Mar Biol (2007) 151:1899–1906
DOI 10.1007/s00227-007-0625-0

RESEARCH ARTICLE

On the consortium of the tintinnid *Eutintinnus* and the diatom *Chaetoceros* in the Pacific Ocean

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Received: 14 November 2006 / Accepted: 16 January 2007 / Published online: 6 February 2007

Abstract The morphology and distribution of the diatoms *Chaetoceros tetrastichon* and *Ch. dadayi* as epiphytes on the loricae of the tintinnids *Eutintinnus apertus* and *E. pinguis* investigated in the open waters of the Pacific Ocean. The *Eutintinnus–Chaetoceros* consortia was encountered in 38 of the 52 sampling stations from 34°N to 33°S, and together were among represented the most wide-spread species. The abundance was low with a maximum of 32 consortia l^{-1} and *E. apertus* was often the most abundant species of the genus. The free-living *Eutintinnus* congeneric species showed a wider vertical distribution, whereas *E. apertus–Chaetoceros* tended to be near the surface. The success of *E. apertus* in consortium with *Chaetoceros* may be due to increase of the clearance rate and/or the lower susceptibility to predation. *Chaetoceros* modifies its morphology to adapt the epiphytic life, especially *Ch. dadayi*. The shorter curved setae may facilitate the transfer to the lorica of the daughter tintinnid after the cell division. The free-living *Ch. tetrastichon* and *Ch. dadayi* are very rare and *Chaetoceros* remained attached to empty loricae or encysted tintinnid cells. This suggests that the *Eutintinnus–Chaetoceros* consortium is obligate for the success of the diatom and renders the tintinnid more competitive versus congeneric species.

Communicated by S.A. Poulet.

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Introduction

The paucity of nutrients in the epipelagic ocean imposes constraints on plankton growth. Some groups have developed strategies to survive based on symbiotic associations. The diatoms, typical of eutrophic and well mixed waters, are also present in stratified, oligotrophic waters. The symbiotic association of diatoms with diazotrophic cyanobacteria explains the presence and sometimes the blooming of diatoms in oligotrophic regions of the world's ocean (Venrick 1974). Beyond these diatom-cyanobacterium associations, the diatoms *Chaetoceros tetrastichon* Cleve and *Ch. dadayi* Pavillard attached to a tintinnid are often encountered in these regions. Tintinnids (Choreotrichida) are ubiquitous planktonic ciliates with a characteristic test, the lorica, secreted around the cell body. Planktonic ciliates are consumers of pico- and nano- primary producers, and also regenerate nutrients. They are also important food sources of metazoan zooplankton and fish larvae (e.g. Pierce and Turner 1992). The tintinnid attached to *Chaetoceros tetrastichon* and *Ch. dadayi* has most often been identified as *Eutintinnus apertus* Kofoid and Campbell and less frequently as *E. pinguis* Kofoid and Campbell (Kofoid and Campbell 1939; Taylor 1982). Several other, more rare, diatom-tintinnid associations have been reported, including *Planktoniella sol* (Wallich) Schütt, *Hemiaulus hauckii* Grunow *ex* Van Heurck, and *Chaetoceros peruvianus* Brightwell with *Eutintinnus lusus-undae* Entz (Rampi 1952; Kofoid and Campbell 1939) and *Fragilariopsis doliolus* (Wallich) Medlin and Sims with *Eutintinnus* spp. (Pavillard 1935; Balech 1962) and *Salpingella subconica* Kofoid and Campbell (Froneman et al. 1998). For these tintinnids, the association may be completely non-adaptive and only represent the accidental adhesion of diatoms (and possibly other debris) to the sticky loricae. The consortium between *E. apertus* and the diatoms *Chaetoceros tetrastichon* and *Ch. dadayi* suggests some adaptive significance, because the diatoms appear to closely fit the loricae of *E. apertus* with modified setae that embraced the tintinnid. These diatoms, furthermore, are extremely rare in the plankton as non-epiphytic colonies (Hernández-Becerril 1992). Taylor (1982) noted that *E. apertus* is capable of moving the entire *Chaetoceros* colony through the water, thus rendering it motile. Beyond a few diatoms associated with cyanobacteria (e.g. Gómez et al. 2005), *Ch. tetrastichon* and *Ch. dadayi* were the only diatoms able to survive in the surface oligotrophic regions investigated in this study.

This study reports, for the first time, on the spatial and vertical distribution of the *Eutintinnus–Chaetoceros* consortia. Several contrasting regional seas of the north east Pacific: a transect of 4,400 km in the western and central equatorial Pacific, and ~8,000 km along the southeast Pacific were investigated. The distributions *Eutintinnus–Chaetoceros* consortia were examined with regard to: environmental conditions such as temperature and fluorescence, as an indicator of the primary producers. The possibility that the association makes *E. apertus* more competitive than the morphologically related congeneric species is also investigated. These relationships as well as the morphology were examined in an attempt to determine the nature of the *Eutintinnus–Chaetoceros* consortia.

