Descriptions of caligiform copepods in plankton samples collected from East Asia: Accidental occurrences or a new mode of life cycle?

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Abstract: Parasitic copepods usually have one or more free-swimming larval/juvenile stages for dispersal or infection. However, the present study has revealed that adults and chalimus stages of caligiform copepods have often been discovered in plankton samples collected from East Asia. This is the first report on free-swimming adults of caligiform copepods from Japanese and Korean waters. Adults of the following species have been discovered in this study. In Japanese waters: *Caligus coryphaenae* (4♂♀), *Caligus* sp. (1♂), *Pandarus* sp. (4♂♀, 16 chalimi) off Nansei Islands in May 2003 and 2006; *C. sclerotinosus* (1♀) near a fish farm, Ehime Prefecture in December 2006; *C. undulatus* (1♂) off Ube, the Seto Inland Sea in July 2006; and *C. undulatus* (1♂) in the Ariake Sea in June 2007. In Korean waters: *C. orientalis* (1♀, 1♂) from brackish waters of the Mankyong River and *C. undulatus* (1♂) from the Seomjin River in October 2006. It is interesting to point out that *C. undulatus* has never been recorded as a parasite infecting any host, but has been collected from plankton samples in East Asia, India and Brazil. It is also noteworthy to mention that males (80%) were found more frequently than females (20%) in this study. We considered the following possibilities for the occurrences of caligiform adults originally infecting fish: (1) escaping from irritation or diseases in the host, (2) looking for an opportunity to switch hosts, (3) change in their life mode, and (4) accidental detachment. In the case of chalimi, it could be accidental, because they would be tightly attached to the host using a special organ called the “frontal filament”, and cannot grow up to the adult stage without nutrient supply from the host.

Key words: Caligidae, caligiform, fish parasite, Pandaridae, plankton

Introduction

The caligiform copepods (Caligidae and its allies) are well known and economically important parasites in aquaculture (Boxshall & Defaye 1993). Hence much attention has been paid to their parasitic mode of life, though their planktonic stages have not been sufficiently characterized. The distribution of their free-swimming naupliar and copepodid stages have been reported only in the Atlantic (Costello et al. 1998, Penston et al. 2004, Copley et al. 2005, Todd 2007). Most of these caligiform copepods have been directly collected from their hosts as parasites, however it is not uncommon to find caligiforms in plankton samples (Kabata 1979). Ho & Lin (2004a) reported 14 species of the siphonostomatoid family Caligidae as planktonic forms from all over the world. In the present study, most of the caligiform adults collected from plankton samples can be assigned to the Caligidae. It is the most speciose family parasitic on fish, comprising over 465 species in 33 genera (Boxshall & Halsey 2004).

The developmental stages of caligiform copepods have been described for some species (Johnson & Albright 1991, Schram 1993, Lin et al. 1996, Ho & Lin 2004b): after hatching from paired egg-strings, they spend a planktonic period consisting of 2 free-living naupliar stages, and 1 infective copepodid stage; after settlement, the copepodid moults into the chalimus phase which is comprised of 4–6 stages characterized by permanent attachment to the host with a frontal filament; in the subsequent preadults either none (*Caligus*) or 2 stages (*Lepeophtheirus*) are recognized, though there is still debate over whether or not molting occurs during this phase (cf. Ho & Lin 2004b, Boxshall & Halsey 2004); finally the adult stage is involved in reproduction, usually moving around the host freely.

Apart from the family Caligidae, adults and chalimus
stages of planktonic copepods belonging to the siphonostomatoid family Pandaridae were also collected from plankton samples in the present study. The Pandaridae consists of 14 valid genera (Dippenaar & Jordan 2006). Their hosts and infection-sites are specific, being found attached mainly on the body surfaces or gill arches of elasmobranch fishes (Benz 1992, Benz et al. 2003), however this is the first record of occurrences in the plankton. The present study describes caligids and pandarids discovered from plankton samples in East Asia, with a consideration of their ecological and adaptive meanings.

Materials and Methods

Plankton samples were collected from 12 stations in brackish, coastal and oceanic waters in Japan and Korea using plankton nets (Fig. 1, Table 1). Collections along the Nansei Islands, southern Japan were carried out by surface towing using an ORI net (diameter 1.6 m; mesh size 0.33 mm) for 10–20 min with the TR/V Toyoshio-maru, Hiroshima University, at 7 stations in 2003 and 2006. Samples from Yamaguchi, Ehime and Saga Prefectures, Japan, and near the mouths of the Mankyong and Seomjin Rivers, Korea, were collected by small plankton nets (diameter 30 or 45 cm; mesh size 0.1 mm or 0.3 mm). After collection, samples were fixed in 10% neutralized formalin seawater. Caligid and pandarid specimens were sorted out from the pool of samples and then preserved in 70% ethanol. Later, specimens were cleared in lactophenol for 1–2 h and observed through a differential interference contrast microscope at magnifications up to 1000X (Olympus BX50) for the identification. All drawings were made with the aid of a camera lucida. Some specimens were dissected to examine the details of the appendages. Mean body measurements are given in millimeters, followed by the range in parentheses. Terminology follows Ho & Lin (2004b).

Specimens are deposited at the Kitakyushu Museum of Natural History & Human History, Japan (KMNH IvR).

