Production of *Oikopleura dioica* (Appendicularia) following a picoplankton 'bloom' in a eutrophic coastal area

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Abstract. The ecological importance of the appendicularian *Oikupleura dioica* as a picoplankton predator and a metazoan secondary producer was assessed in summer 1995 in the Seto Inland Sea, Japan. Just after the collapse of a red tide of *Gymnodinium mikimotoi*, the abundances of bacteria and picocyanobacteria increased rapidly and attained values of 4.6×10^6 and 5.6×10^5 ml^{-1}, respectively. Concurrent with a subsequent sharp decrease in picoplankton abundance, the abundance and biomass of *O.dioica* increased drastically, and reached levels of 57 individuals l^{-1} and 12 µg C l^{-1}, respectively. During this period, the carbon-based growth rate of *O.dioica* was estimated by a bottle incubation experiment. The value was very high (1.66 day^{-1}) for a metazoan and its production was comparable with that of copepods reported previously in the Seto Inland Sea in summer. A carbon budget analysis indicates that ingesting picoplankters as main food sources, *O.dioica* grew rapidly and its biomass attained the high value. Furthermore, the sharp decrease in picoplankton abundance was at least partly attributable to the ingestion by *O.dioica*.

Introduction

In the last two decades, the fate of picoplankton production has drawn much attention in order to understand the carbon flow in marine ecosystems (e.g. Azam *et al.*, 1983). However, the link between picoplankton production and higher trophic levels is still a matter of debate (e.g. Ducklow *et al.*, 1986; Sherr *et al.*, 1987). From the standpoint of food-chain efficiency, the most efficient pathway that connects picoplankton production to fish would be through zooplankters that graze picoplankton and are directly consumed by fish. Appendicularians may be such zooplankters.

Appendicularians live in a mucous 'house' equipped with food-concentrating filters (Alldredge, 1976). The food-concentrating filter of the appendicularian *Oikopleura dioica* Fol, which is distributed worldwide throughout coastal waters, is capable of retaining pico- and nanoplankton-sized particles (Flood, 1978), and bacteria seem to form a substantial portion of its diet (King *et al.*, 1980). Furthermore, weight-specific filtering rates and growth rates of *O.dioica* are higher than those of copepods (Paffenhöfer, 1976; Alldredge, 1981; Hopcroft and Roff, 1995) and its abundance sometimes attains very high values [10–50 individuals (ind.) l^{-1}; Seki, 1973; Uye and Ichino, 1995]. Thus, *O.dioica* may have a significant impact on picoplankton assemblages (heterotrophic bacteria plus picoplankton-sized autotrophs), and its production could equal or exceed that of copepods (Hopcroft and Roff, 1995). However, there are no published data that describe the changes in the abundance of *O.dioica* and pico-/nanoplankton-sized particles simultaneously with the growth rates of the appendicularian in natural populations: the lack of these data makes it difficult to assess the ecological importance of *O.dioica*.

In summer 1995, we monitored the abundance and biomass of *O.dioica*

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populations, together with abundances of its potential prey (pico-/nanoplankters) in the Seto Inland Sea, Japan. Furthermore, one of the field experiments which was originally planned to examine microzooplankton–copepod interactions also enabled us to estimate the *in situ* growth rate of *O.dioica*. In the present paper, results of the field observations/experiments are described, and the ecological importance of *O.dioica* as a picoplankton predator and a metazoan secondary producer is assessed.

Method

Field observations

In summer 1995 (15 July–8 August), a field survey was conducted at Station B (34°35′N, 134°30′E, 21 m depth; see Nakamura *et al.*, 1993) around the Ie-shima Islands in the Seto Inland Sea. Monitoring and sampling were conducted daily in the morning (06:20–07:00 h). Changes in water temperature, salinity, nutrients and chlorophyll *a* were summarized in a previous paper (Nakamura *et al.*, 1996). Wax and wane of a red tide of *Gymnodinium mikimotoi* Miyake et Kominami ex Oda (Dinophyceae) and its potential predators (ciliates and heterotrophic dinoflagellates) were also described in that paper.

