A dense swarm of *Acartia omorii* (Copepoda, Calanoida) with a high female:male sex ratio in Tokyo Bay

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Acartia omorii is a common neritic calanoid copepod of the coastal waters of Japan, adapted to highly variable environments (Uye, 1982). A swarm of this species has been recorded previously in the northern part of Tokyo Bay (Nomura et al.,1993), and there are many records of swarming conspecifics in other marine environments (Ueda et al., 1983; Kouwenberg, 1993; Norrbin, 1994). However no swarms were recorded for A. omorii over 9 months in the Inland Sea of Japan (Liang and Uye,1996). The observation described here is the highest density of this species recorded, with a comparatively high density with respect to conspecifics and other copepods (Table 1).

As part of a large project investigating the annual succession of plankton in Tokyo Bay, water samples were taken at 3 stations (Figure 1- Stn. 1= 35 35.32, 139 50.96; Stn. 2= 35 28.04, 139 55.25; Stn. 3= 35 35.66, 140 00.99) everyday, excluding weekends, for 11 months from 8th June 1995 to 30th April 1996. The results presented here refer directly to a swarm observed at Station 1 on 26th April 1996.

Samples were taken from surface waters (0 m) with a bucket and from 5 m depth with a Van Dorn sampler. A 250 ml sub-sample for macroplankton analysis was fixed with 1% formalin. Plankton were identified and counted later in the laboratory after settling under a light microscope. Identification of A. omorii females and males, was based on the presence/absence of a swollen 1st abdominal segment and the number of abdominal segments. Copepod prosome length was measured with an optical micrometer.

The sample taken from surface waters at Stn. 1 on the morning of April 26, 1996 revealed a density of 10920 inds./L *A. omorii* - the highest density recorded for this species (Table 1). Temperature at 0 m was 16.0 C and salinity 29.01 psu. Samples from the other two stations and also Stn. 1 at 5 m depth had comparatively few *A. omorii*: Stn. 1 -5 m = 0; Stn. 2 - 0 m = 30 inds./L,Stn. 2 -5 m = 60 inds./L; Stn. 3 - 0 m = 0, Stn. 3 - 5 m= 120 inds./L. These observations suggest that the swarm was localised to the surface waters of Stn. 1.

A. omorii, adults and juveniles, constituted 93.3% of the zooplankton by number and 94.0% of the copepods by number (Figure 2) indicating a highly species specific swarm. Centropages abdominalis was also found in the swarm although they comprised only 5.4% of the copepods by number. Abundance of copepod nauplii at Stn. 1 was low: 48 inds./L. Nomura et al. (1993) described a similar swarm of A. omorii from the same area of Tokyo Bay although the density of the 1993 swarm (7553 inds./L) was considerably less than the swarm described here (10920 inds./L). C. abdominalis also constituted a much greater percentage of total swarming copepods in the 1993 swarm at 52.8% (Nomura et al., 1993).

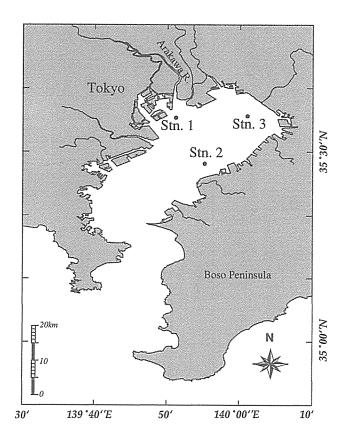


Fig. 1. Sampling stations in Tokyo Bay.

Table 1: Densities of previously reported copepod swarms (in alphabetical order). In most cases only maximum densities are listed.