Materials and methods

Samples were collected during five cruises in the western Pacific Ocean (Fig. 1). Two cruises were carried out on board R/V *Soyo Maru* (13–20 May and 3–10 July 2002) along the 138°E meridian in the vicinity of the Kuroshio Current. Nine stations were sampled from 30°30′N to 34°15′N in May and 10 stations from 30°0′N to 34°20′N during the July cruise. At each station, 15 depths from 5 to 200 m were sampled; a third cruise on board R/V *Hakuho Maru* visited the Celebes, Sulu and South China Seas from November 7 to December 18, 2002. Samples were collected from ten stations at six depths from 0 to 150 m depth. A fourth cruise on board R/V *Mirai* (15–28 January 2003) traversed the equator from 160°E to 160°W. Samples were collected from 9 stations at 14 depths between 5 and 200 m depth. In the SE Pacific, one hundred samples were collected at 14 stations from 5 to 270 m depth during the BIOSOPE cruise on board R/V *L'Atalante* from October 26 to December 12, 2004 (Fig. 1). All samples were collected by Niskin bottles were preserved with acidified Lugol's solution and stored at 5°C. Samples of 500 ml were concentrated via sedimentation in glass cylinders. During a six day settling period, the top 450 ml of sample was progressively slowly siphoned off with small-bore tubing. Fifty ml of concentrate representing 500 ml whole water was settled in composite settling chambers. The entire chamber was scanned at 200× magnification under either Nikon or Olympus inverted microscope equipped with a digital camera.

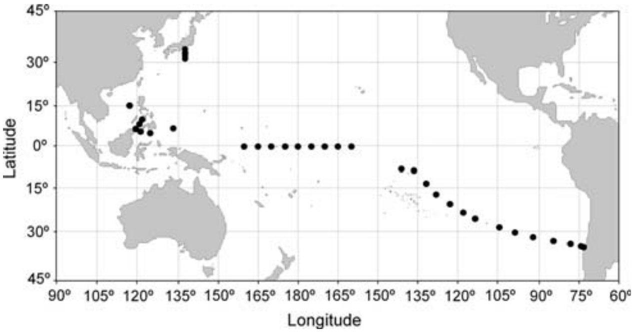

Fig. 1 Map of the stations occupied (*full circles*) in the Pacific Ocean

Results

Spatial and vertical distributions

Kuroshio Current and north Philippine Sea

The Kuroshio Current is one of the world ocean's dominant warm currents. Based on the distribution of the physical variables along the 138°E meridian in the south of Japan it is spatially distinguished into three major regions: the slope waters, the Kuroshio Current and the offshore subtropical waters of the north Philippine Sea. The hydrographic conditions differed between the two cruises. In May, a cyclonic gyre in slope waters made the Kuroshio Current narrower than in the July cruise (Fig. 2a) when the Kuroshio Current was wider and warmer (Fig. 2d). The fluorescence was higher and shallower in the slope surface waters, while a deeper 70–80 m depth maximum was present in the offshore subtropical waters. In July, the fluorescence was lower in the slope waters than in May. Southward, in the Kuroshio Current, the fluorescence values showed a deeper and thinner maxima at 90–100 m depth (Fig. 2d).

In May, *Eutintinnus* species (excluding *E. apertus*) were found in the surface waters of the Kuroshio

