Seasonal fluctuations of the sponge-dwelling gnathiid isopod *Elaphognathia* aff. *cornigera*

Yuzo Ota, Katsuhiko Tanaka and Euichi Hirose

Abstract. —While records of seasonal abundance patterns are available for gnathiids (Crustacea, Isopoda, Gnathiidae) in temperate zones and cold water populations, none exist for tropical and subtropical populations. We found the gnathiid isopod *Elaphognathia* aff. *cornigera* inhabiting sponges on a subtropical tidal flat in the Haneji Island Sea, Ryukyu Archipelago, southwestern Japan. To examine seasonal abundance patterns of this species, we conducted monthly sampling from December 2004 to November 2006 of the demosponge *Haliclona* sp. in which the gnathiids dwelled. All of the adult males, adult females in various reproductive phases, and larvae of *Elaphognathia* aff. *cornigera* were found throughout most of the year, suggesting that the species reproduces year-round. However, gnathiid density showed a remarkable seasonal pattern, with the maximum abundance occurring in spring and the minimum abundance in summer. These results were quite different from temperate species, in which female development and reproduction are restricted to warmer months and the highest densities are often recorded in the summer. Warm subtropical winters would likely not disturb gnathiid growth and reproduction, but extreme environmental conditions, including summer high water temperatures and typhoons, may affect gnathiid density.

Introduction

Gnathiids (Crustacea, Isopoda, Gnathiidae) have a biphasic life cycle with a parasitic larval phase and a nonfeeding adult phase (Hesse, 1864; Monod, 1926). Larval growth proceeds via several alternating periods of ectoparasitic feeding on host fish, followed by molting in the benthic habitat before individuals reach maturity. Finally, larval gnathiids metamorphose into nonfeeding adults with extremely different morphologies (Mouchet, 1928; Stoll, 1962; Wägele, 1988; Klitgaard, 1991; Tanaka & Aoki, 1998).

To date, seasonal abundance patterns have been studied for only five gnathiid species from temperate zones and cold water: *Paragnathia formica* in Europe (Stoll, 1962), *Caecognathia robusta* and *Caecognathia abyssorum* in the Northeast Atlantic deep sea (Klitgaard, 1991, 1997), and *Elaphognathia cornigera* and *Elaphognathia discolor* in Japan (Tanaka, 2003; Tanaka & Nishi, 2008). However, no seasonal abundance pattern studies have been conducted in shallow waters of subtropical or tropical zones. In recent years, gnathiids have been commonly recorded and studied as ectoparasites of elasmobranchs (McKiernan *et al.*, 2005) and teleosts (Cheney & Côté, 2003; Jones *et al.*, 2007) of coral reefs. Furthermore, as ectoparasites, gnathiids participate in cleaning interactions among tropical fishes (Grutter, 1995, 1999a, 1999b, 2003; Arnal & Côté, 2000; Grutter *et al.*, 2000; Sikkell *et al.*, 2006). Thus, obtaining information regarding seasonal abundance patterns from sub-

Fig. 1. Study site. A, Map of Okinawa-jima Island showing the study site; B, The tidal flat in the vicinity of Yagaji-jima Island; C, The sponge *Haliclona* sp. in which *Elaphognathia* aff. *cornigera* dwells. The height of *Haliclona* sp. (ca. 6×4 cm); D, *Elaphognathia* aff. *cornigera* in the sponge *Haliclona* sp. Total length of this specimen was about 2.5 mm.

tropical and tropical zones would be of great benefit to understand gnathiid biology, host-parasite and cleaning interactions.