Results

In total, 11 individuals (3 ♀♀ and 8 ♂♂) of the genus Caligus (Caligidae) and 20 individuals (4 ♀♀ and 16 chal-imi) of the genus Pandarus (Pandaridae) were collected during the plankton surveys.

Family Caligidae Burmeister, 1835

Caligus coryphaenae (Steenstrup & Lütken, 1861) (Fig. 2A–F)

Material examined. Two ♂♂ (KMNH IvR 500,253, 500,254) collected from Stn 11 off the Nansei Islands, Japan on May 24, 2003; 2 ♀♀ (KMNH IvR 500,255, 500,256) from Stn 4 off the Nansei Islands, Japan on May

Fig. 1. Collection sites of planktonic caligiforms off Japan and Korea shown in enlarged box below. Enlarged box on right side shows seven stations off Nansei Islands, Japan. 1. Ube, 2. Uwajima, 3. Ariake Sea, 4. Seomjin River, 5. Mankyong River
Description. Male. Body (Fig. 2A) 5.54 mm long (5.52–5.56, n=4) excluding caudal setae. Cephalothorax subcircular 3.26 (3.22–3.30)×2.92 (2.88–2.96) mm in size. Fourth pediger wider than long, 0.30 (0.29–0.31)×0.68 (0.64–0.72) mm. Genital complex slightly rectangular, 0.61 (0.58–0.64)×0.74 (0.71–0.77) mm. Abdomen 2-segmented with anal somite larger than preceding somite. Caudal ramus longer than wide with 3 long and 3 short setae.

Antenna (Fig. 2B) 3-segmented; proximal segment small, unarmored; middle segment subrectangular, unarmored; distal segment sharply pointed with abruptly bent claw bearing secondary tine midway. Postantennal process absent. Maxillule (Fig. 2B) with broad base. Maxilliped (Fig. 2C) indistinctly 3-segmented; proximal segment robust but unarmored; middle segment and distal segment fused to form robust subchela, sharp claw, armed with short barbel at base. Sternal furca (Fig. 2D) with divergent tines; having 2 knobs nearby, both laterally.

Armature on rami of legs 1–4 as follows: (Roman and Arabic numerals indicating spines and setae, respectively).

Exopod Endopod

<table>
<thead>
<tr>
<th>Leg</th>
<th>Exopod</th>
<th>Endopod</th>
</tr>
</thead>
<tbody>
<tr>
<td>Leg 1</td>
<td>1-0; III, 1, 3</td>
<td>(vestigial)</td>
</tr>
<tr>
<td>Leg 2</td>
<td>1-1; 1-1; II, 1, 5</td>
<td>0–1; 0–2; 6</td>
</tr>
<tr>
<td>Leg 3</td>
<td>1-0; 1-1; III, 4</td>
<td>0–1; 6</td>
</tr>
<tr>
<td>Leg 4</td>
<td>1-0; 1-0; III</td>
<td>(absent)</td>
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Leg 4 (Fig. 2E) with 3-segmented exopod; proximal exopodal segment bearing 3 setules; all outer spines of exopod with pecten at base. Leg 5 (Fig. 2F) represented by 1 long, 1 medium and 2 short setae located on posterolateral corner of genital complex. Leg 6 (Fig. 2F) represented by 1 long and 2 short setae located mediad to leg 5.

Remarks. This is a common parasite on the oceanic dolphinfish Coryphaena hippurus (Linnaeus) all around the world, and has frequently been reported in plankton samples in many different parts of the world (cf. Table 2). Both adult males and “juvenile” (=young) females were collected from plankton samples in previous studies from different localities such as Africa, the Falkland Islands, in the Pacific and around the world (Heegard 1972, Ho & Lin 2004a). However, in the present collection 4 males of this species were found twice, in 2003 (Stn 11) and 2006 (Stn 4). This species differs from most of its congeners by the absence of a postantennal spine (Fig. 2B) and by the presence of accessory sclerotized processes lateral to the sternal furca (Fig. 2D). Recently, Caligus inanis Ho & Lin, 2007 was found from Taiwan with characteristics similar to those of C. coryphaeneae, but it differs in the presence of a tooth-like projection on the cephalothoracic shield in the latter species (Ho & Lin 2007).

Table 1. All plankton sampling stations off Japan and Korea.