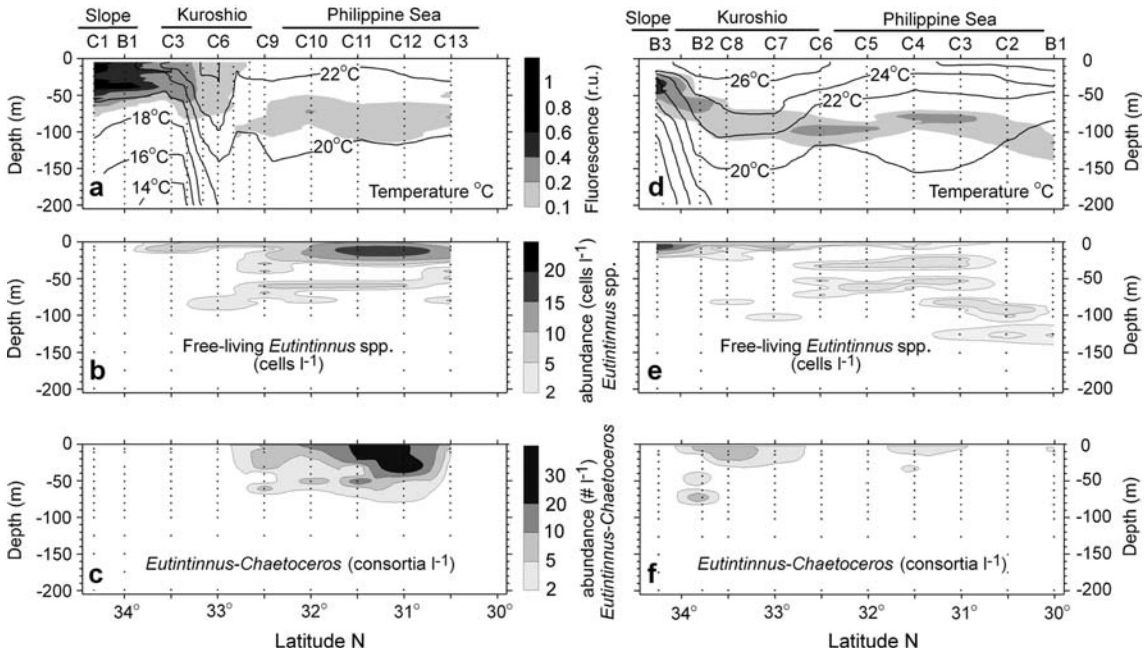

Fig. 2 Section plots of temperature (°C) and fluorescence (as relative units) in the *grey scale* (**a**, **d**). Abundance of *Eutintinnus* spp., excluding *E. apertus* (cells l^{-1}) (**b**, **e**). Abundance of *Eutintinnus–Chaetoceros* consortia (# l^{-1}) in *grey scale* (**c**, **f**). Left and right panels correspond to the distributions along the meridian 138°E in the south of Japan in May and July, respectively

Current and the north Philippine Sea and at subsurface depths (Fig. 2b). The *Eutintinnus–Chaetoceros* consortia were not observed in the slope waters or the Kuroshio Current (Fig. 2c), but occurred, instead, in the upper 40 m depth in the north Philippine Sea, with a maximum of 32 consortia l^{-1} at 31°N, 138°E.

More oligotrophic conditions prevailed in July and the abundance of tintinnids decreased (Fig. 2d, e). *Eutintinnus* spp. were encountered in the slope waters but showed a wider distribution in the offshore waters (Fig. 2e). The abundance of *Eutintinnus–Chaetoceros* consortia was low (<8 consortia l^{-1}) with the higher value in the Kuroshio Current (Fig. 2f).

Celebes, Sulu and South China Seas

The Celebes and Sulu Seas are one of the least investigated regions of the world's oceans. Oligotrophic conditions prevailed in the open waters of the regional seas of the western Pacific Ocean. In the Celebes Sea, upwelling is induced by wind-driven surface water circulation through the Shibutu Strait that connects the Sulu and Celebes Seas. The ascent of the isotherm of 28°C was associated with a surface increase of the fluorescence (Fig. 3a). *Eutintinnus* spp. were restricted to a surface peak in the Shibutu Strait and the subsurface chlorophyll maxima in the South China Sea (Fig. 2b). The distribution of *Eutintinnus–Chaetoceros* consortia was wider than *Eutintinnus* spp., with a low abundance (<6 consortia l^{-1}).

Western and central equatorial Pacific Ocean

A longitudinal transect of 4,400 km along the equator between 160°E and 160°W was investigated during El Niño-Southern Oscillation conditions in January–February 2003. The Western Pacific Warm Pool showed a deep fluorescence maximum (90–120 m depth) (Fig. 3d). The abundance of *Eutintinnus* spp. was very low and tended to appear at subsurface depths (Fig. 3e). The *Eutintinnus–Chaetoceros* consortia were found at all stations, predominantly near the surface, with abundance that did not exceed 6 consortia l^{-1} (Fig. 3e). In the equatorial upwelling region, the fluorescence was higher and shallower (Fig. 3d). *Eutintinnus* spp. showed a surface peak and the *Eutintinnus–Chaetoceros* consortia showed a wider distribution with a surface peak of 10 consortia l^{-1} (Fig. 3e, f).

South East Pacific Ocean

The transect along ~8,000 km in the SE Pacific included several contrasting regions. The surrounding waters of the Marquesas Islands Archipelago are under the influence of the high-nutrient low-chlorophyll conditions of the equatorial upwelling region. The central

