Further observations on the penaeid shrimp *Funchalia sagamiensis* FUJINO 1975 and pelagic tunicates (Order: Pyrosomatida)

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An association between the penaeid shrimp *Funchalia sagamiensis* FUJINO 1975 and pelagic tunicates of the Order Pyrosomatida was confirmed through in situ submersible and shipboard observations. Information on this association, including behavioural, morphological and distributional data is presented. The association is "strong", possibly obligate for the shrimp during this life history phase, and does not appear to be species-specific. Further information is presented on the taxonomic standing within the genus *Funchalia* of the enigmatic species *F. sagamiensis*. Evidence is also presented that the supposed blinding of organisms due to the bright lights of research submersibles does not always hold, even within the decapod crustaceans. The utility of submersibles for in situ behavioural research is discussed.

Keywords : *Funchalia*, pyrosome, association, midwater, submersible, ROV

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Introduction

The structural complexity introduced both spatially and temporally to the midwater zone by gelatinous members of the macroplankton has increasingly been recognised as a major factor contributing to the "paradoxically" high species diversities of many pelagic ecosystems (Harbison *et al.*, 1977; Hutchinson, 1961; Kingsford, 1993). Since the advent of crewed research submersibles, gelatinous macroplankton have been observed in close association with members of many different groups of midwater organisms. A non-exhaustive list includes the following. Fish: (*Caristius* sp. and the siphonophore *Bathyphysa conifera* (Janssen *et al.*, 1989), a Caristiid sp. and the siphonophore *Praya* sp. (J.H., unpubl.), *Leuroglossus stilbius*, *Stenobrachius leucopsarus* and the siphonophore *Apolemia* sp. (Robison, 1983), and *Tetragonurus* sp. and salps (Janssen and Harbison, 1981). Shrimps: *Notostomus robustus* and the medusa *Atolla wyvillei* (Moore *et al.*, 1993). Pycnogonids: *Pallenopsis scoparia* and the medusa *Periphylla periphylla* (Child and Harbison, 1986). Isopods: *Anuropus* sp. and the medusa *Deepstaria reticulum* (Larson et al., 1988). Amphipods: most if not all hyperiids (Harbison et al., 1977). Cnidarians: *Bythotiara* sp. and an undescribed doliolid (Raskoff, 1998). These associations can be parasitic (Ohtsuka *et al.*, 2000), commensal, symbiotic (Thiel, 1976), or predominantly predator/prey-based in character (Moore *et al.*, 1993).

In some cases, such as with the amphipod *Phronima* and its gelatinous barrel, the animals in question are relatively robust and able to be sampled using conventional sampling tools − allowing direct observations on their behaviour and accurate characterization of the interaction (Laval, 1968). Although many further associations between members of the midwater fauna have been proposed (Dall, 1957, p. 165; Harbison *et al.*, 1973; Mauchline, 1984), direct confirmation and characterization is difficult as most associations are disrupted in net trawls − still the most common sampling method in use today. It is often only with in situ observations from crewed submersibles and ROVs that direct confirmation and characterization of any associations can be made (Child and Harbison, 1986; Hunt and Lindsay, 1998; Janssen *et al.*, 1989).

An association between the penaeid shrimp *Funchalia sagamiensis* FUJINO 1975 and pelagic tunicates of the Order Pyrosomatida was recently confirmed through in situ submersible and shipboard observations. Information on this association, including behavioural, morphological and distributional data is presented. Further information is presented on the taxonomic standing within the genus *Funchalia* of the enigmatic species *F. sagamiensis*. Critics of submersible research contend that observations conducted under the bright lights of a submersible or ROV will affect the organism's behaviour, thereby invalidating the observations. These lights may also blind the animal (Herring *et al.*, 1999). Evidence is presented that the supposed blinding of organisms due to the bright lights of research submersibles does not always hold, even within the decapod crustaceans. The utility of submersibles for in situ behavioural research is discussed.

