JOURNAL OF PLANKTON RESEARCH | VOLUME 27 | NUMBER 12 | PAGES 1301–1306 | 2005

SHORT COMMUNICATION

First record of the calanoid copepod *Acartia omorii* (Copepoda: Calanoida: Acartiidae) in the southern bight of the North Sea

LAURENT SEURONT

ECOSYSTEM COMPLEXITY RESEARCH GROUP, STATION MARINE DE WIMEREUX, CNRS UMR 8013 ELICO, 28 AVENUE FOCH, 62930 WIMEREUX, FRANCE AND SCHOOL OF BIOLOGICAL SCIENCES, FLINDERS UNIVERSITY, GPO BOX 2100, ADELAIDE SA 5001, AUSTRALIA

CORRESPONDING AUTHOR: laurent.seuront@univ-lille1.fr

Received July 18, 2005; accepted in principle August 25, 2005; accepted for publication October 12, 2005; published online October 19, 2005

Communicating editor: K.J. Flynn

The occurrence of the calanoid copepod, Acartia omorii, is reported for the first time in the coastal waters of the Southern bight of the North Sea, off Calais harbour. Acartia omorii males and females were consistently found in four plankton samples. The collected specimens were compared with A. omorii individuals collected from the type locality (Tokyo Bay, Japan). The capture of A. omorii, a species native to Japanese coastal waters, is in agreement with the recent observation of the Japanese macroalgae Undaria pinnatifida within Calais harbor and the hypothesis of passive transport in ship's ballast water.

INTRODUCTION

Copepods of the family Acartiidae are common inhabitants of coastal and estuarine environment in all oceans of the world. They are thought to be mainly adapted to high food concentrations, which are encountered in estuaries and upwelling regions. Paffenhöfer and Stearns (Paffenhöfer and Stearns, 1988) demonstrated that *Acartia tonsa* have to be restricted to coastal waters, because they cannot obtain enough food for reproduction offshore where food concentration is low. However, alternative factors which could contribute to the nearshore affinity of *A. tonsa* include limited salinity tolerances (Tester and Turner, 1991; Cervetto *et al.*, 1999), a proper combination of warm water and low salinity favourable to naupliar survival (Tester and Turner, 1991) and omnivorous feeding characteristics (Johnsson and Tiselius, 1990). Their space–time distribution may owe a lot to the fact that a number of *Acartia* species produce diapause eggs which allow them to lie dormant in the sediment and to appear suddenly in the plankton when conditions are favourable (e.g. Viitasalo and Katajisto, 1994). Diapause eggs may also have played a role in the dispersion of *Acartia omorii* by transportation in ship's ballast water to other parts of the world (Hirakawa, 1988).

While large copepods (mainly *Calanus* spp.) are abundant in the Northern North Sea and the western English Channel, small species such as *Acartia clausi*, *Centropages hamatus* and *Temora longicornis* dominate in the eastern English Channel and the southern bight of the North Sea (e.g. Fransz *et al.*, 1991; Williams *et al.*, 1993). To our knowledge, the only copepods of the family Acartiidae reported in the coastal waters of the eastern English Channel and the southern bight of the North Sea are *A. clausi*, *A. tonsa*, *Acartia discaudata* and *Acartia bifilosa*, the last three being mainly restricted to the waters of Dunkirk harbour (Brylinski, 1981, 1984;

doi:10.1093/plankt/fbi088, available online at www.plankt.oxfordjournals.org

Bradford-Grieve, 1999). *Acartia clausi* Giesbrecht has long been considered as an abundant and widespread plankton calanoid copepod in Japanese inlet waters and as a good indicator species of these waters (Yamazi, 1956). Bradford (Bradford, 1976), however, making a revision of Acartiidae species, distinguished the Japanese *A. clausi* from Giesbrecht's *A. clausi* s. str. and described the new species *A. omorii* from Tokyo Bay.