<table>
<thead>
<tr>
<th>Stations</th>
<th>Lat. &amp; Long.</th>
<th>Time &amp; Date</th>
<th>Depth at station (m)</th>
<th>Gear</th>
</tr>
</thead>
<tbody>
<tr>
<td>Japan Nansei Islands</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Stn 6</td>
<td>27°49, 50°N, 128°40.00'E</td>
<td>1015–1200, May 22, 2003</td>
<td>80–77</td>
<td>ORI net (φ 1.6 m; mesh size 0.33 mm)</td>
</tr>
<tr>
<td>Stn 10</td>
<td>26°49, 50°N, 127°42.00'E</td>
<td>0910–1003, May 24, 2003</td>
<td>494–391</td>
<td>Small conical net (φ 30 cm; mesh size 0.33 mm)</td>
</tr>
<tr>
<td>Stn 11</td>
<td>26°19, 18°N, 127°25.56'E</td>
<td>1220–1325, May 24, 2003</td>
<td>606–596</td>
<td>Small conical net (φ 45 cm; mesh size 0.1 mm)</td>
</tr>
<tr>
<td>Stn 13</td>
<td>26°33. 00’N, 127°32. 30’E</td>
<td>1525–1608, May 25, 2003</td>
<td>237–223</td>
<td>Small conical net (φ 30 cm; mesh size 0.1 mm)</td>
</tr>
<tr>
<td>Stn 4</td>
<td>30°14. 73’N, 130°44. 25’E</td>
<td>0912–0923, May 24, 2006</td>
<td>83–70</td>
<td></td>
</tr>
<tr>
<td>Stn 9</td>
<td>26°49, 51°N, 127°51. 87’E</td>
<td>1600–1640, May 27, 2006</td>
<td>329–322</td>
<td></td>
</tr>
<tr>
<td>Stn 11</td>
<td>30°53. 75’N, 131°02. 58’E</td>
<td>0812–0846, May 29, 2006</td>
<td>160–138</td>
<td></td>
</tr>
<tr>
<td>Ube City, Yamaguchi</td>
<td>33°54’N, 131°14’E</td>
<td>Daytime, July 2, 2006</td>
<td>Shallow</td>
<td></td>
</tr>
<tr>
<td>Uwajima City, Ehime</td>
<td>33°13’N, 132°34’E</td>
<td>Daytime, Dec. 11, 2006</td>
<td>Shallow</td>
<td></td>
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<tr>
<td>Ariake Sea, Saga</td>
<td>33°25’N, 129°67’E</td>
<td>0800, June 15, 2007</td>
<td>Shallow</td>
<td></td>
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<tr>
<td>Korea</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Seomjin River</td>
<td>34°03’42. 00’N, 127°44’24. 9’E</td>
<td>Daytime, Oct. 26, 2006</td>
<td>Shallow</td>
<td></td>
</tr>
<tr>
<td>Mankyong River</td>
<td>35°52’55. 8’N, 126°45’04. 8’E</td>
<td>Daytime, Oct. 28, 2006</td>
<td>Shallow</td>
<td></td>
</tr>
</tbody>
</table>
Leg 4 (Fig. 2J) with 2-segmented exopod; proximal segment carrying spine on outer distal corner; distal segment bearing 3 slender spines, outer terminal spine two times longer than next 2 spines; digitiform structure present at base of terminal spine. Leg 5 (Fig. 2K) represented by 2 papillae, one with pinnate seta, another with 1 long and 1 short setae.

**Male.** Body (Fig. 2L) length 3.07 mm long excluding caudal setae. Cephalothoracic shield subcircular 1.91× 1.64 mm. Fourth pediger wider than long. Genital complex

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**Fig. 2.** *Caligus coryphaenae* (Steenstrup & Lütken, 1861), male (A–F); A. Habitus, B. Antenna and maxillule, C. Maxilliped, D. Sternal furca with 2 knobs, E. Leg 4, F. Legs 5 and 6. *Caligus orientalis* Gussev, 1951, female (G–K); G. Habitus, H. Caudal ramus, I. Maxilliped, J. Leg 4, K. Leg 5; *Caligus orientalis* Gussev, 1951, male (L–M); L. Habitus, M. Genital complex. Scale bars: A, L = 1 mm; B–F, H–K = 0.1 mm; G = 0.5 mm; M = 0.2 mm.
(Fig. 2M) 0.52×0.59 mm with serrated lateral margins, with sharp posterolateral projection of leg 5. Abdomen small, 0.26×0.29 mm, 2-segmented with large anal somite. Caudal ramus wider than long, with 3 short and 3 long setae.

Antenna (Fig. 3A) 3-segmented; proximal segment slender, with long, corrugated patches; middle segment largest, armed with adhesion pads; terminal segment smallest, with 2 medial setae and 5 overlapping pointed cuticular flaps at tip. Post antennal process (Fig. 3A) longer, pointed at tip carrying 2 papillae each with 4 setules, another similar papilla located nearby sternum. Maxillule (Fig. 3A) bearing corrugated pad midway. Maxilliped (Fig. 3B) indistinctly 3-segmented; proximal segment stout, robust with 3 prominent knobs at midlength; distal segment bearing claw, sharp, bent towards knobs, carrying subterminal small seta and long barbel at base. Leg 5 (Fig. 3C) represented by sharp projection on genital complex with 3 pinnate setae, 1 on posterolateral side and 2 on posterior corner. Leg 6 (Fig. 3C) represented by 1 small and 1 minute setae on posterior ventral surface of genital complex.

Remarks. This species is closely related to Caligus punctatus Shinjo, 1955 in all characteristic features. However, the male of C. punctatus (see Fig.138 in Ho & Lin 2004b) differs in its lacking of serrated lateral margins on the genital complex in contrast to C. orientalis (Fig. 2M). Another main difference between the two species is the presence of a medial digital (tooth-like) process on the exopod of female leg 4 in C. orientalis (Ho & Lin 2004b).

This is a common parasite in Asia, severely infecting fish in aquaculture farms in both fresh (Suzumoto 1974, Matumoto 1980) and sea waters (Hwa 1965, Urawa et al. 1979, Urawa & Kato 1991, Kim 1998, Ho & Lin 2004b), sometimes causing mass mortality of cultured fish (Nagasawa 2004). Caligus orientalis has been considered as a serious pest in Korea, appearing as a parasite of cultured mullets (Kim 1998).