Species	Recorded	Equivalent	Sampling	Area	Reference
	density ^a	density (inds/ml) ^b	technique		
Acartia australis	166.8 x 10 ³ inds/m ³	0.167	diver operated net	Great Barrier Reef, Australia	Hamner and Carleton 1979
Acartia australis	$210 \times 10^3 \text{ inds/m}^3$	0.21	571 plastic bag	Great Barrier Reef, Australia	Hamner and Carleton 1979
Acartia clausi	$3 \times 10^5 \text{ inds/m}^3$	0.3	Van Dorn water sampler	Shijiki Bay, Japan	Ueda <i>et al.</i> 1983
Acartia australis	$325 \times 10^3 \text{ inds/m}^3$	0.325	still photography	Great Barrier Reef, Australia	Hamner and Carleton 1979
Acartia steuri	$5 \times 10^5 \text{ inds/m}^3$	0.5	resin tube samplers	Shijiki Bay, Japan	Ueda <i>et al.</i> 1983
Acartia australis	586 x 10 ³ inds/m ³	0.586	still photography	Great Barrier Reef, Australia	Hamner and Carleton 1979
Acartia sinjiensis °	$2 \times 10^6 \text{ inds/m}^3$	2.0	diver operated net	Inaizura Bay, Japan	Ueda <i>et al.</i> 1983
Acartia omorii	7553 inds/l	7.553	bucket at surface	Tokyo Bay, Japan	Nomura <i>et al.</i> 1993
Acartia omorii	10902 inds/l	10.902	bucket at surface	Tokyo Bay, Japan	Current study
Acartia tonsa	10 ⁸ inds/m3	100.0			C. Davis and L. Haury, unpublished e
Calanus finmarchicus	351948 inds/m³	0.352	335µmnet tow	Gulf of Maine, USA	Wishener <i>et al.</i> 1995
Calanus pacificus californicus	26.5 x 10 ⁶ inds/m ³	26.5 ^f	diver operated suction sampler	Santa Barbara Basin, USA	Alldredge <i>et al.</i> 1984
Centropages abdominalis	8541 inds/l	8.541	bucket at surface	Tokyo Bay, Japan	Nomura <i>et al.</i> 1993
Dioithona oculata	$4 \times 10^5 \text{ inds/m}^3$	0.4	Van Dorn water sampler	Tanabe Bay, Japan	Ueda <i>et al.</i> 1983
Dioithona oculata ^d	$640 \times 10^3 \text{ inds/m}^3$	0.640	diver operated net	Great Barrier Reef, Australia	Hamner and Carleton 1979
Dioithona oculata d	$1558 \times 10^3 \text{ inds/m}^3$	1.558	still photography	Great Barrier Reef, Australia	Hamner and Carleton 1979
Dioithona oculata	23.2 inds/ml	23.2	hand held net/plastic bag	Mangrove cays, Belize	Ambler <i>et al.</i> 1991
Dioithona oculata	91.7 inds/ml	91.7	video/ plastic bag	Mangrove cays, Belize	Buskey et al. 1996
Oithona davisae	$1.337 \times 10^6 \text{ inds/m}^3$	1.337	95μm Kitahara net tow	Ariake-kai, Japan	Hirota and Tanaka 1985

^a total number of adults, copepodites and nauplii (if determined to species)

^b Size of all swarms not known or smaller than 1m³ so all standardised to inds/ml

° reported as Acartia plumosa

d reported as Oithona oculata

° Cited in Haury and Yamazaki 1995 ^f Stage V copepodids

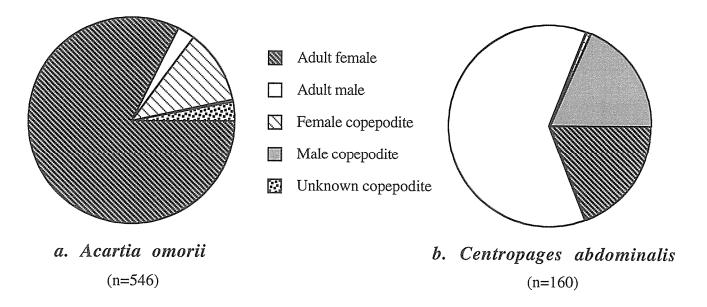


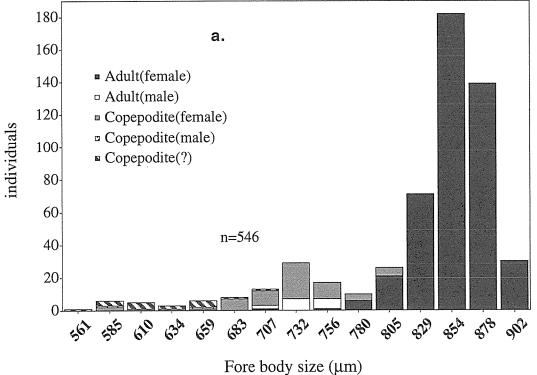
Fig. 2. Sex composition of the two main copepod species.

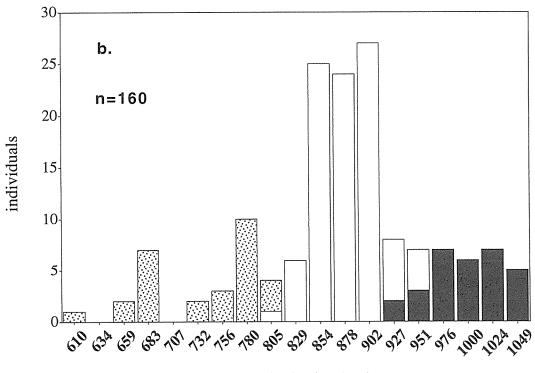
Stages for each group are adults (males and females)- stage VI;
copepodites (males and females) - stages IV- V; and copepodites of unknown sex - stages I- III.