Materials and Methods

Shrimp/pyrosome associations were observed using the crewed submersible *Shinkai 2000* and the ROVs *Dolphin 3K* and *Kaiko* in several areas around Japan. The *Shinkai 2000* and *Dolphin 3K* observational platforms have previously been described by Hunt and Lindsay (1999). The ROV *Kaiko* was equipped with a pan-tiltable Victor/TV3100XDB three chip CCD camera and three tiltable Sony/XC-999 cameras mounted in an array to give a 118 degree angle of view. There were six lights: two 500-W MaxSeaLite ML-120/500 halogen lamps, two 500-W Deep-SeaLite ML-120/500 halogen lamps and two 400-W SeaArc2 HMI metal halide lamps. Video footage from the *Shinkai 2000* and ROV *Dolphin 3K* dives was recorded simultaneously on ST-120PRO S-VHS and BCT-D124L Digital Betacam tapes. Footage from all of the ROV *Kaiko*'s four cameras was recorded on ST-120PRO S-VHS tapes and that from the Victor/TV3100XDB three chip CCD camera was also recorded on BCT-90MLA BetacamSP tapes. The in situ dimensions of animals were estimated if they came in contact with an object that was of known size. Physico-chemical data were collected using a SeaBird SBE19 CTD with an SBE13 oxygen sensor. CTD and dissolved oxygen data were correlated to the presence of the animals by matching the time record on the CTD series to the time record on the video.

Specimens were collected on ROV *Dolphin 3K* Dive 426 using a single detritus sampler (Youngbluth, 1984), and by a 6-cannister suction sampler with a hose diameter of 5.5cm on *Shinkai 2000* Dive 950. Animals were transferred to shipboard aquaria or plankton kreisels (Hamner, 1990) for behavioural observation. Observations of the live animals were also made in the laboratory under a Nikon SMZ-U dissecting microscope and recorded on BCT-90MLA BetacamSP tape. Specimens from ROV *Dolphin 3K* Dive 426 were fixed in 10% formalin-seawater solution. The formalin-preserved specimen from ROV *Dolphin 3K* Dive 426 was compared with three small specimens of *Funchalia* spp. deposited at the National Fisheries University (NFU): *Funchalia* sp. from near Okinotorishima Island, St. 1, 20˚21.8'N, 136˚18.5'E, 40-70 m deep, Sept. 21, 1988, coll. U. Yamada − 8.4mm in carapace length (CL) (NFU 530-2-2076); *Funchalia* sp. from near Okinotorishima Island, St. 2, 20˚22.1'N, 136˚18.2'E, collected together with 2 males of *F. taaningi* Burkenroad, 90-120 m deep, Sept. 22, 1988, by U. Yamada − CL ca. 3.6mm (NFU 530-2-2066); *Funchalia* sp. from the Indian Ocean, St. 10, 02˚43'S, 94˚13'E, 10 foot net, Dec. 2-3, 1962, collected by TS *Koyo-Maru* − CL 7.7mm (NFU 530-2-2072).

The shrimp specimen from ROV *Dolphin 3K* Dive 426 was transferred to 70% ethanol solution for approximately two months before being post-fixed for SEM observation with 2% OsO_4 in sea water for 60 minutes at 4˚C. After rinsing in distilled water, it was dehydrated through a graded ethanol series to 100% ethanol before transfer to a t-butyl alcohol solution. The sample was freeze-dried and coated with platinum/palladium (80:20) before being observed with a JSM 5800-LV scanning electron microscope at an accelerating voltage of 5kV.

Results

Morphological Observations

The species *Funchalia sagamiensis* has hitherto been known only from the original description of a single immature specimen from Sagami Bay, Central Japan (Fujino, 1975) and from a partial description of another immature specimen from Okinotorishima Island at 20˚21.8'N, 136˚18.5'E (Hayashi, 1992). The latter was suggested to be a juvenile of either *F. villosa* or *F. taaningi* (Hayashi, 1992), while the former has been likened to *F. woodwardi* (Grippa, 1987). A specimen with similar characters was also described by Monod (1972), and subsequent authors have likened this specimen to both *F. sagamiensis* (Fujino, 1975) and *F. taaningi* (Crosnier, 1985). In view of the paucity of information on this species and the ongoing debate on its taxonomic position and validity, a description of this specimen is presented here with notes on other juvenile specimens of the genus *Funchalia*.

The following features characterise the present specimen: Small size (CL 5.6mm). Body entirely naked without setae on surface. Rostrum nearly horizontal and with six dorsal teeth (of these, posterior one on carapace as epigastric spine, second one just above orbital margin). Carapace with distinct hepatic spine followed by well-defined longitudinal ridge extending to posterior margin of carapace. Anterior margin of carapace with small spine on postorbital angle and branchiostegal region both supported by short carina. Abdomen slender, first two somites dorsally rounded, but third to sixth somites with middorsal carina. Pleura of first five somites rounded. Well-marked longitudinal carina present on central part of lateral surfaces from distal half of fourth somite to near end of sixth somite. Sixth somite long, 2.8 times as long as fifth somite. Telson 0.9 times as long as sixth somite, with median groove dorsally. Uropods 1.3 times length of telson. Distal margin of telson truncated with strong median spine and three lateral spines near distal end.