Water samples (40 l) for mesozooplankton enumerations were obtained from depths of 0 and 10 m using a 5 l plastic bucket and a 10 l Van Dorn-type bottle, respectively. The samples were concentrated by a hand net (mesh size 100 μm) to a volume of ~100 ml and fixed by neutralized formalin (final concentration 5%). *Oikopleura dioica* and other mesozooplankters from split subsamples (half of the original samples) were enumerated. The trunk length (TL) of *O.dioica* was measured for all individuals present in a half of the original samples or >100 individuals to the nearest 10 μm using a dissecting microscope. The enumeration and TL measurements were conducted within 3 months after collection. TL (μm) was converted into ash-free dry weight (AFD, μg) with the regression equation given by Paffenhöfer (1976):

$$\log AFD = 2.49 \log TL - 6.22$$

The degree of TL shrinkage due to fixation varied from not significant (King *et al.*, 1980) to 6% (Alldredge, 1981). In the present study, we did not make corrections for the shrinkage. However, if we assume 6% shrinkage, the corrected AFD is ~15% higher than uncorrected values. The carbon-based biomass of *O.dioica* was calculated from numerical abundance and TL distributions of the population assuming that carbon content was 45% of AFD (Uye, 1982; Uye and Ichino, 1994).

We also measured the abundance and TL distribution of *O.dioica* that passed the 100 μm net on four dates (17, 23 and 28 July, and 4 August): 1000 ml of the surface seawater filtered through the net were fixed with neutralized formalin, and the abundance and TL distributions were measured as described above. These samples were collected as part of the field experiments (see below).

Samples (80 ml) for the enumeration of bacteria, picocyanobacteria and autotrophic/heterotrophic nanoflagellates were obtained from depths of 0 and

10 m, fixed by glutaraldehyde (final concentration 1%), stained with DAPI (final concentration 1 μg l^{-1}) and concentrated onto black Nuclepore filters. Pico-/nanoplankters were enumerated by observing the filters using an epifluorescent microscope within a few days after collection. Conditions for enumerations were summarized in a previous paper (Nakamura *et al.*, 1995).

Field experiments

These were initially planned to examine the ingestion of microzooplankton by a copepod *Paracalanus* sp. and one experiment fortunately enabled us to estimate the *in situ* growth rate of *O.dioica*. On the morning of August 4 (08:20–08:40 h), 20 l of the surface seawater at Station B were gently filtered through a 100 μm mesh to remove large mesozooplankton and the filtrate was returned to the field laboratory within 10 min. The filtrate was then mixed gently and siphoned into six glass bottles (1160 ml each) using silicon tubing. Adult females of *Paracalanus* sp., which had been collected in gentle vertical tows from 15 m using a 45 cm ring net of 200 μm mesh and acclimated for 20 h at 25°C, were introduced to the three bottles (10 individuals per bottle) and the other bottles served as 'controls'. The bottles were free of air space or bubbles, wrapped with black sheeting to suppress algal growth and suspended at 3 m depth (temperature 25–26°C) from the pontoon of the field laboratory for 23.5 h. In parallel with the above procedures, an 80 ml aliquot of the filtrate was fixed and used for the enumeration of pico-/nanoplankton (see above). Another 400 ml aliquot was fixed with acid Lugol's (2%), stored at 5°C, and used for ciliate enumeration by an inverted microscope (Utermöhl, 1958). We also fixed the filtrate (1000 ml) with neutralized formalin (final concentration 5%) and used it for abundance and TL measurements of *O.dioica* that passed the 100 μm net. Following the enumeration of ciliates, the rest of the acid Lugol's-fixed sample was also used for TL measurements. TL distribution in the acid Lugol's-fixed sample was not significantly different from that in the formalin-fixed sample (Student's *t*-test, $P > 0.1$).