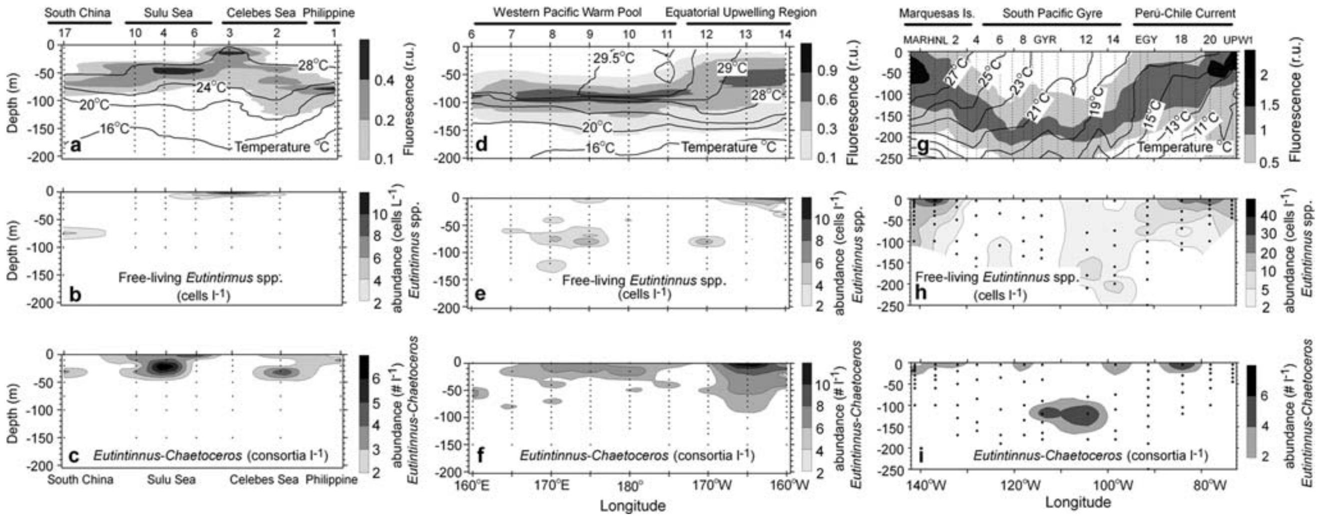

Fig. 3 Section plots of temperature (°C) and fluorescence (as relative units) in the *grey scale* (**a**, **d**, **g**). Abundance of *Eutintinnus* spp., excluding *E. apertus* (cells l^{-1}) (**b**, **e**, **h**). Abundance of *Eutintinnus*–*Chaetoceros* consortia (# l^{-1}) in *grey scale* (**c**, **f**, **i**). *Left panel* Celebes, Sulu and South China Seas, *Central panel* western and central equatorial Pacific, *Right panel* SE Pacific Ocean

part of the transect, the South Pacific Gyre, covered some of the most oligotrophic waters of the world's oceans. The fluorescence maxima were located at 180–200 m depth (Fig. 3g). The Perú-Chile Current was associated with a shallower fluorescence maxima progressively increasing towards the region of upwelling off the Chilean coast (Fig. 3g). The abundance of *Eutintinnus* spp. was higher in the surface waters in the more eutrophic stations near the Marquesas Is. Archipelago and the Perú-Chile Current. The records of *Eutintinnus* spp. were scarce in the extremely oligotrophic waters of the South Pacific Gyre (Fig. 3h). In contrast to other regions, the abundance of the *Eutintinnus*–*Chaetoceros* was very low compared to *Eutintinnus* spp. (Fig. 3i). The records were restricted to the surface waters and a few records at about 100 m depth at the southern limit of the South Pacific Gyre (Fig. 3i).

Morphology of the *Eutintinnus*–*Chaetoceros* consortia

The *Eutintinnus*–*Chaetoceros* consortia imply the association of two morphologically, closely related species diatoms: *Ch. tetrastichon* and *Ch. dadayi* and two tintinnid species of the genus *Eutintinnus*. The diatoms are easily identifiable taxa, while the identity of the tintinnid is more difficult. The genus *Eutintinnus*, characterized by a large transparent lorica, is one of the most widespread and species-rich genera (Kofoid and Campbell 1929, 1939). The species showed a very pronounced polymorphism and nearly allied and so closely connected by intermediate forms, making it very difficult to draw any line of separation between the species. The tintinnids have been identified as *E. apertus*, however, in a few cases, the *Eutintinnus*–*Chaetoceros* consortia includes *E. pinguis*. The lorica of *E. apertus* does not noticeably differ from other congeneric species. *E. apertus* tended to be the most common species of the genus and this success is attributable to the consortium with *Chaetoceros*.

Chaetoceros tetrastichon and *Ch. dadayi*

The two *Chaetoceros* species are distinctive taxa with closely related morphologies. Both diatoms form short and straight chains with long, thick, spine-bearing setae arising from the corners of the valves. These setae diverge, curve and lie parallel to the transapical axis. The setae of *Chaetoceros* are oriented toward the posterior part (aboral aperture of the tintinnid). One pair of setae is generally curved more strongly to embrace the lorica. The species showed several small, round chloroplasts in the valves and the setae. The colonies of *Chaetoceros* are invariably located in the anterior part near the oral aperture (Fig. 4a–n). In the species, *Ch. dadayi* (Fig. 4a–k) the disposition and morphology of the setae are more modified than in *Ch. tetrastichon* (Fig. 4a–j). *Chaetoceros dadayi* showed at least two setae directed toward the anterior or apical region of the tintinnid (oral aperture) in the direction of normal movement of the tintinnid.

