D (1981) Tidal and lunar rhythms. In "Handbook of Behavioral Neurobiology. Vol. 4: Biological Rhythms" Ed by J Aschoff, Plenum Press, New York, pp 351–380

Neumann, D (1987) Tidal and lunar rhythmic adaptations of reproductive activities in invertebrate species. In "Comparative Physiology of Environmental Adaptation: Tide, Moon, Magnetic Field and Rhythmic Functions, Vol. 3", Ed by P. Pévet, S. Kager, Basel, pp 152–170

Nishimura S (ed) (1995) Guide to Seashore Animals of Japan with Color Pictures and Keys, Vol. II. Hoikusha, Tokyo (in Japanese)

Oishi K, Saigusa M (1999) Rhythmic patterns of abundance in small sublittoral crustaceans: variety in the synchrony with day/night and tidal cycles. Mar Biol 133: 237–247

Palmer JD (1995) The Biological Rhythms and Clocks of Intertidal Animals. Oxford University Press, New York

Palmer JD, Round FE (1967) Persistent, vertical-migration rhythms in benthic microflora. VI. The tidal and diurnal nature of the rhythm in the diatom *Hantzschia virgata*. Biol Bull 132: 44–55

Reid DG, Naylor E (1989) Are there separate circatidal and circadian clocks in the shore crab *Carcinus maenas*? Mar Ecol Prog Ser 52: 1–6

Saigusa M (1982) Larval release rhythm coinciding with solar day and tidal cycles in the terrestrial crab *Sesarma*. Biol Bull 162: 371–386

Saigusa M (1988) Entrainment of tidal and semilunar rhythms by artificial moonlight cycles. Biol Bull 174: 126–138

Saigusa M (1992) Phase shift of a tidal rhythm by light-dark cycles in the semi-terrestrial crab *Sesarma pictum*. Biol Bull 182: 257–264

Saigusa M (1997a) The circatidal clock of an estuarine semi-terrestrial crab, *Sesarma erythrodactylum*. Benthos Res 52: 21–33

Saigusa M (1997b) Hatching and its control by the circatidal clock in marine crustaceans. Proc Arthropod Embryol Soc Jpn 32: 1–23

Saigusa M, Akiyama T (1995) The tidal rhythm of emergence, and the seasonal variation of this synchrony, in an intertidal midge. Biol Bull 188: 166–178

Saigusa M, Kawagoye O (1997) Circatidal rhythm of an intertidal crab, *Hemigrapsus sanguineus*: synchrony with unequal tide height and involvement of a light-response mechanism. Mar Biol 129: 87–96

Ueda H, Kuwahara A, Tanaka M, Azeta M (1983) Underwater observations on copepod swarms in temperate and subtropical waters. Mar Ecol Prog Ser 11: 165–171

(Received April 6, 1999 / Accepted September 1, 1999)