At the end of the experiment, the bottles were retrieved and the survival of *Paracalanus* sp. was assured. Then, 80 and 250 ml aliquots were taken from each bottle, preserved with glutaraldehyde and acid Lugol's, and used for the enumeration of pico-/nanoplankton-sized particles and ciliates, respectively (see above). After the completion of ciliate enumeration, the rest of the acid Lugol's-fixed samples (~200 ml × 6) was used for the TL measurements. Since the presence of *Paracalanus* sp. did not affect the TL distribution significantly (Student's *t*-test, $P > 0.1$), all the TL data were combined. The growth rate of *O.dioica* (μ) was calculated using the following equation:

$$\mu = (\ln <C>_f - \ln <C>_i)/T$$

where $<C>_i$ and $<C>_f$ are the averaged carbon content (ind.$^{-1}$) of *O.dioica* in initial and final samples, respectively, and T is the incubation period. Since the growth rate of *O.dioica* does not depend on body size (Paffenhöfer, 1976), its

production (P) for the natural population was calculated from $P = \mu B$, where B is the biomass and μ is the growth rate obtained from the above experiment.

Estimation of prey biomass

Since we did not measure the cell size of pico-/nanoplankton, equivalent spherical diameters (ESD) of 0.4, 1, 4 and 10 μm were assumed for bacteria, pico-cyanobacteria and nanoflagellates (2–8 μm) and nanoflagellates (8–20 μm), respectively (cf. Nakamura *et al.*, 1993, 1994). Using these values, together with an abundance and carbon/volume conversion factor of 0.1 pg C μm^{-3} (e.g. Watson *et al.*, 1977), prey biomass was roughly estimated.

Results

Background

During the survey period, the weather was sunny and calm. The water was thermally stratified and the temperature at the surface and 10 m ranged from 22.4 to 27.4 and 20.6 to 26.7°C, respectively. An autotrophic dinoflagellate, *G.mikimotoi*, developed its population in the subsurface layer (5–15 m) from 23 to 29 July, accumulated at the surface layer after 29 July and formed a red tide (Nakamura *et al.*, 1996). Then the abundance of a tintinnid ciliate *Favella ehrenbergii* increased drastically by ingesting *G.mikimotoi* and the red tide collapsed by 4 August (Figure 1; Nakamura *et al.*, 1996).

Pico- and nanoplankton

From 15 July to 1 August, the abundance of bacteria was relatively constant at around 3 × 10^6 ml^{-1}. Coupled with the collapse of the red tide, it increased and reached the maximum of ~4.5 × 10^6 ml^{-1} on 3–4 August and then decreased
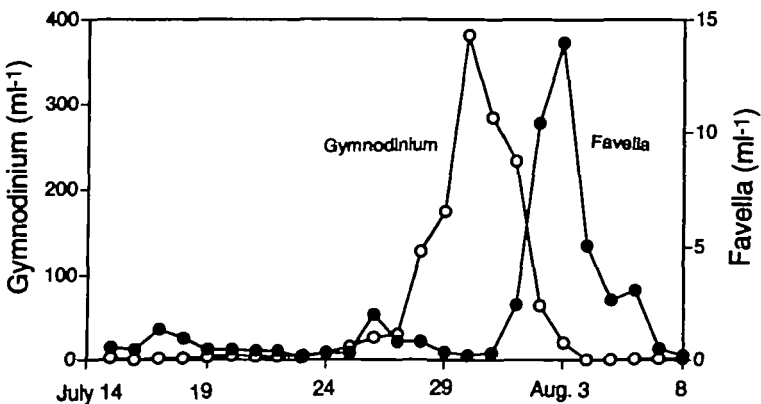

Fig. 1. Temporal changes in the abundance of *G.mikimotoi* (○) and *F.ehrenbergii* (●); average of values for 0 and 10 m.

sharply (Figure 2). The abundance of picocyanobacteria increased gradually from 15 to 29 July (1.5×10^4 to 1.3×10^5 ml^{-1}), then increased rapidly, exhibiting very high values from 31 July to 5 August ($3-6 \times 10^5$ ml^{-1}). Abundance then suddenly decreased to ~1×10^5 ml^{-1} within a day (Figure 3).