Chaetoceros remain attached to empty and even damaged loricae (Fig. 4e–g), although it is possible that mechanical disturbance associated with sample handling may cause the soft cell body to detach from the loricae (Paranjape and Gold 1982). *Chaetoceros* also appeared to be attached to encysted tintinnid cells

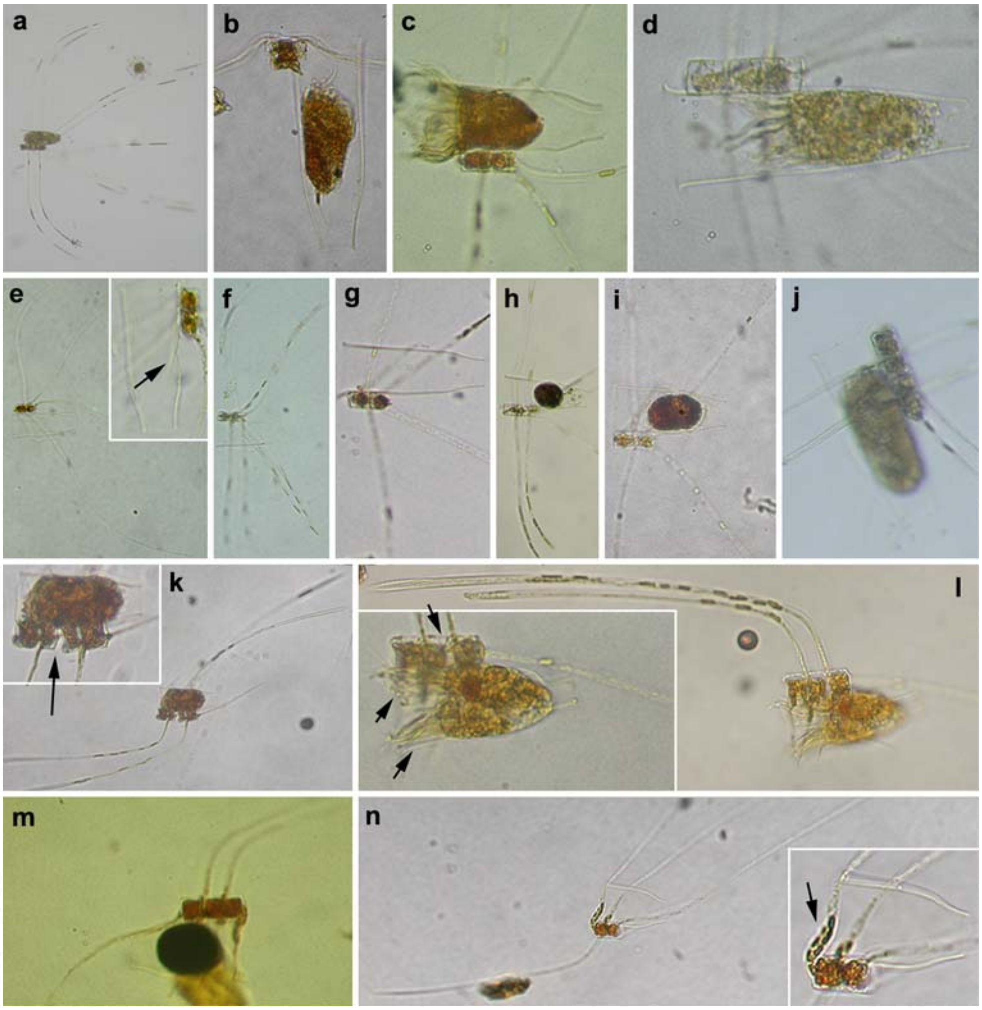

Fig. 4 Photomicrographs of *Eutintinnus–Chaetoceros* consortia from the Pacific Ocean, bright field optics. **a–c** *Eutintinnus apertus–Ch. tetrastichon* (**a** 0°, 165°W, 10 m depth; **b** 33°45′N, 138°E, 40 m; **c** 0°, 180°, 15 m). **d** *Eutintinnus pinguis–Ch. tetrastichon* (0°, 160°W, 40 m). (**e**) *Ch. tetrastichon* in an empty lorica of *E. apertus* (0°, 170°E, 0 m). The *arrow* indicates the damage contour of the lorica. **f**, **g** *Ch. tetrastichon* in an empty lorica of *E. apertus* (**f** 0°, 170°E, 80 m; **g** 5°10′N, 124°05′E, 30 m). **h** Cyst of *E. apertus* with *Ch. tetrastichon* (0°, 165°W, 70 m). **i** *E. apertus-Ch. tetrastichon* (7°25′N, 121°12′E, 10 m). **j** *Eutintinnus–Ch. tetrastichon*, four cells-chain (0°, 165°W, 20 m). **k** *E. apertus–Ch. dadayi*. The *arrow* indicates the recently divided chain of *Ch. dadayi* (31°30′N, 138°E, 5 m). **l** *E. apertus–Ch. tetrastichon*. Note the thick, anterior setae. The *arrows* indicate *Eutintinnus* under division and the fragmented cells of *Chaetoceros* (32°N, 138°E, 10 m). **m** Cyst of *E. apertus* with *Ch. dadayi* (0°, 180°, 15 m). **n** Empty lorica of *E. apertus* with *Ch. dadayi* (7°25′N, 121°12′E, 30 m). The *arrow* indicates the thick setae that embrace the lorica. *Scale bar* 20 µm

(Fig. 4h, i, m). In these cases, the tintinnid remained attached to the lorica, even when the ciliate was no longer motile.