Some copepods formerly attributed to *A. clausi* in the Northwest Pacific have thus been showed to consist of at least two species, i.e., *A. omorii* and *Acartia hudsonica* (Ueda, 1986). While extensively studied in terms of vertical distribution (Tanaka *et al.*, 1987a,b; Kimoto, 1988), physiology (Laguna and Uye, 2001), feeding (Ishii, 1990; Uye and Takamatsu, 1990), egg production (Ayukai, 1987), population dynamics (Liang and Uye, 1996) and taxonomy (Yoo *et al.*, 1991), *A. omorii* have only been observed once outside Japanese waters, in the coastal waters of southern Chile (Hirakawa, 1988; Bradford-Grieve, 1999; Bollens *et al.*, 2002). To date, *A. omorii* have never been recorded in the coastal waters of the eastern English Channel and the southern bight of the North Sea, although many zooplankton surveys have been carried in this area (e.g. Brylinski, 1981, 1984; Brylinski *et al.*, 1988; Seuront, 1999; Breton, 2000; Cotonnec, 2001).

In this article, *A. omorii* collected in the coastal waters of the southern bight of the North Sea are described. Their relative abundance is compared to indigenous zooplankton taxa, and their body proportions compared to those of the indigenous *A. clausi*, *A. omorii* specimens from the type locality and to previous taxonomic studies. A mechanism for their introduction in the study area is proposed with regard to a recent evidence for the presence of another non-indigenous marine species. The potential consequences of their successful establishment and dispersal are briefly discussed.

METHOD

Zooplankton were collected by vertical hauls of a WP2 net (200-μm mesh size), on 10 May 2004, during a routine survey cruise. The net was hauled vertically at 50 cm s^{-1}, and filtered volume was estimated from the flowmeter reading and the net diameter. The specimens were netted in three different hauls, taken at four stations with coordinates 50°58′788 N/1°51′230 E, 50°58′855 N/1°52′194 E, 51°59′438 N/1°53′901 E, and 51°59′594 N/1°54′334 E. Immediately after sampling, zooplankton were fixed and preserved in 5% paraformaldehyde (final concentration).

Calanoida and Harpacticoida species were identified according to Farran (Farran, 1948a,b, 1951a,b) and Wells (Wells, 1970). The Acartiidae species were identified following Bradford (Bradford, 1976), Chihara and Murano (Chihara and Murano, 1997) and Bradford-Grieve (Bradford-Grieve, 1999). *Acartia omorii* is closely related to *A. hudsonica* and *A. clausi* (e.g. Barthélémy, 1999; Bradford-Grieve, 1999) and has sometimes been confused with *A. hudsonica* and *A. omorii* (Ueda, 1986). *Acartia omorii* was mainly distinguished from *A. clausi* by the absence of posterodorsal spines and posterior hairs on the posterior prosome of *A. omorii* for females and for males (i) the absence of posterodorsal spines and posterior stiff hairs on the posterior prosome of *A. omorii* and (ii) the posteroventral hairs on the posterior prosome of *A. omorii* (Table I). The criteria used to distinguished *A. omorii* from *A. hudsonica* were the proportion of length to width of the genital double somite for females and the shape of the inner lobe of the third exopodal segment of the right fifth leg for the males. In *A. hudsonica*, the genital segment of the female is long (i.e. ratio of genital segment length/width is bounded between 1.20 and 1.34; Chihara and Murano, 1997; Bradford-Grieve, 1999) and the inner projection on the right segment of the right fifth leg of the male has a rounded distal end (Ueda, 1986; Table I). In contrast, in *A. omorii*, the genital segment of the female is relatively short (i.e. ratio of genital segment length/width is bounded between 0.99 and 1.10; Chihara and Murano, 1997; Bradford-Grieve, 1999) and the inner projection of the right fifth leg of the male has two unequal distal processes (Ueda, 1986; Table I). We finally ensure the relevance and the generality of our determination by comparing *A. omorii* specimens observed in the present work with specimens of *A. omorii* sampled from the type locality (i.e. Tokyo Bay, Japan; Bradford, 1976) at an anchor station (35°23′55 N, 139°46′45 W) on October 24, 2000. The sampling strategy employed was identical to the one described above. Copepods were identified under a dissecting microscope (Olympus SZX12), and for *A. clausi* and *A. omorii* the sex of individuals and body proportions were measured using an ocular micrometer.