Eyes with large hemispherical cornea. Antennular peduncle slightly overreaching distal end of antennal scale. First antennular segment subrectangular in dorsal view, as long as distal two segments combined, distolateral corner ending in sharp spine. Stylocerite short, only reaching basal third of first segment. Antennal scale roughly oblong, outer distal spine as long as end of lamella. Mouth bundle illustrated in Figure 1. First three pereopods chelate. Chelae with several teeth on cutting edges. First and second pereopods unarmed on basis and ischium. Fifth pereopod similar to fourth pereopod in general shape and proportion of each segment. Dactylus conical, about one-fifth length of propodus in fourth and fifth pereopods. No pereopod bearing exopod. No particular structure of genital organ is differentiated on thoracic sternum and/or pleopods. First abdominal sternite between first pleopods bearing small median subconical spine bent anteriorly. Similar rather long spine present on second abdominal sternite.

These characters can be seen in SEM photographs posted on the internet at [http://www.jamstec.go.jp/jamstec/MESOPELAGIC/SEMofFunchaliasagamiensis.html], though short spine-like processes are visible on the distal margin of the telson in the SEM photographs, a feature which was not observable under the binocular microscope.

In situ and Shipboard Observations

Since the initiation of a mesopelagic biology research program at the Japan Marine Science and Technology Center (Hunt *et al.*, 1997), six observations of pyrosome-shrimp interactions have been documented (Table 1). These observations have ranged from 2 seconds to

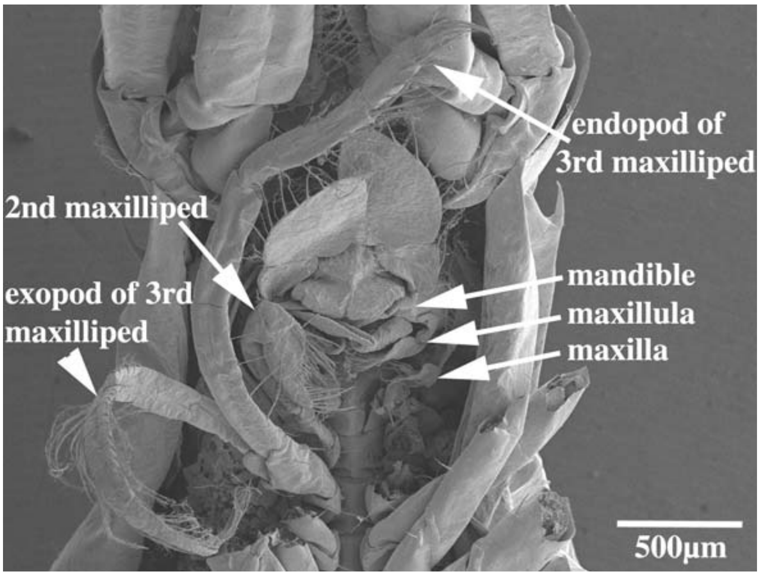

Fig. 1 Scanning electron micrograph of the mouth bundle of *Funchalia sagamiensis* Fujino collected on *Dolphin 3K* Dive 426.

Table 1 In situ observations of pyrosome-shrimp associations in the mesopelagic zone.
Eye position is recorded as the percentage of the pyrosome's length from the apex at which the shrimp's eyes were situated;
Cloacal angle is the deviation of the pyrosome from a horizontal attitude based on the position of the cloacal opening.
The entry "n.a." signifies that the association was not captured on the video record.