Rampi (1952) described *Chaetoceros dadayi* var. *pacifica* from the central equatorial Pacific. This form, which has not been reported in the literature since the initial description, is characterized by two anterior setae that thickened in the proximal and central parts with a transversal striation. Figure 4n showed the anterior thick seta of *Ch. dadayi* that accumulated numerous chloroplasts (Fig. 4n). Other *Chaetoceros* specimens showed thickening in the distal part of the anterior setae (Fig. 4l).

The chains were usually formed of three cells, followed by 2-cells chains and rarely 4-cells chains (Fig. 4j, k). No chain longer than 4 cells was observed. One *Eutintinnus–Chaetoceros* consortium was composed of only one *Chaetoceros* cell (Fig. 4b). In the absence of sampling induced damage, this observation of the diatom adhering to the lorica on the valve surface suggests that the setae are not necessary. The shorter setae that embraced the lorica may reinforce, but they are not essential for the adhesion to the lorica (Fig. 4b).

One of the 4-cells chains showed the chain separated into 2 chains of 2-cells that suggested a recent division (Fig. 4k). A 3-cell chain was encountered attached to a tintinnid in division (Fig. 4l). One of the cells of *Chaetoceros* was slightly separate from the rest of the colony. The synchrony of the division of *Chaetoceros* and *Eutintinnus* cannot be demonstrated based on fixed specimens. The present observations suggest that the shorter setae of the colony that embraced the lorica might facilitate the transfer of the diatom to the new lorica of the daughter tintinnid cell after the chain fragments (Fig. 4k, l).

Eutintinnus apertus and E. pinguis

The lorica of *E. apertus* corresponds to a slightly tapering cylinder, narrowing abruptly near the aboral aperture to a width of about half of the mouth (Fig. 4a–c, e–m). The oral (anterior) margin may be slightly flared. The lorica length is 70–110 µm and the oral diameter is 25–40 µm. The lorica of other specimens showed a narrower aboral diameter when compared to that of *E. apertus* and more closely resembled *Tintinnus angustatus* Daday (Fig. 4n).

Eutintinnus pinguis showed a similar or slightly larger oral diameter (30–40 µm) (Fig. 4d, j) than *E. apertus*, but tended to be longer (100–140 µm) with a less abrupt tapering of the aboral aperture. Hada (1938) considered *E. pinguis* and *E. pacificus* Kofoid and Campbell as synonyms.

Discussion and conclusions

The association of *Eutintinnus–Chaetoceros* is well known (Kofoid and Campbell 1939; Taylor 1982). To date, however, the nature of this association has remained uncertain. The term symbiosis is currently used in three different ways: in the broadest sense, to include all physical associations regardless of benefit or harm; in the narrowest sense, applying only to associations of mutual benefit (i.e. as a synonym for mutualism) or to non-parasitic associations subdivided into commensalisms (no benefit or harm to the host) and mutualism (mutual benefit) (Taylor 1982). To date, the nature and distribution of the *Eutintinnus–Chaetoceros* consortia have not been investigated. Historical studies based on net hauls resulted on the separation of members of the fragile *Chaetoceros–Eutintinnus* consortia. For example, Hada (1938, p. 182) reported for *E. apertus*: "specimens from European waters often carry a colony of *Chaetoceros*...but there is no record of such an example from the Pacific". However, Ikari (1926) had already reported both *Ch. tetrastichon* and *Ch. dadayi* attached to *Eutintinnus* in the surrounding waters of Japan.

Diatoms such as *Chaetoceros* are typical organisms of well mixed and eutrophic waters, however, when forming consortia this genus can also be found in stratified oligotrophic surface waters. In some locations, such as the SE Pacific, *Chaetoceros* in consortium with *Eutintinnus* was the only diatom in the upper 150 m depth. *Chaetoceros tetrastichon* and *Ch. dadayi* never reached high abundances, but they constituted one of the most ubiquitous diatoms in the surface open waters of the Pacific from 34°N to 33°S. For the diatom, the association with a tintinnid appears to be obligate for its widespread distribution.