RESULTS AND DISCUSSION

Seven copepod species were identified: the calanoid copepods *A. clausi*, *A. omorii*, *Centropages typicus*, *Paracalanus parvus*, *Pseudocalanus minutus* and *T. longicornis*, and the harpacticoid copepod *Euterpina acutifrons*. No significant differences in copepod absolute or relative abundance were found between the four sampling stations. The zooplankton assemblage was strongly dominated by *T. longicornis* (1430 ± 112 individuals m^{-3}; 42.8 ± 1.1%) and *A. clausi* (1028 ± 102 individuals m^{-3}; 31.7 ± 1.4%). The abundance of *P. parvus* and *P. minutus* was fairly similar (420 ± 41 individuals m^{-3} and 12.6 ± 1.4%, and 365 ± 32 individuals m^{-3} and 10.9 ± 1.3%, respec-

Table I: Comparisons of distinctive characters of Acartia species closely related to each other

	Acartia omorii	*Acartia clausi*	*Acartia hudsonica*
Female			
Last pedigerous somite posterodorsally with spines	No	No	No
Posterior prosome	Ventral hairs	Posterodorsal spines and posterior stiff hairs	Ventral hairs
Proportion of length to width of genital double somite	0.99–1.10[abc]	1.10–1.20	1.20–1.34
Posterodorsal margin of genital somite	Naked	Bordered posterodorsally with conspicuous spines	Naked
Male			
Posterior prosome	Posteroventral hairs	Dorsal spines and posterior stiff hairs	Two rows of lateral hairs
First exopodal segment of right fifth leg	With a long setae	With a long hairy setae	With a long setae
Inner lobe of third exopodal segment of right fifth leg	With two unequal distal processes	With a rounded distal end	With a rounded distal end

[a]Referred from Ueda (1986).
[b]Referred from Chihara and Murano (1997).
[c]Referred from Bradford-Grieve (1999).

tively), and significantly higher than the abundance of *C. typicus* (50 ± 6 individuals m^{-3}; 1.5 ± 0.4%), *A. omorii* (12 ± 3 individuals m^{-3}; 0.3 ± 0.1%) and *E. acutifrons* (7 ± 2 individuals m^{-3}; 0.2 ± 0.1%). Apart from the newly observed *A. omorii*, the abundances of all other reported species are congruent with previous studies conducted in the same area (e.g. Brylinski, 1986; Breton, 2000; Cotonnec, 2001). The abundance of *A. omorii*, observed here for the very first time in the southern bight of the North Sea, is 88 times smaller than the one of *A. clausi*, the only other Acartiidae species identified here. The sex ratio of *A. clausi* (0.51 ± 0.05) is significantly higher ($P < 0.05$) than the one of *A. omorii* (0.30 ± 0.02), potentially suggesting different mating strategies as it would be more difficult for a *A. omorii* male to find a female than for a *A. clausi* male.

Measurements of body proportions of *A. omorii* and *A. clausi* males and females are shown and compared in Table II. The prosome lengths (PL) of both *A. omorii* males and females are significantly higher (Wilcoxon-Mann–Whitney U-test, $P < 0.05$) than those of *A. clausi* and similar to previous measurements found in the literature (Bradford, 1976; Ueda, 1986; Chihara and Murano, 1997; Bradford-Grieve, 1999; Soh and Suh, 2000; Table II; see also www.copepodes.obs-banyuls.fr). For both species, males are significantly smaller than females (U-test, $P < 0.05$; Table II), and there is a significant negative correlation (Spearman test, $P < 0.01$) between the female prosome length/width ratio (PL/PW) and PL length size. The male PL/PW, however, is independent of body size ($P > 0.05$). The mean ratio does not significantly differ between male and female within a same species (*U*-test, $P > 0.05$) and is significantly higher for *A. omorii* than *A. clausi* ($P < 0.01$; Table II). The length/width ratio of the genital segment (GL/GW) is positively correlated with body size for both species ($P < 0.05$). Finally, the caudal ramus length/width ratio (RL/RW) varies greatly and within the same species, it is significantly higher ($P < 0.05$) for females than males. This ratio is not significantly different for male *A. omorii* and *A. clausi* but is significantly higher ($P < 0.05$) for female *A. clausi* (Table II).

The previous results are specified by the comparison of the body proportions of males and females of *A. omorii* sampled in the southern bight of the North Sea and in the type locality (Tokyo Bay, Japan). No significant differences are observed between the specimens sampled in the North Sea and Tokyo Bay, both in terms of specific morphologic characters (Table I) and body proportions (Table II). The allometric relationships observed between (i) males and females prosome length and prosome length/width ratio, (ii) female prosome length and the length/width ratio of the genital segment, and (iii) males and females prosome length and the caudal ramus length/width ratio are not distinguishable for the specimens from the North Sea and Tokyo Bay (*t*-test, $P > 0.05$; Table III), providing sufficient evidence to support the identification of collected specimens as the exotic Japanese species, *A. omorii*, and suggesting that the European and Japanese cannot be distinguished morphologically.