We found a gnathiid species inhabiting sponges on a subtropical tidal flat in the Haneji Island Sea, Yagaji-jima Island, Ryukyu Archipelago, southwestern Japan ($26^{\circ}28'N$, $128^{\circ}0'E$). The gnathiid species is morphologically similar to *Elaphognathia cornigera* but a few differences exist between the two species. Thus, the present species is temporarily called *Elaphognathia*

aff. *cornigera*. *Elaphognathia cornigera* was originally described from Amakusa, Kyushu, southwestern Japan ($32^{\circ}33'N$, $130^{\circ}6'E$) (Nunomura, 1992) and its life cycle (Tanaka & Aoki, 1998) and population dynamics (Tanaka, 2003) were investigated in temperate waters (Izu Peninsula, southern Japan: $34^{\circ}40'N$, $138^{\circ}57'E$). In this paper, a seasonal abundance pattern in a subtropical population of *Elaphognathia* aff. *cornigera* is discussed based on the results of monthly sampling over two years to better understand

Fig. 2. Ventral view of adult females of *Elaphognathia* aff. *cornigera*. Adult females were classified into three reproductive phases (Ph. 1, embryos or eggs in the adult female; Ph. 2, embryos having prominent eyes in the breeding pouch; Ph. 3, an empty breeding pouch after larvae were released larvae). Scale bar = 1 mm.

the ecology of gnathiid isopods in the sub-tropics.

Materials and Methods

A tidal flat in the vicinity of Yagaji-jima Island (26°28'N, 128°0'E) was chosen as the collection site for materials (Fig. 1). The tidal flat is primarily composed of muddy sand littered with rocks. Several sponge species grow on the rocks at depths up to 50 cm during the lowest water levels of the spring tide. Surface seawater temperature was inferred from coastal observations at Sesoko Station, Tropical Biosphere Research Center, University of the Ryukyus (26°38'N, 127°51'E).

Elaphognathia aff. *cornigera* has been found from rocks and several sponge species. Among the sponge habitats of the present gnathiid, a reddish purple sponge, *Haliclona* sp., is conspicuous at the collec-

tion site. *Haliclona* sp. is distributed in infralittoral zone (0–50 cm depth below the water level at the spring low tide). The softness of the sponge also makes it suitable for dissection. Therefore, we collected *Haliclona* sp. monthly from December 2004 to November 2006 at the point of the lowest water level of the spring tide. During each sampling period, 5–12 sponge colonies were collected by hand, and each colony was put in a plastic bottle (500–1000 ml) filled with seawater. After the samples were taken back to the laboratory, each colony was dissected into smaller pieces with forceps to collect infaunal gnathiids. Latex gloves were worn during the dissection because the sponges are venomous. Dissected sponges and gnathiids were fixed in 70 % ethanol. The dissected sponges were dried at 80 °C for 48 h in a forced convection oven (FV-630, Advantec) and weighed with an electromagnetic weight-measuring scale (HF-400, A&D

Company).

Under a binocular stereomicroscope (SZX12, Olympus), the gnathiids from each sponge colony were classified as larvae, adult males, or adult females on the basis of morphological characteristics, and the adult females were further classified into three reproductive phases (phase 1, females with eggs or early-stage embryos lacking prominent eyes; phase 2, females with embryos having prominent eyes; phase 3, females that had released larvae from their ventral brood pouch) (Fig. 2). None of the adult females were found prior to oviposition.

Body lengths of adult males, adult females, and larvae were measured with an ocular micrometer. Larvae and adult females often rolled up during fixation, and thus body length was defined as the distance from the head to the tip of pleotelson without the mandibles for adult males, from the head to the tip of pereonite 6 for adult females, and from the head, without mandibles, to pereonite 6 for pre-feeding and post-feeding larvae. Deformed gnathiids, such as metamorphosing individuals, were not measured because their pereonites were deformed.

Spearman's rank correlation coefficient was used to assess the relationship between the numbers of *Elaphognathia* aff. *cornigera* and dry sponge colony weight (= size). Furthermore, to examine gnathiid distribution patterns, Morisita's Index I_{δ} , a measure of aggregation (Morisita, 1959), was calculated using the number of gnathiids in each sponge from each sampling, and the randomness of the distribution was tested by comparing the variance-mean ratio of the number of gnathiids in each sponge to F-values.