This is the first report of the occurrence of C. orientalis from plankton samples in Korea. Even worldwide this is only the second record of its occurrence in the plankton (Table 2), since the first report from the estuary of the Yellow River in China (Shen 1957). These present specimens (1♀, 1♂) were collected from the surface water, in which temperature and salinity were recorded at 18.7°C and 29.2 psu, respectively, near the surface of the Mankyong River, Korea.

Caligus sclerotinosus Roubal, Armitage & Rhode, 1983 (Fig. 3D–I)

Material examined. One ♀ (KMNH IvR 500,259) collected from near a fish farm in Uwajima, Ehime Prefecture, Japan on December 11, 2006 (I Madinabeitia pers comm).

Description. Female. Body (Fig. 3D) 2.41 mm long excluding caudal setae. Cephalothoracic shield subcircular 1.68×1.64 mm, slightly wider than long. Fourth pediger wider than long. Genital complex 0.42×0.79 mm, wider than long with broadly protruded posterolateral corners carrying seta bearing process on leg 5. Abdomen (Fig. 3E) small, 0.29×0.36 mm, wider than long. Caudal ramus (Fig. 3E) armed with 2 long and 4 very short setae of irregular lengths. Maxilliped (Fig. 3F) indistinctly 3-segmented; proximal segment long and narrow with bump at lower region; middle segment small, partly fused with long and thin distal segment to form subchela, small, pointed claw armed with short barbel at base. Sternal furca (Fig. 3G) short, with broad tines.

Armature on rami of legs 1–4 as in C. orientalis. Leg 5 (Fig. 3H) represented by 2 papillae at blunt posterior corner carrying 1 and 2 setae respectively.

Remarks. In Japan, infections by C. sclerotinosus are becoming increasingly intensive as it becomes a notorious parasite at fish farms with the red sea bream Pagrus major (Temminck & Schlegel), but it has so far not been recorded from the same wild fish host anywhere (I Madinabeitia pers comm). Caligus sclerotinosus was first reported from the sparid host Chrysophrys auratus (Forster) in Australia (Roulal et al. 1983); after that it was recorded in fish farms raising P. major in Oita Prefecture, Japan (Ho et al. 2004) and recently in fish farms in Ehime Prefecture, Japan (I Madinabeitia pers comm).

Recently, C. sclerotinosus was identified as a parasite at fish farms in Mie Prefecture, Japan (K Ogawa pers comm). The present specimen was collected for the first time from plankton samples (surface water) nearby the aquafarm where water temperature and salinity were measured at 19.6°C and 34.3 psu, respectively. It might have escaped from a fish host due to overcrowding or irritation, since the maximum prevalence reached up to 35 per fish in the fish farms of Uwajima, Ehime (I Madinabeitia pers comm).

Caligus undulatus Shen & Li, 1959 (Figs. 3I–O, 4A–M)

Material examined. One ♀ (KMNH IvR 500,260) with broken egg sacs collected from off Ube City, Yamaguchi Prefecture, Japan on July 2, 2006 (R Yoshizaki pers comm); 1♂ (KMNH IvR 500,261) in the Ariake Sea, Saga Prefecture, Japan on June 15, 2007; 1♂ (KMNH IvR 500,262) near the mouth of the Seomjin River, Korea on October 26, 2006.

Description. Female. Body (Fig. 3I) 4.25 mm long excluding caudal setae. Cephalothoracic shield longer than wide, slightly ovoid, 2.01×1.49 mm. Fourth pediger 0.26×0.38 mm, wider than long. Genital complex, longer than wide, 1.20×0.89 mm with ridges. Abdomen long, 0.74×0.32 mm. Caudal ramus longer than wide carrying 0.77 mm long setae. Egg-sac partly broken, containing 3 eggs on each side.

Antennule (Fig. 3J) 2-segmented; stout, proximal segment with 27 setae; distal segment longer than proximal, with subterminal seta on posterior margin and 11 setae plus 2 aesthetasc on distal margin. Antenna (Fig. 3K) 3-seg-
mented; proximal segment rounded, unarmed; middle segment broad, unarmed; distal segment with acutely pointed claw carrying 2 setae, one at midlength and another proximal. Postantennal process (Fig. 3K) long and narrow, slightly curved, carrying 2 basal papillae each with 2 setules; another similar papilla located nearby sternum. Maxillule (Fig. 3K) long, and pointed at base. Mandible (Fig. 3L) comprised of 2 sections; with 12 teeth on medial margin of distal blade. Maxilla (Fig. 3M) 2-segmented; proximal segment large and unarmed; distal segment slender with small subterminal hyaline membrane on outer edge and 2 unequal elements at terminal end. Maxilliped (Fig. 3N) indistinctly 3-segmented; proximal segment stout and unarmed with small swelling at midlength; distal segment with sharp, robust claw carrying barbel at base. Sternal furca (Fig. 3O) with long tines bearing membrane on lateral sides (broken at right tip).