Table II: Prosome length and body proportions of Acartia omorii males and females sampled in the Southern bight of the North Sea and the type locality (Tokyo Bay, Japan) and Acartia clausi males and females sampled in the southern bight of the North Sea (France)

	Species											
	Acartia omorii (North Sea)				Acartia omorii (Tokyo Bay)				*A. clausi*			
	Male	*n*	Female	*n*	Male	*n*	Female	*n*	Male	*n*	Female	*n*
PL	1.03 (0.01)	10	1.12 (0.02)	10	1.10 (0.02)	25	1.15 (0.02)	30	0.80 (0.01)	15	1.01 (0.02)	15
	1.00–1.19		*0.94–1.22*		*1.00–1.19*		*0.94–1.22*		*0.71–1.31*		*0.81–1.47*	
PL/PW	2.45 (0.04)	10	2.48 (0.04)	10	2.41 (0.05)	25	2.50 (0.04)	30	2.32 (0.02)	15	2.36 (0.03)	15
GL/GW	–		1.02 (0.02)		–		1.00 (0.02)		–		1.15 (0.02)	
	–		*0.99–1.07*		–		*0.99–1.07*		–		*1.10–1.20*	
RL/RW	1.14 (0.04)	10	1.45 (0.05)	10	1.17 (0.04)	25	1.48 (0.06)	30	1.13 (0.04)	15	1.94 (0.05)	15
	1.10–1.25		*1.05–1.84*		*1.10–1.25*		*1.05–1.84*		*1.02–1.24*		*1.83–2.08*	

GL and GW, genital segment length and width; *n*, number of individuals considered; PL and PW, prosome length and width; RL and RW, right caudal ramus length and width. The numbers in parentheses and in italic are the standard deviations obtained in the present work and the range of values reported in Bradford-Grieve (1999), respectively.

Table III: Allometric relationships obtained between prosome length and different morphometric ratios for Acartia omorii adult males and females sampled in the southern bight of the North Sea (France) and in the type locality (Tokyo Bay, Japan)

	Acartia omorii (North Sea)		*Acartia omorii* (Tokyo Bay)	
	PL_{male}	PL_{female}	PL_{male}	PL_{female}
PL/PW	NS	$PL/PW = 4.2 - 1.1PL$ ($\rho = 0.76$; $P < 0.01$; $n = 10$)	Ns	$PL/PW = 3.9 - 1.2PL$ ($\rho = 0.41$; $P < 0.05$; $n = 30$)
GL/GW	–	$GL/GW = 1.1 + 0.6PL$ ($\rho = 0.79$; $P < 0.01$; $n = 10$)	–	$GL/GW = 1.2 + 0.7PL$ ($\rho = 0.32$; $P < 0.05$; $n = 30$)
RL/RW	NS	NS	NS	NS

GL/GW, genital segment length/width ratio; *n*, the number of individual considered; NS, not significant; PL/PW, prosome length/width ratio; RL/RW, right causal ramus length/width ratio; ρ, Spearman's rank correlation coefficient.

To our knowledge, this is the first record of the calanoid copepod *A. omorii* in the coastal waters of the southern bight of the North Sea. It is even the first report of a non-indigenous zooplankton species in this area and the second record of *A. omorii* outside Japanese waters (Hirakawa, 1988; Bradford-Grieve, 1999; Bollens *et al.*, 2002). *Acartia omorii* has already been demonstrated to be able to be transported in ship's ballast water from Japan to southern Chile (Hirakawa, 1988). In the present case, the observation of *A. omorii* in the coastal waters of the southern bight of the North Sea off Calais harbour is congruent with the first identification in 1998 and the subsequent proliferation of the Japanese macroalgae *Undaria pinnatifida* within one of the harbour basins (Leliaert *et al.*, 2000). It is notable that a similar sampling strategy, conducted over the same period in the coastal waters of the Eastern English Channel, never identified *A. omorii* but only *A. clausi* (Flamme, 2004). Assuming that *A. omorii* has been introduced in Calais harbour, the absence of *A. omorii* in the eastern English Channel could be related to the tidally driven residual circulation parallel to the coast with nearshore coastal waters drifting toward the North Sea (Brylinski *et al.*, 1991). The observed non-indigenous *A. omorii* cannot spread southward in the eastern English Channel but are likely instead to disperse northward into the North Sea as suggested by the first record of *U. pinnatifida* in Zeebrugge harbour (Belgium) in 2001 (Dumoulin and De Blauwe, 1999; De Blauwe, 2000).