Dive No.	Area	Date	Time	Depth	Temp.	Sal.	σT	Oxygen	Attachment	Eye position	Pyrosome	Cloaca
3K#325	Sagami Bay 35˚00.00'N, 139˚14.00'E	29-May-97	16:00:15	460m	6.4˚C	34.2	26.9	2.6 ml/L	ventral	25% from apex	*Pyrostremma agassizi*	80˚ up
2K#950	Suiyo Seamount 28˚34.16'N, 140˚38.74'E	9-Jun-97	11:10:16	742m	6.0˚C	34.1	26.9	2.7 ml/L	ventral	75% from apex	*Pyrosoma atlanticum* 52mmX_19mm	70˚ down
3K#426	Sagami Bay 34˚59.89'N, 139˚13.83'E	10-Jun-99	14:10:04	490m	6.0˚C	34.2	26.9	2.2 ml/L	ventral	15% from apex	*Pyrostremma agassizi* 130mmX_19mm	15˚ down
2K#1106	An'ei Seamount 29˚16.00'N, 138˚37.78'E	19-Jun-99	11:41:10	804m	7.4˚C	34.1	26.7	3.1 ml/L	n.a.	n.a.	*Pyrosoma atlanticum*	n.a.
2K#1106	An'ei Seamount 29˚16.00'N, 138˚37.78'E	19-Jun-99	11:41:43	806m	7.4˚C	34.1	26.7	3.1 ml/L	ventral	25% from apex	*Pyrostremma agassizi*	5˚ up
10K#114	Japan Trench 40˚06.69'N, 144˚10.21'E	22-Apr-99	9:08:28	247m	11.2˚C	34.3	26.2	5.8 ml/L	dorsal	5% from apex	*Pyrosoma atlanticum*	45˚ up

over 14 minutes in length. Positive species identification of both members involved in this association (*Funchalia sagamiensis* and *Pyrostremma agassizi*) was made for the single observation during ROV *Dolphin 3K* Dive 426 in Sagami Bay (34°59.89'N, 139°13.83'E). Both animals were collected and fixed in a 10% formalin-seawater solution after shipboard and laboratory-based observations. Identification to the genus level (*Funchalia sp.*) was possible for the shrimp captured during *Shinkai 2000* Dive 950 (28°34.16'N, 140°38.74'E). However, during a shipboard feeding experiment, this shrimp was consumed by the cranchid squid *Liocranchia reinhardtii*. Several characters suggested that this shrimp was also *F. sagamiensis*. In particular the colouration was similar to that of the specimen from ROV *Dolphin 3K* Dive 426, with the distal four-fifths of the antennae and the distal third of the uropodal exopods tinged blue-white. The distal ends of both the fourth and fifth pereopods, the distal end of the antennal scale, the entire carpocerite, and the anterior ends of the flagellae were flecked orange, as with the positively identified specimen (Fig. 2a). The gross morphology and the total body length of 25mm also corresponded closely with *Funchalia sagamiensis*. Apart from the specimen observed during ROV *Kaiko Dive* 114, all other specimens also exhibited white colouration on the distal ends of the antennae and the uropodal exopods, a similar body shape and size, and similar behaviour.

ROV Dolphin 3K Dive 426

Funchalia sagamiensis was found attached to a 130mm long, 19mm wide colony of *Pyrostremma agassizi* at 14:10:04 local time (GMT+9h) at 490m depth on ROV *Dolphin 3K* Dive 426 in Sagami Bay, Central Japan (Table 1). The pyrosome was oriented with the cloacal opening at a declination approximately 15° from the horizontal plane. The shrimp was attached ventrally to the external surface, facing the closed end of the test