Armature on rami of legs 1–4 as follows:

Fig. 3. Caligus orientalis Gussev, 1951, male (A–C); A. Antenna, postantennal process and maxillule, B. Maxilliped; C. Legs 5 and 6. Caligus sclerotinosus Roubal, Armitage & Rhode, 1983, female (D–H); D. Habitus, E. Abdomen and caudal ramus, F. Maxilliped, G. Sternal furca, H. Leg 5. Caligus undulatus Shen & Li, 1959, female (I–O); I. Habitus, J. Antennule, K. Antenna, postantennal process and maxillule, L. Mandible, M. Maxilla, N. Maxilliped, O. Sternal furca. Scale bars: A–C, E–H, J–O=0.1 mm; D=0.5 mm; I=0.8 mm.
Exopod | Endopod
---|---
Leg 1 | I-0; III, 1, 3 (vestigial)
Leg 2 | I-1; I-1; II, 5
Leg 3 | I-0; I-1; III, 4
Leg 4 | I-0; I, III (absent)

Leg 1 (Fig. 4A) bearing bulbous, vestigial endopod; distal exopodal segment with 3 long plumose setae. Leg 2 (Fig. 4B) with large spine, pointed on distal exopodal segment; small spine (one third length of preceding spine on distal segment) on middle segment; 1 small and 1 long spine on proximal segment. Leg 3 (Fig. 4C) as in *C. orientalis*. Leg 4 (Fig. 4D) with 2-segmented exopod; all outer spines on both segments of exopod with pecten at base. Leg 5 (Fig. 4E) represented by 2 pinnate setae on posteroventral part of genital complex.

**Male.** Body (Fig. 4F) 3.50, 3.52 mm long excluding caudal setae. Cephalothoracic shield longer than wide, slightly

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**Fig. 4.** *Caligus undulatus* Shen & Li, 1959, female (A–E). A. Leg 1, B. Leg 2, C. Leg 3, D. Leg 4, E. leg 5. *Caligus undulatus* Shen & Li, 1959, male (F–M); F. Habitus, G. Genital complex, H. Caudal ramus, I. Antenna, postantennal process and maxillule, J. Maxilliped, K. Post oral pad, L. Sternal furca, M. Legs 5 and 6. Scale bars: A–E, G–M=0.1 mm; F=0.6 mm.
ovoid, 1.86, 2.06×1.26, 1.31 mm. Genital complex (Fig. 4G) with constriction next to fourth pediger, longer than wide 0.50, 0.60×0.38, 0.40 mm. Abdomen 2-segmented, subequal in length. Caudal ramus (Fig. 4H) long, with 3 long and 3 short setae.

Antenna (Fig. 4I) 3-segmented; first segment long with adhesion pad, second segment with 2 adhesion pads; third short, with 2 spines (one outwardly projected, another inwardly projected). Postantennal process (Fig. 4I) long, acutely pointed at tip, carrying 2 basal papillae each with 2 setules; another similar papilla located nearby sternum. Maxillule (Fig. 4I) pointed at tip, with adhesion pad and seta at midlength. Maxilliped (Fig. 4J) indistinctly 3-segmented; proximal segment largest with well protruded knob at midlength; distal segment long, acutely pointed, crossing over knob on proximal segment, armed with short barbel at base. Pair of post oral pads (Fig. 4K) present just below oral cone. Sternal furca (Fig. 4L) with long, divergent tines. Leg 5 (Fig. 4M) represented by 2 pinnate setae on posterolateral part of genital complex. Leg 6 (Fig. 4N) represented by 2 small setae nearby leg 5.

Remarks. The present single female specimen of C. undulatus differs in the structure of the genital complex without prominent ridges, compared to that reported from China (Shen & Li 1959). The two males (3.50, 3.52 mm) collected in the present study are larger than those from China (3.08 mm) (Shen & Li 1959), but similar to that from India (3.50 mm) (Pillai 1966). However, legs 5 and 6 of male were overlooked in the previous descriptions (Shen & Li 1959, Pillai 1966), these are provided herein.

Caligus undulatus is closely related to its congener C. chelifer Wilson, 1905, and shares the following features: (1) 2-segmented exopod of leg 4; (2) longer genital complex and caudal rami. However, it differs from C. chelifer chiefly by the presence of 3 long outer setae on the exopodal segment of leg 1 (smaller in C. chelifer).

Caligus undulatus was first identified from plankton samples in China (Shen & Li 1959). After that, it was found in Brazil (see Ho & Lin 2004a and India (Pillai 1966) and now from Japan and Korea (present study). However, C. undulatus has not hitherto been reported as a parasite on any host. It is likely that this species is more easily detached from its host than others. Likewise, the closely related congener C. chelifer was also found in plankton samples from Florida (Kabata 1972) and the Gulf of Mexico (Suárez-Morales et al. 1998), though it was recovered from different fish hosts like the Atlantic cutlassfish Trichurus lepturus (Linnaeus), the menhaden Brevoortia tyrannus (Hildebrand), the sword fish Xiphias gladius (Linnaeus) and some elasmobranchs (Wilson 1905, Cressey 1991).

Caligus sp. (Fig. 5A–I)

Material examined. One ♀ (KMNH IvR 500,263) collected at Stn 9 on May 27, 2006 off the Nansei Islands, Japan.

Description. Male. Body (Fig. 5A) 3.13 mm long excluding caudal setae. Cephalothorax suborbicular 2.31×1.94 mm, comparatively long. Fourth pediger wider than long. Genital complex triangularly rounded 0.53×0.74 mm carrying setules; blunt corners bearing legs 5 and 6 (Fig. 5B). Abdomen small, rectangular-shaped, wider than long 0.17×0.30 mm. Caudal ramus (Fig. 5B) longer than wide, with 3 long and 3 short setae.