The introduction and successful establishment of non-indigenous species (NIS) in marine and estuarine habitats has become a major global concern (see Bollens *et al.*, 2002 for a review), as the number of aquatic NIS taxa is now suspected to total in the hundreds (e.g. Carlton and Geller, 1991, 1993). The vector of transport of *A. omorii* and *U. pinnatifida* is likely to be the release of ballast water of ships (Ruiz *et al.*, 2000) rather than accidental or intentional release by aquaculture, fisheries or pet industries (Ruiz *et al.*, 1997). Yet the consequences, or ecological impacts, of NIS are not always understood (Parker *et al.*, 1999), especially in planktonic systems. Despite a large number of NIS taxa being identified from marine and estuarine habitats, little is still known on the potential consequences of their dispersal, physiology, feeding and community interactions in their new habitats. Even at the low relative abundance described here, the identification of *A. omorii* in the southern bight of the North Sea raises several critical issues such as the possibility and consequences of interbreeding with the native *A. clausi* species, its trophic impact on other zooplankton species or more generally the resilience and resistance of the North Sea coastal ecosystems, already heavily threatened by anthropogenic and climatic changes (e.g. Beaugrand *et al.*, 2003; Seuront and Prinzivalli, 2005), to invasions.

ACKNOWLEDGEMENTS

I am grateful to the captain and the crew of the NO 'Sepia II' (CNRS-INSU) and the RV 'Shinyo-maru' (Tokyo University of Fisheries) for their help during the sampling experiment, D. Devreker and G. Flamme for their contribution to the sampling in the southern bight of the North Sea, Dr. Raechel Waters for critically reading drafts of this note, Mojito Seuront for his contagious peacefulness and three anonymous reviewers whose suggestions and comments greatly improved this manuscript. This work was financially and infrastructurally supported by the CNRS, the Université des Sciences et Technologies de Lille, the Flinders University, the Australian Research Council and the Tokyo University of Fisheries. The Japanese component of this work was supported by a postdoctoral fellowship from the Japan Society for the Promotion of Science and a Monbusho Grant-in-Aid for JSPS Fellows (No. 99756).

REFERENCES

Ayukai, T. (1987) Feeding by the planktonic calanoid copepod *Acartia clausi* Giesbrecht on natural suspended particulate matter of varying quantity and quality. *J. Exp. Mar. Biol. Ecol.*, **106**, 137–149.

Barthélémy, R. M. (1999) Functional morphology and taxonomic relevance of the female genital structures in Acartiidae (Copepoda: Calanoida). *J. Mar. Biol. Ass. U. K.*, **79**, 857–870.

Beaugrand, G., Brandel, K. M., Lindley, J. A. *et al.* (2003) Plankton effect on cod recruitment in the North Sea. *Nature*, **426**, 621–664.

Bollens, S. M., Cordell, J. R., Avent, S. *et al.* (2002) Zooplankton invasions: a brief review, plu two case studies from the northeast Pacific Ocean. *Hydrobiologica*, **480**, 87–110.

Bradford, J. M. (1976) Partial revision of the Acatia subgenys Acartiura (Copepoda: Calanoida: Acartiidae). *N. Z. J. Mar. Freshw. Res.*, **10**, 159–202.

Bradford-Grieve, J. M. (1999) Copepoda, sub-order Calanoida, genera Acartiidae, Paracartia, Pteriacartia. *ICES Identification Leaflets for Plankton*. International Council for the Exploration of the Sea, Copenhagen, Denmark, p. 19.

Breton, E. (2000) Feeding of pelagic copepod in the Eastern English Channel. PhD Thesis. Université du Littoral Côte d'Opale, France.

Brylinski, J. M. (1981) Report of the presence of *Acartia tonsa* Dana (Copepoda) in the harbour of Dunkirk (France) and its geographical distribution in Europe. *J. Plankton Res.*, **3**, 255–260.

Brylinski, J. M. (1984) Anomalies morphologiques chez le genre *Acartia* (Crustacea: Copepoda): description et essai de quantification. *J. Plankton Res.*, **6**, 961–965.