Beyond the *Eutintinnus–Chaetoceros* consortium, another well-known association, although less ubiquitous, is the ciliate *Vorticella*, an aloricate ciliate with contractile stalks that can be found on colonies of *Chaetoceros coarctatum* Lauder. A single chain may support twenty or more of the ciliates and the motions of the ciliary beating move the chains in an irregular manner (Taylor 1982). According to Taylor, *Vorticella* is the epibiont and *Chaetoceros* is the host, whereas for the *Eutintinnus–Chaetoceros* association, *Chaetoceros* is the epibiont and *Eutintinnus* is the host. Taylor (1982) reported, based on the observation of living cells, that the tintinnid is capable of swimming rapidly through the water and consequently constitutes a phoretic association. In both, *Chaetoceros–Vorticella* and *Eutintinnus–Chaetoceros* the ciliate renders the association motile. The literature reports other, less common, attachments between tintinnid species and diatoms such as *Chaetoceros peruvianus*, *Fragilariopsis doliolus*, *Hemiaulus hauckii* or *Planktoniella sol* (Pavillard 1935; Kofoid and Campbell 1939; Rampi 1952; Balech 1962; Froneman et al. 1998). These epiphytic associations were encountered in waters where the diatoms as free-living cells were very abundant. None of these diatoms modify their morphology to adapt to life as an epiphyte, suggesting an accidental adhesion to a sticky lorica. Whether the epiphytic life is beneficial for the diatom, the lack of an apparent mechanism for transfer of the diatom to the new lorica of the daughter tintinnid cells may limit the dispersal of the association.

Chaetoceros tetrastichon and *Ch. dadayi* showed distinct morphological adaptations to an epiphytic lifestyle, such as the orientation of the setae. Both diatoms were extremely rare as free-living colonies; the few records that exist may be attributed to the disruption of the consortia due to rough sample treatment. This study suggests that the diatom remains attached to the lorica even if it is empty, damaged or the tintinnid is encysted (Fig. 4e–i). The species of the genus *Chaetoceros* are typically composed of colonies in a par number or single cells. Chains of 2 or 3 cells are exceedingly uncommon. *Chaetoceros tetrastichon* and *Ch. dadayi* usually form 3-cell chains and never exceeded 4 cells per chain or a chain length of about one half of the lorica length. The *Eutintinnus–Chaetoceros* consortium is motile (Taylor 1982) and a very long *Chaetoceros* chain would encumber the locomotion of the consortium. The longer setae are directed toward the posterior part (except the two anterior setae of *Ch. dadayi*). Consequently, a prospective tintinnid predator approaching from the rear, will find the pointed spine-bearing setae. The role of the shorter setae seems to be to reinforce the adhesion to the colony. However, these short setae are not strictly required for the adhesion to the lorica (Fig. 4b). Another unsolved question relating to this association concerns the mechanism of transfer of the diatom cells to a new lorica. The short setae that embrace the lorica may detect the newly forming lorica and facilitate the transfer to the tintinnid daughter cell. The present study illustrates a tintinnid in division where the diatom chain is fragmented (Fig. 4l). The induction of the fragmentation of the colony is a common strategy for the dissemination of the colonial diatoms (Smetacek 1985).

Benefit for the diatom

Traditionally, the success of phototrophic species such as *Chaetoceros* is believed to be a function of photosynthetic efficiency (nutrient uptake and light availability) and grazing pressure. The irradiance level depends on the position in the water column. In stratified open waters, heavily silicified diatoms can become light limited as they sink to depth. *Rhizosolenia* is a genus that is often associated with pelagic, oligotrophic regions of the world's oceans. These often large, yet lightly silicified, diatoms have large vacuoles that may facilitate buoyancy. Heavily silicified *Chaetoceros* spp., such as those in this study, lack large vacuoles or other obvious mechanisms to improve cell buoyancy. Doubtless, the locomotion of the tintinnid is responsible for the occurrence of these heavily silicified *Chaetoceros* in stratified surface open waters.

Diatoms such as *Chaetoceros* are more typical habitants of nutrient rich waters. Nutrient concentrations in the stratified, epipelagic, oligotrophic waters are expected to be too low to support the growth of this species. In contrast to other diatoms, *Ch. tetrastichon* and *Ch. dadayi* are able to survive in these nutrient limited regions when associated with the tintinnid. Both *Chaetoceros* species belong to the *Phaeoceros* group, that beyond some minor ultrastructural differences (Hernández-Becerril 1992), is characterized by the presence of chloroplasts in the setae. The chloroplasts in the setae increase the photosynthetic capacity and the extension of the cytoplasm in the setae increases the surface area for nutrient uptake (nonmotile autotrophic organisms will easily deplete the nutrients from the surrounding waters). The motile tintinnid provides its epiphytes with greater access to new nutrient-rich patches in the water column. One source of nutrients in oligotrophic waters is excretion by heterotrophic organisms. Epiphytic *Chaetoceros* spp. are invariably attached to the oral aperture of the tintinnid. In this position, the nutrients excreted by the ciliate may contribute to the requirements of *Chaetoceros*.