Results

The gnathiid species in this study

The gnathiids found in *Haliclona* sp. individuals were morphologically similar to *Elaphognathia cornigera* (Nunomura, 1992) as for whole proportions, cephalosomes, and

mouthparts. This species was originally found in the sponge *Haliclona permollis* and later rediscovered from the sponge *Halichondria okadai* (Nunomura, 1992; Tanaka & Aoki, 2000). However, a few differences exist between the present species and *E. cornigera*. The present species lives in sponges found on a muddy tidal flat, whereas *E. cornigera* inhabits sponges on rocky bottoms. We preliminarily compared detailed morphologies between the present species and *E. cornigera* collected in Shimoda (Izu Peninsula, Japan). In the present species, the adult male had nine plumose setae on pylopod, the adult female had 22 plumose setae on maxilliped, and the larva had 16 setae on lateral margin of pleotelson. In *E. cornigera*, the adult male had six plumose setae on pylopod, the adult female had 20 plumose setae on maxilliped, and the larva had 18 setae on lateral margin of pleotelson. Furthermore, in the present species, larval gnathopods had several notches, but such notches were absent in *E. cornigera*. However, we have also observed strong variations in the morphologies of the cephalosome and appendages within populations of the present species. Detailed examination will be necessary to clarify the taxonomic status of the present gnathiid and its relationship with *E. cornigera*. Therefore, the present species is called *Elaphognathia* aff. *cornigera* in this paper.

Distribution pattern of gnathiids among sponges

Haliclona sp. has always been found at the study site, and we examined 168 colonies in total. However, we could not obtain weight data for each sponge colony in June 2005 and in February and March 2006 because of technical errors. In July 2006, no sponges were collected because of stormy weather. During sampling in December 2004, eight sponge colonies were collected and deposited together in a bucket. The gnathiids in the sponges mixed within the bucket before sorting, and thus data from that month were not used in examining the

Table 1. The results of statistical analyses of the relationship between the sponge *Haliclona* sp. and *Elaphognathia* aff. *cornigera* and the number of gnathiids in each month. Morisita's index is also shown in the left column.

Year	Month	Morisita's Index I_{δ}	Spearman's rank correlation coefficient		Total N. of sponge	% of sponge inhabited by gnathiids	Total N. of gnathiid
			rs	P *			
2004	Dec	–	–	–	8	No data	71
2005	Jan	5.54	0.2	0.35	5	80	77
	Feb	1.4	-0.3	0.8	5	100	56
	Mar	1.76	0.7	0.25	5	100	141
	Apr	1.29	0.4	0.07	5	100	128
	May	2.17	-0.38	0.82	5	60	80
	Jun**	2.6	–	–	5	100	55
	Jul	2.55	0	0.56	5	80	39
	Aug	1.78	-0.81	0.95	6	83	80
	Sep	3.61	0.75	0.03	7	43	27
	Oct	3.09	0.71	0.08	6	33	22
	Nov	3.58	0.6	0.02	9	44	39
	Dec	4.48	-0.05	0.6	11	55	80
2006	Jan	2.82	0.1	0.63	10	50	100
	Feb**	2.12	–	–	9	77	116
	Mar**	2.57	–	–	8	75	199
	Apr	1.79	0.21	0.46	8	88	174
	May	7.03	0.58	0.44	12	58	96
	Jun	3.91	0.21	0.56	8	38	10
	Jul	–	–	–	No data	No data	No data
	Aug	–	–	–	8	0	0
	Sep	4.31	-0.43	0.82	6	33	13
	Oct	3.15	0.27	0.45	8	38	22
	Nov	2.86	-0.14	0.78	9	56	31
Total					168 (160)***		1656

* Significant correlation ($P<0.05$) in bold.
** Spearman's test could not be applied, because weight data of each sponge colony were not available.
*** Total number of sponge excluding the data in Dec. 2004 is in parenthesis.

relationship between the number of gnathiids and sponge dry weight.