Antenna (Fig. 5C) 3-segmented, long proximal segment with corrugated patches; middle segment with 2 adhesion pads; distal segment bearing 3 small pointed spines. Postantennal process (Fig. 5C) long, curved, pointed at tip, carrying 2 basal papillae each with 2 setules; another similar papilla located nearby sternum. Maxillule (Fig. 5C) triangular, bearing 3 plumose setae anteriorly. Maxilliped (Fig. 5D) indistinctly 3-segmented; proximal segment long, robust with rectangular-shaped ridge at midlength; distal segment long with pointed bent claw, carrying barbel at base. Sternal furca (Fig. 5E) with slightly wider tines fringed with membrane at proximity.

Armature on rami of legs 1–3 (Figs. 5F–H) as in C. orientalis. Leg 4 (Fig. 5I) with 2-segmented exopod; proximal segment bearing smooth spine; distal segment carrying 3 slender spines, however only distal 2 terminal spines with serration; outermost terminal spine comparatively longer than other 2 inner spines. Leg 5 (Fig. 5B) represented by 2 prominent spines at posterior corner of genital complex. Leg 6 (Fig. 5B) represented by 2 papillae with 1 and 2 small setae at ventrolateral part of genital complex.

Remarks. The male of Caligus sp. has a close resemblance with that of Caligus oviceps Shiino, 1952. These two species share some common features in: the barrel-shaped genital complex and the presence of setules on the genital complex; the position of leg 6 as a posteriorly produced knob. However, Caligus sp. can be distinguished from C. oviceps by: relatively higher ratio of the cephalothorax to abdomen (2.3 in C. oviceps vs 3.71); 1-segmented abdomen (2-segmented in C. oviceps); leg 4 with terminal serrated spines (no serration in C. oviceps).

It also has a resemblance with the body structure of male C. orientalis and C. punctatus. However, they significantly differ from the present male of Caligus sp. in: the serration of genital complex (lateral margin not serrated in Caligus sp., serrated in C. orientalis and not serrated, but a row of setules found along the lateral margin and posterior lateral corner in C. punctatus) and the presence of terminal serrated spines on leg 4 in Caligus sp. (absence in C. orientalis and C. punctatus). Both of these species were also found in plankton samples (Ho & Lin 2004b). Although there is a possibility that it is an undescribed species, descriptions of caligid species usually depend on females. Therefore, we defer the description until a female is discovered.
Family Pandaridae Milne-Edwards, 1840

Pandarus sp. (Figs. 5J–K, 6A–J)

Material examined. Sixteen specimens of chalimi: 3 (KMNH IvR 500,264–500,266) from Stn 6 on May 22, 2003; 8 (KMNH IvR 500,267–500,274) from Stn 10 on May 24, 2003; and 5 (KMNH IvR 500,275–500,279) from Stn 11 on May 29, 2006. Four \( \delta \delta \) (KMNH IvR 500,280–500,283) each from Stn 11 on May 24, from Stn 13 on May 25, 2003 and from Stn 4 on May 24, from Stn 9 on May 27, 2006 off the Nansei Islands, Japan. The body length of chalimus stages were measured as 1.74–1.98 mm. Only males are described herein.

Description. Male. Body (Fig. 5J) 3.38 mm long (3.18–3.58, \( n=4 \)) excluding caudal setae. Cephalothorax suborbicular, longer than wide 2.22 (2.18–2.26),\( \times 1.98 \) (1.95–2.01) mm. Genital complex, not well expanded, wider than long 0.58 (0.53–0.63)\( \times 0.64 \) (0.60–0.68) mm. Abdomen (Fig. 5K) 0.36 (0.33–0.39)\( \times 0.42 \) (0.40–0.44) mm, 2-segmented,
small, unequal in length. Caudal ramus (Fig. 5K) not long, but with 4 long and 2 small setae.

Antennule (Fig. 6A) 2-segmented; proximal segment broad with 16 plumose setae; distal segment small with 6 long hirsute setae; 4 naked setae and aesthetasc present distally. Antenna (Fig. 6B) 3-segmented; proximal segment small, bluntly pointed towards maxillule, unarmed; middle segment unarmed, rectangular; distal segment with inwardly bent, pointed claw bearing 1 proximal and 1 medial setae. Postantennal process (Fig. 6B) small, slightly rectangular bearing 2 basal papillae each with 2 setules, another similar papilla located nearby sternum. Maxillule (Fig. 6B) acutely pointed at tip. Maxilla (Fig. 6C) 2-segmented; proximal segment robust; distal segment ornamented with hyaline membrane at midlength; 2 distal spinules with hyaline membrane. Maxilliped (Fig. 6D) incompletely 3-segmented; proximal segment largest, with small knob at midlength, 3 cup-like adhesive pads present at inner part of midventral region; middle segment small, partly fused with distal segment to form subchela; distal segment long, robust pointed claw, armed with short seta subterminally. Sternal furca (Fig. 6E) slightly squared, stout with sharply pointed tines.