Benefit for the tintinnid

The success of a heterotrophic species such as *Eutintinnus* spp. would mainly depend on feeding efficiency as well as an ability to escape from predation. Investigations of feeding revealed that tintinnids ingest a large variety of pico- and nano-sized prey, ranging in size from about 2 μm to particles about one half the lorica oral diameters (Spittler 1973). The average oral diameter of *Eutintinnus apertus* is ~30 μm. The *Eutintinnus–Chaetoceros* consortia tended to appear in the surface waters (Figs. 2, 3). Larger nanoplankton cells tend to be more abundant near the deep chlorophyll maxima. Free-living unicellular cyanobacteria, mainly *Prochlorococcus*, Chisholm et al. and *Synechococcus* Nägeli, are a ubiquitous component of the picoplankton, with abundances of ~10 × 10^6 cells l^{-1} (Blanchot et al. 2001). The genus *Eutintinnus* is composed of numerous closely related species with quite similar oral diameters (Kofoid and Campbell 1939). The success of a *Eutintinnus* species could depend on the higher clearance rate versus congeneric species. In some ocean regions, *E. apertus* was the most abundant species of the genus (Figs. 2, 3). At a first sight, the main difference of *E. apertus* is its association with a diatom. There is no direct evidence for the transfer of any *Chaetoceros*' metabolite to the tintinnid; however, an advantage for *E. apertus* may be inferred from the physical association.

Jonsson et al. (2004) reported that *Tintinnus inquilinum* O.F. Müller attached to aggregates has a feeding rate 80% higher than free-swimming individuals. This is due to the change in the fluid dynamics of the feeding current, which leads to steeper velocity gradients and higher flow rates close to the lorica. Jonsson et al. (2004) reported that this mechanism would also operate for swimming suspension feeders attached to smaller particles that significantly increase the hydrodynamic drag. Jonsson et al. (2004), based on published illustrations of *E. apertus* with attached *Ch. dadayi*, calculated that the drag resulting from the exposed surface, could increase the flow through the ciliary filter by a factor of three. A higher clearance rate of *E. apertus* with attached diatoms could explain the success of this species versus congeneric species in epipelagic, oligotrophic waters were the food resources are low.

The success of a species would also depend on predation avoidance. As an example, the delicate, tropical ciliate *Vorticella* spp. can be found as an epizoid among the setae of the diatom, *Chaetoceros coarctatus*, where it appears to be less vulnerable to predation. The swimming pattern typical for many free-living tintinnids has been described as steep, helical trajectories and without jumps (Broglio et al. 2001). This mobility is likely impaired in the *Eutintinnus–Chaetoceros* consortia due to the drag created by the long diatom chain, and could make escape from predation more difficult. The predators of the *Eutintinnus–Chaetoceros* consortia, however, encounter the long, spine-bearing setae of *Chaetoceros* when approaching the small ciliate. Furthermore, the presence of the epiphyte increases the effective size of the tintinnid by a factor of about 5, thus exceeding the feeding-particle size spectra of its small predators. Jonsson et al. (2004) reported that the predation rate by calanoid copepods on *Tintinnus inquilinum* with attached aggregates was three times less than the predation rate on similar congeneric, free-swimming tintinnids. Thus, epiphytic *Chaetoceros* may act as a grazing deterrent for *Eutintinnus* against small size predators.

Eutintinnus apertus is morphologically, and likely physiologically, similar to other, exclusively free-living, congeneric species. As a consortium with *Chaetoceros*, however, it is one of the most ubiquitous species of the Pacific Ocean. The association is very likely, mutually beneficial for both species. The association between *E. apertus* and the diatoms *Chaetoceros tetrastichon* and *Ch. dadayi* suggests an adaptive significance and a mutual benefit for both taxa, especially for species of *Chaetoceros* that constitute the only members of that genus in surface oligotrophic waters. Further studies of the nature of the *Eutintinnus–Chaetoceros* consortia will contribute to a better knowledge of symbiosis in the sea.

Acknowledgments The studies in the NE and equatorial Pacific were supported by a fellowship of the European Commission (ICB2-CT−2001-80002) held at the University of Tokyo with K. Furuya as host. I am grateful to the scientists and crew of R/V *Soyo Maru* (Nat. Res. Inst. Fish. Sci.), R/V *Hakuho Maru* (ORI, Tokyo University), R/V *Mirai* (JAMSTEC) and R/V *L'Atalante* (IFREMER). I thank to H. Claustre for the seawater samples and J. Ras for collecting assistance. I thank S. Coale for improving on the manuscript. This is a contribution to a Grant-in-aid for Creative Basic Research (12NP0201, DOBIS) from the MEXT, Japan; BIOSOPE of the LEFE-CYBER and the French IFB 'Biodiversité et Changement Global' programs.

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