Elaphognathia aff. *cornigera* was found in *Haliclona* sp. during every sampling period except August 2006. Gnathiids were present in 96 of 160 sponge colonies collected from January 2005 to November 2006 (Table 1), excluding specimens from December 2004, and the total number of gnathiids found during the study was 1656, including specimens

from December 2004. One adult male was often found with one female and one premature larva in sponge oscula.

Correlation analysis found no statistically significant relationship between the number of gnathiids and sponge dry weight during most months (Table 1). Morisita's indices were larger than 1 in every month (Table 1), suggesting that the present gnathiid species tends to aggregate in a particular sponge

colony. Furthermore, the variance-mean ratio significantly supports the aggregate distribution in every month ($P < 0.05$).

Seasonal fluctuations

Adult males, adult females, and post-feeding larvae of *Elaphognathia* aff. *cornigera* were found in *Haliclona* sp. throughout the year at the study site (Fig. 3A–C) and pre-feeding larvae were found from January to May 2006 (Fig. 4C). The proportion of sponges that contained gnathiids tended to increase from winter to spring and decrease in the summer (Table 1).

Because the number of gnathiids was not related to sponge dry weight, the relationship was not used as an index of gnathiid abundance. Instead, the number of gnathiids per sponge colony was applied to assess seasonal changes in population abundance (Fig. 3A–C). The abundance of gnathiids was low at the beginning of the investigation (December 2004). Then, the abundances of both larval and adult gnathiids increased after January/February 2005 (Fig. 3A–C). The abundance of gnathiids tended to be low in a warm period and high in a cold period (Fig. 3). Larval abundance peaked in March 2005 (Fig. 3C) and the abundances of both adult males and females increased until April 2005 (Fig. 3A, B). The numbers of both larvae and adults then declined. Although a small peak was observed in August 2005, gnathiids were relatively scarce until November 2005. The seasonal population changes observed in the second year were comparable to the results from the first year.

Male gnathiids outnumbered females in most months (Fig. 3A, B). The male ratio (no. of males / no. of both adults $\times$ 100) ranged from 46.5 to 89.8 %, increasing from February to March, decreasing during June and July, increasing again around September and October, and diminishing by January (Fig. 3A). Three female reproductive phases were observed almost year-round (Fig. 3B).

Body lengths were not measured for 109 gnathiids because of deformations. Adult

males had body sizes (from the head to the tip of the pleotelson without the mandibles) ranging from 1.27 to 2.67 mm (mean $\pm$ SD, 2.03 ± 0.22 ; $N = 665$) and adult females (from the head to the tip of pereonite 6) were between 1.25 and 2.31 mm (mean $\pm$ SD, 1.77 ± 0.14 ; $N = 405$). Monthly average body lengths for both sexes tended to increase from fall to winter and decrease from spring to early summer (Fig. 4A, B).

Body size for larvae (from the head without the mandible to pereonite 6) ranged from 0.36 to 1.60 mm ($N = 477$). Average body sizes were not shown for larvae because the samples likely included several developmental stages. For example, two size-groups are separated by a broken line in Fig. 4C. Among the larvae measured, 34 individuals were pre-feeding larvae (shown as gray ellipses in Fig. 4C) while the others were post-feeding larvae. Pre-feeding larvae were found from January to May 2006 but not observed in other months. They were small in size (< 1 mm), except for one individual found in March 2006, and were distributed below the broken line in Fig. 4C. However, most of the larger larvae were post-feeding and as large as adults.