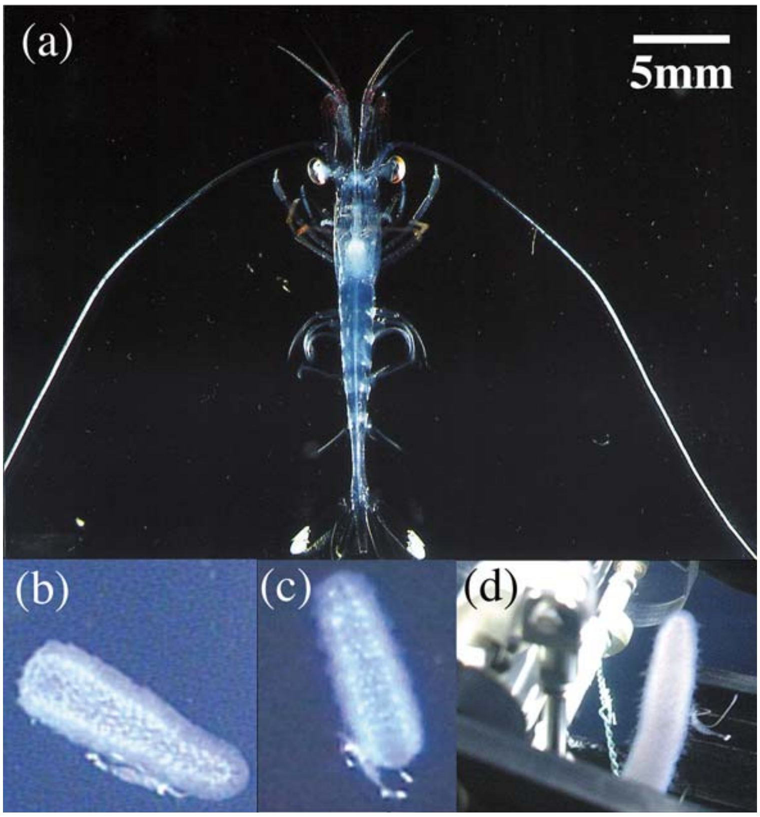

Fig. 2 a) The colouration and gross morphology of a living specimen of *F. sagamiensis* (*Dolphin 3K* Dive 426).
b) *F. ?sagamiensis* on *Pyrosoma atlanticum* (*Shinkai 2000* Dive 1106).
c) *F. ?sagamiensis* on *Pyrosoma atlanticum* (*Shinkai 2000* Dive 950).
d) *F. sagamiensis* remained attached to its pyrosome even in the wash of the ROV's thrusters (*Dolphin 3K* Dive 426).

(hereafter referred to as the apex.) Its eyes were positioned about 2cm from the pyrosome's apex and its long axis was aligned with that of the pyrosome. The two animals disappeared off-screen at 14:10:21 and reappeared at 14:11:04 in the same coupling. At 14:11:07 the shrimp rotated in place and, keeping the body of the pyrosome between it and the ROV, moved around to sit on the dorsal surface of the pyrosome. Its new position was again facing the apex of the pyrosome with its eyes approximately 6cm from that end. At 14:11:28 the pyrosome was once again between the shrimp and the ROV. At 14:11:42 the pyrosome had rotated and the shrimp was again clinging to the ventral surface. At 14:11:54 the shrimp's midline was skewed approximately 30° to that of the long axis of the pyrosome. Only the white-coloured distal end of an antenna and the uropods and telson were visible. The tail was spread so that the distance between the white-coloured distal ends of the uropodal exopods was at a maximum.

At 14:13:10 the attitude of the pyrosome began to change rapidly in the wash of the ROV's thrusters. When viewed dorsally, the only areas of the nearly-transparent shrimp that were visible above the background of the pyrosome's surface were the eyes and the white areas of the uropodal exopods. The shrimp stayed attached firmly to the pyrosome even when it collided with the sample basket or was tumbled in the current. During a particularly strong wash, the posterior end of the shrimp was swept out to lie perpendicular to the long axis of the pyrosome (Fig. 2d). It tucked its pleopods up along its ventral surface, presumably to reduce drag, and held them stationary while firmly clasping the surface of the pyrosome with its pereopods. The shrimp maintained its position with its eyes approximately 6cm from the apex and its long axis skewed approximately 30° to that of the pyrosome until collection at 14:18:09. Several centimetres of the posterior end of the pyrosome were sheared off by the closing door of the D-sampler. The shrimp however remained attached to the pyrosome. At 14:53:07 at 929m depth the D-sampler was opened for 11 seconds in an attempt to sample the Scyphozoan medusa *Deepstaria enigmatica* and its two associated crustaceans. During this time the shrimp remained attached at a distance approximately two thirds along from the apex and at an orientation perpendicular to the long axis of the pyrosome. The shrimp remained firmly attached even as the pyrosome tumbled in the current and collided with the interior walls of the D-sampler. A maximum depth of 1215m was attained on this dive. During the time on the bottom the shrimp changed orientation but remained attached to the pyrosome at a distance approximately two thirds along from the apex. During ascent at 15:44:35 and at a depth of 914m the shrimp's orientation was almost perpendicular to the long axis of the pyrosome and only slightly angled towards the apex. At 15:52:07 and 652m depth the shrimp was still stationary in the same position. Within five seconds of directly training a 400-W SeaArc HMI/MSR metal halide lamp on the D-sampler, the shrimp began beating its pleopods actively as if to swim away from the light but its pereopods remained firmly attached to the pyrosome's external surface. At 15:58:38 and at a depth of 428m the shrimp was stationary with its midline skewed 45 degrees to the long axis and facing the apex of the pyrosome. Within three seconds of being exposed to the light, it repositioned itself so that its long axis was perpendicular to that of the pyrosome and began beating its pleopods. At 16:01:17 and at a depth of 263m the shrimp, perpendicular to and positioned about halfway along the pyrosome, turned in place to face the cloacal opening. At 16:05:15 and at a depth of 129m the shrimp was again attached ventrally about halfway along the pyrosome's length and perpendicular to its long axis. It began swimming in place, still attached to the pyrosome, approximately four seconds after being exposed to direct light from the metal halide lamp.