The abundance of autotrophic nanoplankton (ANP; 2–8 μm) showed high values ($3-7 \times 10^3$ ml^{-1}) from 15 to 28 July, then decreased and reached the minimum (~0.5×10^3 ml^{-1}) from 3 to 7 August (Figure 4). The abundance of heterotrophic nanoflagellates (HNF; 2–8 μm) was in the range $1-3 \times 10^3$ ml^{-1} throughout the survey period, except on 15 and 26 July when it reached 4×10^3 ml^{-1} (Figure 4). The abundances of ANP (8–20 μm) were in the range 30–750 ml^{-1} throughout the survey period and were <100 m^{-1} from 30 July to 6 August (Figure 5). The abundance of HNF (8–20 μm) was in the range 10–150 ml^{-1} throughout
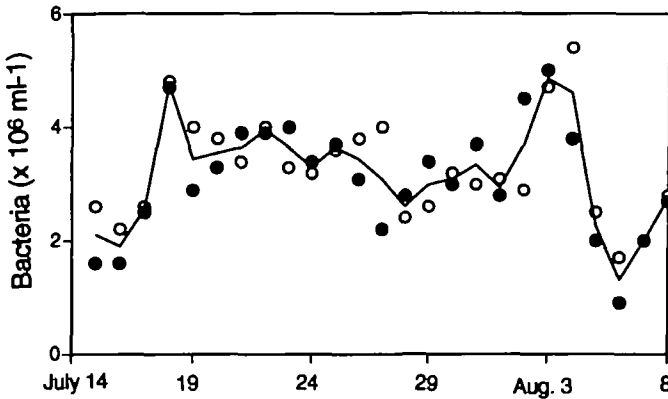

Fig. 2. Temporal changes in the abundance of bacteria. O, 0 m; ●, 10 m. The solid line is the average of values for 0 and 10 m.
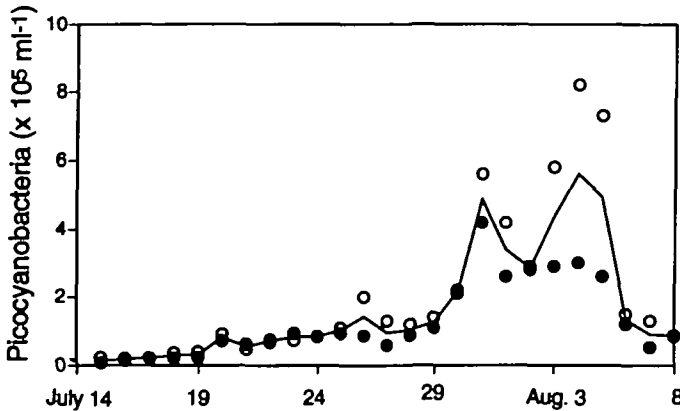