Discussion

The use of Haliclona sp. by Elaphognathia aff. cornigera

Gnathiid species are generally found in, for example, sponges, rocks and dead coral crevices, tubes of terrellid polychaetes, and mud burrows (Tanaka, 2007), but habitat use has been discussed for only a few gnathiids. In the Antarctic species *Caecognathia calva*, premature larvae and adults mainly dwell in hexactinellid sponges, but young larval stages are less frequent there and some adults and young larvae also occur in sediments (Wägele, 1988). *Elaphognathia cornigera* in Izu Peninsula, southern Japan, dwell in some sponge species (Nunomura, 1992; Tanaka & Aoki, 1998). In this species, individuals of all life stages were found abundantly in the sponge

Fig. 3. Seasonal changes of the densities of adult males (A), adult females (B), and larvae (C) of *Elaphognathia* aff. *cornigera* and water temperature (D). A and B also showed seasonal changes in the male ratio (no. of males / no. of both adults $\times$ 100) of adult gnathiids, and the number of adult females at each reproductive phase, respectively. The asterisk in January 2005 indicates broken specimens and unknown phases. In July 2006, sponge colonies could not be collected because of stormy weather.

Fig. 4. The size distributions of adult males, adult females, and larvae of *Elaphognathia* aff. *cornigera* during each month. Body sizes are defined as the length from the head to the tip of the pleotelson without the mandibles for adult males, from the head to the tip of pereonite 6 for adult females, and from the head without mandibles to pereonite 6 for larvae. Lines indicate the average sizes for adult males and adult females. Average lengths are not shown for larvae because the samples likely included multiple developmental stages. The broken line indicates a gap in the larval sizes and gray ellipses indicate pre-feeding larvae. In June 2006, sponge colonies could not be collected because of stormy weather. In July 2006, sponge colonies could be collected but no gnathiids were found.

Halichondria okadai although larvae showed different vertical distributions from those of adults (Tanaka & Aoki, 1999). Thus, this gnathiid species was thought to utilize the sponge throughout its life cycle (Tanaka & Aoki, 1998).

In the present study, most larval *Elaphognathia* aff. *cornigera* were of similar size to adults, suggesting that most of the larvae in *Haliclona* sp. were premature individuals. In contrast, small larvae were relatively scarce in our surveys. Thus, we hypothesize that *Haliclona* sp. is mainly used by *Elaphognathia* aff. *cornigera* during metamorphosis and reproduction, and young larvae use other habitats such as rock crevice and muddy substrata. In the present study, however, we did not collect young larvae from the habitats other than *Haliclona* sp. because we could not make specific identification of the young larvae that might include other gnathiid species. This type of habitat utilization may be similar to the Antarctic *C. calva*, and different from *E. cornigera*, a congener of the present gnathiid, which utilizes demosponges throughout its life cycle. Note that *Haliclona* sp. colonies were not the only habitat available for gnathiid reproduction because adults were occasionally collected from other sponge species and rock crevices.

During most months, *Elaphognathia* aff. *cornigera* tended to aggregate in particular sponge colonies. Factors influencing benthic distribution patterns of gnathiids are not fully understood but chemical communication among individuals has been reported. Upton (1987b) observed that all larval stages of *Paragnathia formica* were attracted to mud containing adult males. The presence of benthic conspecific individuals was hypothesized to indicate suitable benthic settlement sites, where post-settlement mortality due to anoxic mud was low for post-feeding larvae, which would have previously been on host fishes (Upton 1987b). Although further investigation is needed to confirm this conclusion, the detection of chemicals released from congeners might

cause an aggregated distribution of *Elaphognathia* aff. *cornigera* and improve settlement success and encounter rates.

Seasonal fluctuations of Elaphognathia aff. cornigera

Differences in occurrence patterns between sexes by season have been recorded for a few temperate gnathiid species. In the Afro-European species *P. formica*, adult females are absent and only adult males and larvae remain during colder months (Upton, 1987a). The absence of adult females in the winter has also been recorded for the population of *E. cornigera* in the Izu Peninsula (southern Japan) (Tanaka & Aoki, 2000; Tanaka, 2003). In these gnathiid species, larval growth is thought to halt during cold conditions and development from larvae to adults stops from autumn onward. Semelparous females die after this developmental pause, and only larvae and adult males with greater longevity than females survive during colder months (Upton, 1987a; Tanaka & Aoki, 2000; Tanaka, 2003).