When viewed under the dissecting microscope, the exopod of the third maxilliped was held such that the tip brushes or lies just below the ventral surface of the eye. The endopod of the third maxilliped and the first three pereopods were held forward such that their tips brushed the surface the shrimp was resting on, and they were brought back to the mouth bundle intermittently − presumably for cleaning. The hepatopancreas and digestive tract were coloured the same orange as the branchial basket of the pyrosome (*P. agassizi*) to which the shrimp was attached upon collection.

Shinkai 2000 Dive 950

The behaviour of the shrimp captured during *Shinkai 2000* Dive 950, which was also identified to the genus level *Funchalia*, is described below. *Funchalia* sp. was found attached to a 52mm long, 19mm wide colony of *Pyrosoma atlanticum* at 11:10:16 local time (GMT+9h) at 742m depth on *Shinkai 2000* Dive 950 over Suiyo Seamount in the Izu/Ogasawara Island Chain (Table 1). The pyrosome was oriented with the cloacal opening at a declination approximately 70˚ from the horizontal plane. The shrimp was attached ventrally to the external surface, facing the apex and with its tail hanging over the cloacal opening (Fig. 2c). Its eyes were positioned about three quarters of the pyrosome's length from its apex. At 11:12:24 a second, slightly smaller, colony of *Pyrosoma atlanticum* was observed. During collection of the shrimp/pyrosome cohort using the suction sampler at 11:13:36, the shrimp remained firmly attached to the pyrosome. The shrimp remained immobile for the full three minutes and twenty seconds of observation. Five other pyrosomes were observed on this dive, all occurring between 742m and 802m depth. The temperature, salinity and dissolved oxygen ranges were 5.2－6.0˚C, 34.13－34.16 and 2.07－2.69 ml/l, respectively, and both *Pyrosoma atlanticum* and *Pyrostremma agassizi* were observed.

ROV Dolphin 3K Dive 325

During ROV *Dolphin 3K* Dive 325 in Sagami Bay, a shrimp was observed attached ventrally to the external surface of a colony of *Pyrostremma agassizi* at 16:00:15 local time (GMT+9h) and at 460m depth. The pyrosome was oriented with the apex at a declination approximately 80˚ from the horizontal plane. The shrimp faced the apex and its eyes were positioned about one quarter of the pyrosome's length from the apex. The observation lasted for 2 seconds.

Shinkai 2000 Dive 1106

Two shrimp/pyrosome associations were observed during *Shinkai 2000* Dive 1106 at An'ei Seamount, Izu/Ogasawara Islands. Only the second, however, was captured on the video record. The pyrosome colony (*Pyrostremma agassizi*) was oriented with the apex at a slight declination from the horizontal plane. The shrimp was attached ventrally to the external surface of the pyrosome, facing the apex, and its eyes were also positioned about one quarter of the pyrosome's length from the apex (Fig. 2b). The observation lasted for 19 seconds, during which time the shrimp remained immobile.

ROV Kaiko Dive 114

A shrimp was observed attached to a pyrosome at 9:08:28 local time (GMT+9h) at 247m depth during ROV *Kaiko* Dive 114 over the Japan Trench. This shrimp was attached to the dorsal surface of the pyrosome (*Pyrostremma agassizi*), in contrast to the ventral position of the shrimps in the other pyrosome-shrimp observations, and its body shape and colour resembled a sergestid rather than *Funchalia*. The pyrosome was oriented with the apex at a declination approximately 45˚ from the horizontal plane. The shrimp faced the apex and its length was roughly equal to that of the pyrosome. As the bow wave of the ROV Kaiko reached the pyrosome, the shrimp flicked backwards off the pyrosome to a position approximately two shrimp lengths away and proceeded to hover at the same angle as the pyrosome before leaving the field of view at 9:08:32. Only one other pyrosome was observed during this dive; at 537m depth with temperature, salinity and dissolved oxygen at 6.4˚C, 33.61 and 5.7 ml/l, respectively.