Armature on rami of legs 1–4 as follows:

**Fig. 6.** *Pandarus* sp., male (A–J). A. Antennule, B. Antenna, postantennal process and maxillule, C. Maxilla, D. Maxilliped, E. Sternal furca, F. Leg 1, G. Leg 2, H. Leg 3, I. Leg 4, J. Leg 5. Scale bars: A, J=0.5 mm; B–I=0.1 mm.
Leg 1 (Fig. 6F) with 2-segmented exopod; distal segment bearing 3 long plumose setae; endopod prominently 2-segmented; distal segment carrying 3 small plumose setae. Leg 2 (Fig. 6G) with 2-segmented exopod; distal segment carrying 2 smaller and 2 larger spines. Leg 3 (Fig. 6H) with 2-segmented exopod; distal segment armed with 4 small spines of equal length, proximal segment with moderately large spine. Leg 4 (Fig. 6I) with 2-segmented exopod; distal segment carrying 4 large spines fringed with hyaline membrane laterally. Leg 5 (Fig. 6J) represented by 2 papillae, one with seta, another with 2 long and 1 short plumose setae.

Remarks. The present planktonic specimens of Pandarus sp. resemble the young male (preadult) specimens (7.9 mm long) of Pandarus satyrus (Dana, 1852) in the shape of the cephalothorax and genital complex, and this species was reported to infect the body surface of the hammer head shark Sphyrena zygaena (Linnaeus) and the blue shark Isurus glaucus (Linnaeus) in Japanese waters (Shiino 1954). The present specimen chiefly differs with P. satyurs in: (1) the smaller size; (2) the setal structure of legs. Legs 2 and 3 have 5 setae each on the distal exopodal segment (6 in P. satyurs).

Pandarus has a host-specificity to elasmobranchs (Benz 1992). They were collected only from the Nansel Islands, suggesting that oceanic sharks could be a candidate host for this species. Normally they would be attached firmly to the body surface of the sharks, using the prominent maxillipeds (Benz 1992, Benz et al. 2003), but some males and chalimi might have accidentally detached or slipped and then become planktonic forms. This species may be considered as an undescribed species. Since, the identification of caligiforms usually depend on females, discovery of a female of the same species is necessary to describe this species.

Discussion

The present study has revealed that adults and chalimus stages of caligiform copepods mainly infecting fish are not just rarely found in marine plankton samples. According to Kabata (1979), the occurrence of Caligus in plankton is considered as an artifact, because their oral appendages are not suitable for feeding while suspended in the water. Thus, the number of caligids found in plankton samples at any time is reported to be usually one, very rarely two in a sample (Heegard 1972).

A planktonic adult male of Caligus hyalinus Cherniavsky, 1868 was first found in the Black Sea in the 19th century (see Ho & Lin 2004a); subsequently the same species was identified four years later as a parasite of wrasses at the same location. Likewise, an adult female of Caligus planktonis Pillai, 1979 was collected from a plankton sample off India (Pillai 1985). Twenty-five years later, it was isolated from the host Liza macrolepis (Smith) in Taiwan (Ho & Lin 2004a). In total, 15 species of Caligus have been found in plankton samples from all over the world (Table 2), out of which 5 species have not been recorded from any host; these being C. aduncus Shen & Li, 1959, C. costatus Shen & Li, 1959, C. hylaimae Heegard, 1966, C. tripodalis Heegard, 1972 and C. undulatus Shen & Li, 1959. Five species of plankonic caligids have so far been recorded from China, and three each from India and Mexico (Ho & Lin 2004a). Surprisingly, this is the first report of the occurrence of Caligus species in plankton samples from Japan and Korea, even though three-fourths of the parasitic copepods in Asia have been reported from these two countries (Ho & Lin 2004b).

Caligus coryphaenae (4♀♀♂) was more frequently found than any other congener in the present study. It was previously recorded from plankton samples 7 times from 1894 to 1972 at 7 different localities (Ho & Lin 2004a). Caligus coryphaenae (♀♀ and juv. ♂♂) and C. productus (♀♀ and ♂♂) have been reported as planktonic forms from several localities around the world (Heegard 1972, Ho & Lin 2004a), and interestingly, both are parasitic on the dolphinfish C. hippurus, which is distributed throughout the world’s oceans (Froese & Pauly 2008).

It is important to note that C. undulatus has not so far been found as a parasitic form. However, the distribution of free-swimming individuals at these different and distant locations implies that the host might be highly migratory (Ho & Lin 2004a), since it has been recovered from plankton samples in both Asia and South America. Since we collected an ovigerous female of this species in our collection, we can infer that even ovigerous females can become detached from their hosts. However, there is also the possibility that the females actively detach themselves from the host, releasing their nauplii. The closely related species C. chelifer (♀♀) has also been found from zooplankton samples (Kabata 1972, Suárez-Morales et al. 1998), and it is parasitic on elasmobranchs such as the dusky smooth-hound Mustelus canis (Mitchell) (Wilson 1905, Cressey 1991). Caligids infecting elasmobranchs may be found frequently in plankton samples. Another related species, C. rufmaculatus Wilson, 1905 (♀♀ and ♂♂), has been found in plankton samples from the Gulf of Mexico (Suárez-Morales et al. 2003). This species was found infecting many hosts including the snapper Lutjanus synagris (Linnaeus) exclusively on the Atlantic coast of the United States (Cressey 1991).

Apart from caligids, pandarids were also collected and examined during this study. Pandarus sp. was captured in the form of 16 chalimi and 4 adult males. They are essentially parasites of elasmobranchs (Benz 1992, Benz et al. 2003). So far, there have been no reports on pandarids from plankton samples and hence this is the first record of occurrence of the family from plankton samples anywhere in the
Table 2. Caligus species found in plankton samples, some of which have been recorded also from fish hosts (after Ho & Lin, 2004a).