Table 2. Abundance of copepods in the Tokyo Bay swarm.

Species		Sta	Stage		(%)	Copepod (%)
Acartia	omorii	Adult	Female	2250	76.35	77.51
			male	75	2.54	2.58
		Copepodite	Female	315	10.69	10.85
			male	10	0.34	0.34
			?	80	2.71	2.76
Centropages	abdominalis	Adult	Female	30	1.02	1.03
			male	97	3.29	3.34
		Copepodite	Female	1	0.03	0.03
			male	29	0.98	1.00
Oithona	davisae	Adult	Female	1	0.03	0.03
			male	1	0.03	0.03
Pseudodiaptom	us inopinus	Adult	male	2	0.07	0.07
Nauplius of	Copepoda			12	0.41	0.41
Podon	polyphemoides		,	1	0.03	*
Tiarina	fusus			1	0.03	~
Stenosemella	ventricosa			23	0.78	
Favella	ehrenbergii			12	0.41	-
Synchaeta	sp.			1	0.03	-
Oikopleura	dioica			1	0.03	-
Umbo	larva			2	0.07	-
Polycaeta	larva			2	0.07	-
Nauplius of	Balanomorpha			1	0.03	*
	Total			2947	100	-

Fig 3. Size of a. Acartia omorii and b. Centropages abdominalis in swarm





Fore body size (µm)

Stn. 1 is highly eutrophic (DIN 1.8 mg./L during the time of the swarm) and affected greatly by the inflow of water from the Arakawa River. During April , numbers of the dominant diatom species, *Skeletonema costatum* increased at Station 1 with greater than 1000 cells./L present from 24th April onwards.

Both *A. omorii* and *C. abdominalis* had skewed sex ratios although the skew favored different sexes. The *A. omorii* population had a ratio of females to males of 30:1 within the adults (96.8% female) and 31.5:1 (96.9% female) within the juveniles; whereas for *C. abdominalis* the same ratio was 1:3.2 within adults (23.6% female) and 1:29 in copepodites (3.3% females, Table 2). The copepod swarm described by Nomura *et al.* (1993) had a similar sex ratio in *A. omorii* - 98.2% of adults were female - suggesting the possibility that this sex ratio skewedness is a seasonal occurrence. In contrast to the sex ratio of *C. abdominalis* in the swarm we observed, Liang *et al.* (1996) found a fairly constant sex ratio of 1:1 in *C. abdominalis* in the Inland Sea of Japan.

Ueda et al. (1983) described the swarming of 8 species of copepods (including 5 congeneric Acartia spp.) off the Japanese coast, including A. omorii * and concluded that Acartia spp. swarms are both age and species specific and nearing sex specificity as well. Over a year, A. longiremis females constituted nearly 100% of all adults during the months of October to April (Norrbin, 1994). Over a 9 month period, Liang and Uye (1996) reported a mean of 58% males in adults and 53% males in stages CIV-CV of A. omorii in the Inland Sea of Japan, although the percentage of males did drop to approximately 10% in early July. Kouwenberg (1993) found the sex ratio of A. clausi skewed towards females throughout the year in the Mediterranean and suggested that the ratio is related to the swarming behaviour. She proposed that a sex ratio skewed to females provides the females with a greater share of the available food, thus chanelling more energy to production of the more energetically costly eggs.

A further observation that suggests a possible reproductive function of this swarm is the high density of copepods. The high density leads to a very low nearest neighbour distance of 5.4 mm (calculated using the isohedral packing formula from Hamner and Carleton, 1979, and assuming regular distribution within the swarm) which is less than one body length for all individuals observed (Figure 3). This suggests that each individual is in the immediate

sensory range of all its neighbours (Haury and Yamazaki, 1995) and also the average distance between a male and the more populous females would be reduced.

The most common factor thought to determine the overall abundance of copepods is the distribution of food (Paffenh ffer et al., 1987) although Buskey et al. (1996) found that non-swarming Dioithona oculata had greater amounts of food in their gut than swarming individuals, suggesting that there is fierce competition for food within a swarm.

We propose that food availability was the not the causal factor in the formation of this *A. omorii* swarm, but that the swarm actively moved with the higher food concentration so that there was sufficient food for the swarming individuals.

In conclusion, it is possible that the dense awarm of *A. omorii* (10920 inds./L) observed in Tokyo Bay was formed to facilitate reproduction, while its location corresponded with a minor *S. costatum* bloom that increased food availability for the swarming copepod population. The highly skewed sex ratio observed in *A. omorii*, 30:1 in favour of females, may be related to their reproductive behaviour.

* Note Originally reported as *Acartia clausii* but *A. clausi* in Japanese coastal waters was reclassified *A. omorii* in 1986 (Ueda, 1986).

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