Brylinski, J. M. (1986) Méthode de détection des gradients faunistiques: les courbes FCT. Répartition du zooplancton au large du Cap Griz-NeZ. (France). *Oceanol. Acta*, **9**, 457–467.

Brylinski, J. M., Bentley, D. and Quisthoudt, C. (1988) Discontinuité écologique et zooplancton (copépodes) en Manche orientale. *J. Plankton Res.*, **10**, 503–513.

Brylinski, J. M., Lagadeuc, Y., Gentilhomme, V. *et al.* (1991) "Le fleuve côtier": un phénomène hydrologique important en Manche orientale. Exemple du Pas-de-Calais. *Oceanol. Acta*, **11**, 197–203.

Carlton, J. T. and Geller, J. B. (1991) A thousand points of invasion: rapid oceanic dispersal of coastal organisms and implications for evolutionary biology, ecology, and biogeography. *Am. Zool.*, **31**, 127.

Carlton, J. T. and Geller, J. B. (1993) Ecological roulette: the global transport of nonindigenous marine organisms. *Science*, **261**, 78–82.

Cervetto, G., Gaudy, R. and Pagano, M. (1999) Influence of salinity on the distribution of *Acartia tonsa* (Copepoda, Calanoida). *J. Exp. Mar. Biol. Ecol.*, **239**, 33–45.

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

Cotonnec, G. (2001) Les lipides, marqueurs des relations trophiques planctoniques dans les écosystèmes pélagiques côtiers. PhD Thesis. Université du Littoral Côte d'Opale, France.

De Blauwe, H. (2000) *Undaria pinnatifida* te Zeebrugge, het verloop van een groeiseizoen. *De Strandvlo*, **20**, 153–156.

Dumoulin, E. and De Blauwe, H. (1999) Het Bruinwier *Undaria pinnatifida* (Harvey) Suringar (Phaeophyta: Laminariales) aagetroffen in de jachthaven van Zeebrugge: met gegevens over het voorkomen in Europa en de wijze van verspreiding. *De Strandvlo*, **19**, 182–188.

Farran, G. P. (1948a) Copepoda, sub-order. Calanoida, Family: Acartiidae, Genus: Acartia. *Fich. Ident. Zooplancton*, **12**, 1–4.

Farran, G. P. (1948b) Copepoda, sub-order. Calanoida, Family: Centropagidae, Genus: Centropages. *Fich. Ident. Zooplancton*, **11**, 1–4.

Farran, G. P. (1951a) Copepoda, sub-order. Calanoida, Family: Paracalanidae, Genus: Paracalanus. *Fich. Ident. Zooplancton*, **35**, 1–4.

Farran, G. P. (1951b) Copepoda, sub-order. Calanoida, Family: Pseudocalanidae, Genus: Pseudocalanus, Microcalanus. *Fich. Ident. Zooplancton*, **37**, 1–4.

Flamme, G. (2004) Effets de la nourriture et de la température sur les traits du cycle de vie du copépode *Temora longicornis* (Müller): couplage entre un suivi *in situ* et expérimental. Master Thesis. Université des Sciences et technologies de Lille, France.

Fransz, H. G., Colebrook, J. M., Gamble, J. C. *et al.* (1991) The zooplankton of the North Sea. *Neth. J. Sea Res.*, **28**, 1–52.

Hirakawa, K. (1988) New records of the North Pacific coastal planktonic copepods, *Acartia omorii* (Acartiidae) and Oithona davisae (Oithonidae) from southern Chile. *Bull. Mar. Sci.*, **42**, 336–339.

Ishii, H. (1990) In situ feeding rhythms of herbivorous copepods, and the effect of starvation. *Mar. Biol.*, **105**, 91–98.

Johnsson, P. R. and Tiselius, P. (1990) Feeding behavior, prey detection and capture efficiency of the copepod *Acartia tonsa* feeding on planktonic ciliates. *Mar. Ecol. Prog. Ser.*, **60**, 35–44.

Kimoto, K. (1988) Segregation of vertical distribution of calanoid copepod Acartia omorii depending on the developmental stages in Shijiki Bay, western Kyushu, Japan. *Bull. Seikai Natl. Fish. Res. Inst.*, **66**, 35–39.

Laguna, D. G. and Uye, S. I. (2001) Influence of mid-ultraviolet (UVB) radiation on the physiology of the marine planktonic copepod *Acartia omorii* and the potential role of photoreactivation. *J. Plankton Res.*, **23**, 143–155.