Fig. 3. Temporal changes in the abundance of picocyanobacteria. O, 0 m; ●, 10 m. The solid line is the average for 0 and 10 m.
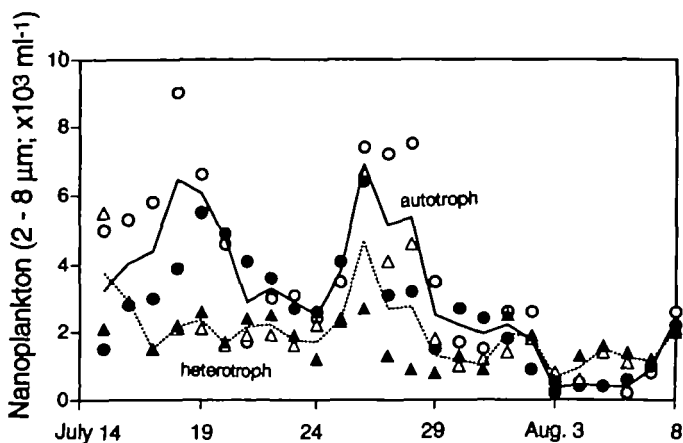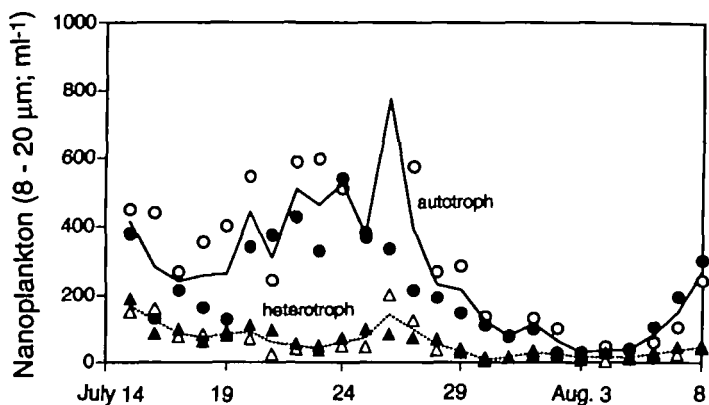
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Fig. 4. Temporal changes in the abundance of autotrophic nanoplankton (ANP) and heterotrophic nanoflagellates (HNF) of 2–8 μm in size. O, ANP 0 m; ●, ANP 10 m; Δ, HNF 0 m; ▲, HNF 10 m. Solid and dotted lines are the average of values between 0 and 10 m for ANP and HNF, respectively.

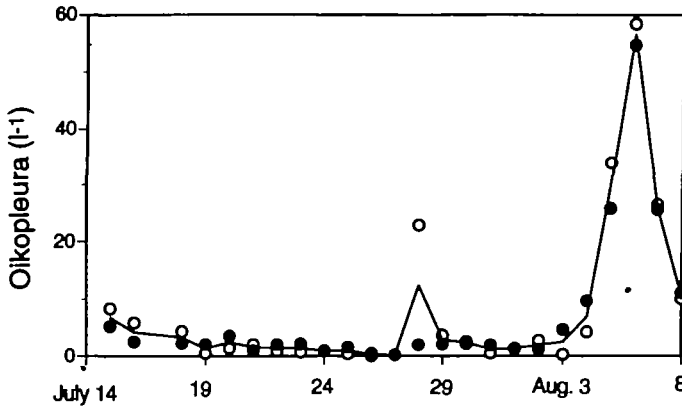**Fig. 5.** Temporal changes in the abundance of autotrophic nanoplankton (ANP) and heterotrophic nanoflagellates (HNF) of 8–20 μm in size. O, ANP 0 m; ●, ANP 10 m; Δ, HNF 0 m; ▲, HNF 10 m. Solid and dotted lines are the average of values between 0 and 10 m for ANP and HNF, respectively.

the survey period and <30 ml^{-1} from 30 July to 6 August (Figure 5). The biomass of picoplankton exceeded that of nanoplankton (2–20 μm) from 30 July to 6 August (Figure 7).

Oikopleura dioica

In July, the abundance of *O.dioica* collected with a 100 μm mesh net was in the range <0.1–6.9 ind. l^{-1} (except for 12.4 ind. l^{-1} on 28 July). Then concurrent with the decrease in picoplankton, the abundance of *O.dioica* increased rapidly, reached a maximum of 56.6 ind. l^{-1} on 6 August and decreased again (Figure 6).