Discussion

Morphological Observations

The present submersible-collected specimen is smaller than the holotype of F. sagamiensis FUJINO 1975, but is readily referable to that species. Fujino (1975) emphasised that the species bore no exopods on any pereopod, no spines on the basis or ischium of either the first or second pereopods and bore a triangularly-projected telson end. These characters, however, seem to change with growth. The smallest specimen from near Okinotorishima Is., CL ca. 3.6mm, bears no pereopodal exopod-like the present specimen and the holotype of *F. sagamiensis*. On the other hand, the slightly larger specimens, one from the same locality, CL 8.4mm, and the other from the Indian Ocean, CL 7.7mm, have a small bud-like process on the bases of all the pereopods. The presence or absence of spines on the basis and/or ischium of the first two pereopods mirrors the results for the pereopodal exopod. The smaller specimens are unarmed, but the larger two carry a spine on the basis and ischium, as does Monod's (1972) specimen. The distal margin of the telson changes in rather a different manner. The present specimen shows a close resemblance to the holotype of F. sagamiensis in this point too. The smallest specimen has a concave distal telson margin, but the remaining two specimens bear a tapered telson end, like in the adults. The distinct hepatic spine is present in all five specimens, including the holotype of *F. sagamiensis*.

Although these small specimens may not all be assignable to a single species, three diagnostic characters of *F. sagamiensis* listed by Fujino (1975) are obviously not defining. The absence of both the pereopodal exopods and the spines on the basis and ischium of the first two pereopods, the truncated telson end, and also the presence of the hepatic spine appear to be characteristic of juvenile specimens of the genus *Funchalia*. Any genital differentiation, moreover, is not evident in the present specimen, as is also the case for the holotype of the species. These observations support the supposition that the present specimen is only a juvenile but no new morphological information was discovered to help identify the adult form. There is therefore not enough information to support Hayashi's (1992) supposition that *F. sagamiensis* is the juvenile of either *F. villosa* or *F. taaningi*.

According to Pérez Farfante and Kensley (1997), *Funchalia contains* five species including *F. sagamiensis*; *F. danae* Burkenroad, 1940; *F. taaningi Burkenroad*, 1940; *F. villosa* (Bouvier, 1905); *F. woodwardi* Johnson, 1867. Of these, *F. danae* and *F. woodwardi* have more than ten rostral teeth and a hepatic spine in the adult stage, while *F. taaningi* and *F. villosa* bear five to seven rostral teeth but no hepatic spine when adults. The present specimen, therefore, has to be tentatively identified as *F. sagamiensis* until more reliable conclusions about the status of each species is obtained.

In situ and Shipboard Observations

Field observations of *F. sagamiensis* suggest that the relationship between this juvenile form and pelagic tunicates of the Order Pyrosomatida is integral to the life history of the shrimp, in contrast to the "perching" behaviour observed in sergestid shrimps. Sergestids are usually observed swimming or floating independently in the water column. No free-swimming juveniles of the genus *Funchalia* have yet been observed during more than 200 hours of submersible dive time around Japan, while six records exist for observations of *Funchalia* juveniles associated with pyrosomatid tunicates (Table 1). No amount of agitation, due either to ROV-induced turbulence or physical collision with the walls of the D-sampler, caused *F. sagamiensis* to detach itself from its pyrosome, even when the pyrosome was sheared in half by the closing doors of the D-sampler.

One previous observation exists in the literature of an association between *Funchalia* sp. (*sagamiensis*) and a pyrosome (Monod, 1972). This animal was captured while inside the cloacal cavity of a pyrosome at 22:00 near the surface at lat. 0˚- long. 151˚W on 27 November 1969. This juvenile *Funchalia* was 8mm in carapace length, compared to the present specimen of 5.6mm CL. Although the present specimen is of a smaller size than that of Monod's, it was found on the outer surface of the pyrosome. Furthermore, some individuals observed in this study were attached to pyrosomes of a relative size too small to enable the shrimp to enter the cloacal cavity. We submit that the more usual habitat of this juvenile shrimp is not within the cloacal cavity of pyrosomes but rather on the outer surface. Monod's specimen may have taken refuge within the cloacal cavity of its pyrosome while in the cod-end of the trawl. Monod's observation, however, suggests that these juvenile *Funchalia* may accompany their pyrosome hosts on their diel vertical migration. Such hitchhiking would allow the juvenile shrimp to take advantage of the higher growth rates afforded by warmer waters during the night while being protected from visual predators during the day. The energy expenditure of the shrimp for this diel vertical migration would be negligible. Furthermore, through attachment to the outer surface of the pyrosome the flow of water through the cloacal cavity of the pyrosome would not be interfered with.

Several reports exist of animals taking shelter within the cloacal cavities of pyrosomes, including juvenile penaeid shrimp such as *Penaeus trisulcatus* (Mayer, 1879), and *Parapenaeus longirostris* (Bianco, 1902), and juvenile fishes (Johnson, 2000). Some animals have been reported to be specifically adapted for life in association with pelagic tunicates (Janssen and Harbison, 1981), invariably within the cloacal cavity in the case of pyrosomes. The present report is to our knowledge the first, however, to identify an organism specifically associated with the external surface of a pyrosome.