Leliaert, F., Kerckhof, F. and Coppejans, E. (2000) Eerste waarnemingen van *Undaria pinnatifida* (Harvey) Suringar (Laminariales, Phaeophyta) en de epifyt *Pterothamnion plumula* (Ellis) Nägeli (Ceramiales, Rhodophyta) in Noord Frankrijk en België. *Dumortiera*, **75**, 421–426.

Liang, D. and Uye, S. (1996) Population dynamics and production of the planktonic copepods in a eutrophic inlet of the Inland Sea of Japan. II. Acartia omorii. *Mar. Biol.*, **125**, 109–117.

Paffenhöfer, G. A. and Stearns, D. E. (1988) Why is *Acartia tonsa* (Copepoda: Calanoida) restricted to nearshore environments? *Mar. Ecol. Prog. Ser.*, **42**, 33–38.

Parker, I. M., Simberloff, D., Lonsdale, W. M. *et al.* (1999) Impact: toward a framework for understanding the ecological effects of invaders. *Biol. Invasions*, **1**, 3–19.

Ruiz, G. M., Carlton, J. T., Grosholz, E. D. *et al.* (1997) Global invasions of marine and estuarine habitats by nonindigenous species: mechanisms, extent, and consequences. *Am. Zool.*, **37**, 621–632.

Ruiz, G. M., Rawlings, T. K., Dobbs, F. C. *et al.* (2000) Global spread of microorganisms by ships. *Nature*, **408**, 49–50.

Seuront, L. (1999) Space-time heterogeneity and bio-physical coupling in pelagic ecology: implications on carbon fluxes estimates, the case of the Eastern English Channel. PhD Thesis. University of Sciences and Technologies of Lille, France.

Seuront, L. and Prinzivalli, P. (2005) Vulnerability of harbour seals, *Phoca vitulina*, to transient industrial activities in the Stait of Dover. *J. Mar. Biol. Ass. U. K.*, **85**, 1015–1016.

Soh, H. Y. and Suh, H. L. (2000) A new species of *Acartia* (Copepoda, Calanoida) from the Yellow Sea. *J. Plankton Res.*, **22**, 321–337.

Tanaka, M., Ueda, H. and Azeta, M. (1987a) Near-bottom copepod aggregations around the nursery ground of the juvenile red sea bream in Shijiki Bay. *Bull. Jpn. Soc. Sci. Fish.*, **53**, 1537–1544.

Tanaka, M., Ueda, H., Azeta, M. *et al.* (1987b) Significance of near-bottom copepod aggregations around the nursery ground of the juvenile red sea bream in Shijiki Bay. *Bull. Jpn. Soc. Sci. Fish.*, **53**, 1545–1552.

Tester, P. and Turner, J. T. (1991) Why is *Acartia tonsa* restricted to estuarine habitats? *Bull. Plankt. Soc. Jpn*, **Spe. Vol.**, 603–611.

Ueda, H. (1986) Redescription of the planktonic calanoid copepod *Acartia hudsonica* from Atlantic and Pacific waters: a new record from Japanese waters? *J. Oceanogr. Soc. Jpn*, **42**, 121–133.

Uye, S. and Takamatsu, K. (1990) Feeding interactions between planktonic copepods and red-tide flagellates from Japanese coastal waters. *Mar. Ecol. Prog. Ser.*, **59**, 97–107.

Viitasalo, M. and Katajisto, T. (1994) Mesozooplankton resting eggs in the Baltic Sea: identification and vertical distribution in laminated and mixed sediments. *Mar. Biol.*, **120**, 455–465.

Wells, J. B. (1970) Copepoda, sub-order *Harpacticoida*. *Fich. Ident. Zooplancton*, **133**, 1–7.

Williams, R., Lindley, J. A., Hunt, H. G. *et al.* (1993) Plankton community structure and geographical distribution in the North Sea. *J. Exp. Mar. Biol. Ecol.*, **172**, 143–156.

Yamazi, I. (1956) Plankton investigation in inlet waters along the coast of Japan XIX. Regional characteristics and classification of inlet waters based on the plankton communities. *Publ. Seto Mar. Biol. Lab.*, **5**, 157–193.

Yoo, K. I., Hue, H. K. and Lee, W. C. (1991) Taxonomical revision on the genus *Acartia* (Copepoda: Calanoida) in the Korean waters. *Bull. Korean Fish. Soc.*, **24**, 255–265.