<table>
<thead>
<tr>
<th>Species</th>
<th>Sex</th>
<th>Locality</th>
<th>Host</th>
</tr>
</thead>
<tbody>
<tr>
<td>Caligus aduncus</td>
<td>♂️</td>
<td>China</td>
<td>No host record</td>
</tr>
<tr>
<td>C. chelifer</td>
<td>♂️</td>
<td>Mexico</td>
<td>Trichurus lepturus (Linnaeus)</td>
</tr>
<tr>
<td>C. coryphaenae</td>
<td>♂️, ♀️</td>
<td>Florida</td>
<td>Coryphaena hippurus (Linnaeus)</td>
</tr>
<tr>
<td>C. costatus</td>
<td>♀️</td>
<td>China</td>
<td>No host record</td>
</tr>
<tr>
<td>C. hyalinae</td>
<td>♂️, ♀️</td>
<td>Texas</td>
<td>No host record</td>
</tr>
<tr>
<td>C. hyalinus</td>
<td>♂️</td>
<td>Black Sea</td>
<td>Symphodus ocellatus (Forsskål)</td>
</tr>
<tr>
<td>C. macarovi</td>
<td>♂️</td>
<td>California</td>
<td>Cololabis saira (Brevoort)</td>
</tr>
<tr>
<td>C. orientalis</td>
<td>♂️, ♀️</td>
<td>China</td>
<td>Chanos chanos (Forsskål)</td>
</tr>
<tr>
<td>C. pelagicus</td>
<td>♂️, ♀️</td>
<td>India</td>
<td>Mugil subviridis (Vælæciennes)</td>
</tr>
<tr>
<td>C. planktonis</td>
<td>♀️</td>
<td>India</td>
<td>Liza macrolepis (Smith)</td>
</tr>
<tr>
<td>C. productus</td>
<td>♂️, ♀️</td>
<td>California, Mexico</td>
<td>Coryphaena hippurus (Linnaeus)</td>
</tr>
<tr>
<td>C. punctatus</td>
<td>♂️, ♀️</td>
<td>China</td>
<td>Gymnogobius castaneus (O’Shaughnessy)</td>
</tr>
<tr>
<td>C. rafmaculatus</td>
<td>♂️, ♀️</td>
<td>Mexico</td>
<td>Lutjanus synagris (Linnaeus)</td>
</tr>
<tr>
<td>C. tripedalis</td>
<td>♂️, ♀️</td>
<td>New Zealand</td>
<td>No host record</td>
</tr>
<tr>
<td>C. undulatus</td>
<td>♂️, ♀️</td>
<td>China, India, Brazil</td>
<td>No host record</td>
</tr>
</tbody>
</table>

In the present study, adult males (80%) of caligiforms have more frequently occurred than adult females (20%) based on the number of individuals. However, the previous data were not clear enough to find the sex ratios of all the individuals collected (cf. Table 2). In general adult males may be more easily detached from the host than do adult females, because the latter may be more firmly attached to them in order to continue absorbing nutrients for laying eggs. There is another possibility that males actively search for their mates on another host after their detachment from one host. In the poecilostomatoid copepod family Ergasilidae there are two types of life modes of females (Ohtsuka et al. 2004). Females of some species never detach from the host, whereas those of others seem to attach themselves to it only for feeding and be free swimming in the waters when in their non-feeding period. The latter exhibits a dual mode of life. It could be predicted that some caligiforms, in particular males, may exhibit such dual modes in their life cycles.

The parasites’ entry into the mode of free-swimming could be a chance for survival. The following possibilities of the occurrences of caligiform adults originally infecting fish can be considered: (1) escaping from irritation or diseases in the host, (2) looking for an opportunity to switch hosts, (3) change in their life mode, and (4) accidental detachment. In the case of chalimi, it could be accidental, because they would be tightly attached to the host using a special organ called the “frontal filament” (cf. Ho & Lin 2004b), and cannot grow up to the adult stage without nutrient supply from the host. Their incompletely developed legs are not suitable for swimming (see Ho & Lin 2004b).

However, how these planktonic adults complete their life cycle is still a mystery. Whether they could find another host immediately or would live only ephemerally and soon die in open waters has not been studied at all. In this study, both sexes of adult forms were found in plankton samples, but how they spend the rest of their lives in a planktonic environment rather than a parasitic environment is completely unknown and imperative to study in the future.

It is worth mentioning that planktonic individuals of C. sclerotinosus have been found from near a fish farm in western Japan (Ho et al. 2004, present study). If they carry some kinds of pathogens, it is probable that the prevalence of diseases could be increased by these free-swimming copepods becoming vectors after resettlement on new hosts. Actually some pathogenic bacteria have been identified from C. sclerotinosus (I Madinabeitia et al. in prep) infecting diseased hosts. We intend to reveal the relationships among hosts, parasites and symbionts on parasites in the near future.

For a fish host to become infected, it must first come into contact with the infective free-swimming stage. This is particularly true in the field of mariculture. As the number of marine fish farms increase, the problems caused by parasites in the operation and efficiency of production are becoming greater. It is now known that some parasitic copepods can become serious pests of cultured fish (Boxshall & Defaye 1993, Ho 2000, Nagasawa 2004, Johnson et al. 2004, Rosenberg 2008). It is, therefore, increasingly important that more attention be paid to the dispersal stages of these parasites, not only the larval/juvenile stages but also...
the adults.

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