In contrast to females of *P. formica* and *E. cornigera*, which have limited reproductive periods (Upton, 1987a; Tanaka & Aoki, 2000), adult females of *Elaphognathia* aff. *cornigera* were collected almost year-round in the present study. Furthermore, three reproductive phases were observed for adult females in most months, while sex ratios showed some fluctuations. This suggests that the present species continued to reproduce during the winter, as well as during the warmer months. The larval growth of *P. formica* was suggested to cease below 4 °C in the laboratory (Stoll, 1962) and almost no adult females of *E. cornigera* emerged when water temperatures were below 18 °C (Tanaka & Aoki, 2000; Tanaka, 2003). However, water temperatures in our subtropical sampling area were always above 20 °C. In the present species, the warm environmental conditions may not prevent larval growth during the winter and likely contributes to the continuous occurrence of adult females throughout the year.

Seasonal changes in the abundance of *Elaphognathia* aff. *cornigera* are also different from those of *P. formica* or *E. cornigera*. In the two temperate species, population density decreases during the winter because no reproduction occurs (Upton, 1987a; Tanaka & Aoki, 2000). In our study, the maximum density of *Elaphognathia* aff. *cornigera* in the sponge *Haliclona* sp. was reached during the winter or spring, while minimum densities occurred in the fall of 2005 and the summer of 2006. Low overall densities during warmer months do not appear to be attributable to seasonality in reproductive activity because ovigerous females were found throughout the year. Similar drastic changes in population density with continuous reproduction in females have been observed in other organisms in warm waters. In the gammarid *Eripisa chilensis* from an estuarine in the southwest coast of India, population density decreased to 0 in February, although breeding occurred almost year-round (Aravind *et al.*, 2007). In an undescribed sponge-dwelling amphipod species, occasionally referred to as *Leucothoe* "spongicola," in the Indian River Lagoon of east-central Florida, juveniles and subadults were only abundant in May even though ovigerous females were observed throughout the year (Thiel, 2000). Aravind *et al.* (2007) thought that a decrease in *E. chilensis* density was associated with environmental conditions such as high salinity and/or high organic matter. Thiel (2000) suggested that the exposure of sponges for long periods during warmer months occurs when water levels are low and *L. "spongicola"* may change habitats in response to severe water loss.

In the tidal flat where the present investigation was conducted, sudden increases or decreases in salinity, extreme high temperature, and eventual exposure of sponges can occur during warmer months (pers. obs.). Such severe environmental conditions provide possible explanations for the low density of *Elaphognathia* aff. *cornigera* during warmer months. Furthermore, from sum-

mer to fall, our study site is characterized by stormy weather, including typhoons. When struck by typhoons, sponges inhabited by gnathiids may be washed out from shallow tidal flats. Rapid water movements may also prevent gnathiids from seeking and settling on favorable habitats. More information is needed on the physical factors affecting the abundance of *Elaphognathia* aff. *cornigera*. Furthermore, the habitats for young larval stages should be disclosed in future studies.

The present species *Elaphognathia* aff. *cornigera* exhibits differences in habitat use and seasonal emergence patterns from the congener *E. cornigera*. Although the taxonomic status of the present gnathiid requires further study, ecological characteristics suggest that *Elaphognathia* aff. *cornigera* is a distinct species. Spatiotemporal distributions of this gnathiid species may be due to as responses to environmental conditions, including physical and biological factors such as the availability of suitable habitats. Further understanding of the ecological plasticity to different environmental conditions exhibited by these animals, as well as intensive taxonomical efforts, are, however, needed to confirm these points.

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Addresses: (YO and EH) University of the Ryukyus, Senbaru, Nishihara, Okinawa, 903-0213, Japan; (KT) Central Research Institute of Electric Power Industry, Gasonji, Chiba 270-1194, Japan
E-mail: (YO) yuzomushi@yahoo.co.jp