Dall (1957) suggested that *Funchalia* spp. "may feed by piercing and sucking the body fluids of some pelagic animal", on the basis of the greatly elongate incisor processes of the mandibles and the absence of teeth in the gastric mill. Although our specimen was not directly observed feeding on the pyrosome, there is anecdotal evidence to suggest it can. Upon collection, the hepatopancreas and digestive tract of *Funchalia sagamiensis* were coloured the same shade of orange as the branchial basket of the *P. agassizi* individual to which it was attached. This orange mass migrated along the digestive tract, getting progressively more diffuse with time. Presumably it would be difficult for the shrimp to obtain other prey items while remaining firmly attached to its pyrosomatid host − as was the case for all observations of *F. sagamiensis* in Japanese waters. *Funchalia sagamiensis* exhibits several features that appear to be either advantageous for, or specifically adapted to, an extended life history stage on the surface of pelagic pyrosomatid tunicates. The conical dactyls of the fourth and fifth pereopods allowed the shrimp to attach securely to the pyrosome's outer surface by embedding them within the test. Adult *Funchalia* are usually red in colour, while juveniles are transparent. Body opacity would almost certainly be disadvantageous for an animal living on the external surface of a light-producing organism such as a pyrosome. The midline of the shrimp was always aligned with the long axis of the pyrosome when first encountered by the submersible, so whether or not the silhouette of the pyrosome was visible from below, the shrimp's silhouette would be obscured. Those portions of the shrimp that lay in direct contact with the pyrosome (eg. conical dactyls of fourth and fifth pereopods, distal end of antennal scale, carpocerite, anterior ends of flagellae) were flecked orange, possibly enhancing its camouflage under natural light. The reaction observed upon exposure to light of positioning the body at an angle, often perpendicular, to the long axis of the pyrosome and swimming while remaining attached in place, probably allows the shrimp to rotate the pyrosome such that it lies between the shrimp and any perceived threat. That the shrimp was able to sense and react to the submersible's lights after repeated exposure to them at close range shows that although some decapod crustaceans may be permanently blinded by submersible lights (Herring *et al.*, 1999), some other species are not adversely affected.

In situ surveys using submersibles can yield important ecological information on species and this is in part because of the vehicle's lights and/or thruster-induced water turbulence. In the case of *Funchalia sagamiensis* and pelagic pyrosomatid tunicates, the association can be classified as "strong" because of the shrimp's reaction to ROV-induced stresses. The shrimp remained attached tightly to the pyrosome even when tumbled in the wash of the thrusters. When bright lights were trained on the shrimp it exhibited a negatively phototactic response but did not leave the surface of the pyrosome. In contrast, the sergestid shrimp that was perched on a pyrosome abandoned its host when stressed by the approaching ROV, suggesting only a "weak" association. A "moderate" association is exemplified by that of the Caristiid sp. and the siphonophore *Praya* sp. (J.H., unpubl.). During collection of the siphonophore, the juvenile Caristiid left its position of ventral surface flush to the siphosome and ventured into the water column. However, after the nectosome of the siphonophore was collected, the Caristiid again associated with the now-detached siphosome. The intrusiveness of submersible surveys can therefore yield valuable information on the strengths of relationships between members of the midwater fauna. Likewise, feeding behaviours of visual predators such as *Loligo opalescens* have been observed in situ precisely because the ROV's lights affect the behaviour of prey items such as euphausids, causing them to aggregate, and provide a light field that allows visual predation to occur (Hunt, 2000). The increased activity of these visual predators around the ROV can in turn stimulate defensive behaviours in other animals as they are affected by the increased activity within the light field of the submersible. When care is taken in the interpretation of behavioural observations made by a submersible, it is precisely the supposedly invalidating intrusiveness of the vehicle that can allow valuable observations to be made.

Submersible-based observations have further illuminated the association between *Funchalia sagamiensis* and pelagic pyrosomatid tunicates. The association is "strong", possibly obligate for the shrimp during this life history phase, and does not appear to be species-specific. This association is yet another example of the importance of the gelatinous macroplankton as both habitat substrates for, and presumably prey items of, other mesopelagic organisms and of the sometimes vastly different ecology of juvenile and adult forms, helping further to explain the "paradox of the plankton".

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