Fig. 6. Temporal changes in the abundance of *O.dioica* retained in 100 μm net. O, 0 m; ●, 10 m. The solid line is the average of the values for 0 and 10 m.
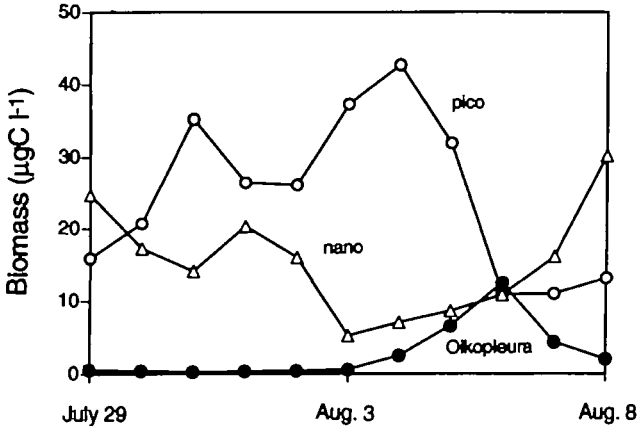
Fig. 7. Temporal changes in the biomass of *O.dioica* retained in 100 μm net (●), picoplankton (O) and nanoplankton (Δ); average of values for 0 and 10 m.

Systematic trends in the vertical distribution of *O.dioica* were not apparent. Throughout the survey period, averaged individual carbon contents were in the range 0.13–0.48 μg C ind.$^{-1}$ and did not show any trends with sampling time and depth. However, from 4 to 8 August, when the abundance of *O.dioica* showed high values, average individual carbon contents were in a much narrower range of 0.17–0.27 μg C ind.$^{-1}$ except for 0.47 μg C ind.$^{-1}$ on 4 August (10 m). The biomass of *O.dioica* retained on a 100 μm mesh net was <2 μg C l^{-1} before 4 August (except for 4.5 μg C l^{-1} on 28 July), and then increased to reach a maximum of 12.4 μg C l^{-1} on 6 August (Figure 7).

The abundance and biomass values for *O.dioica* that passed through the 100 μm mesh net were 5, 16, 3 and 63 ind. l^{-1}, and 0.1, 0.4, 0.1 and 1.7 μg C l^{-1} for 17, 23 and 29 July, and 4 August, respectively.

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Growth rate and production of Oikopleura dioica

Just after the collapse of the red tide of *G.mikimotoi*, we started the field experiment that enabled us to estimate the *in situ* growth rate of *O.dioica*. The planktonic community in this period was characterized by a scarcity of autotrophs other than picocyanobacteria, and high abundance of bacteria and the tintinnid ciliate *F.ehrenbergii* (Table I; cf. Nakamura *et al.*, 1996).

At the start of the experiment, most individuals of *O.dioica* were small, had TLs of around 100 μm and the average carbon content was 0.028 μg ind.$^{-1}$. After the incubation of 23.5 h, TL increased drastically and the average carbon content reached 0.140 μg C ind.$^{-1}$ (Figure 8). The growth rate was calculated to 1.66 day^{-1}. Epifluorescence microscope observations indicated that after the incubation the stomachs of *O.dioica* individuals were filled with picocyanobacteria.

Changes in the abundance of pico-/nanoplankters and *F.ehrenbergii* during the incubation are summarized in Table I. Irrespective of the presence of copepods, the abundance of picocyanobacteria decreased drastically and that of bacteria decreased slightly. The abundance of HNF (2–8 μm) increased ~3 times and ingested picocyanobacterial cells were often observed in the HNF cells.

The production of the natural population of *O.dioica* (P) retained on a 100 μm mesh net was calculated using the growth rate obtained above and the biomass (Figure 9). P was <3 μg C l^{-1} day^{-1} before 4 August (except for 7.4 μg C l^{-1} day^{-1} on 28 July) and reached the maximum of 20.7 μg C l^{-1} day^{-1} on 6 August.

Discussion

The present study provides the first direct measurements of population development and growth rate of *O.dioica* together with changes in the abundance of its potential prey. Our results strongly suggest the ecological importance of *O.dioica* as a component of the mesozooplankton as a predator of picoplankton.

Abundance, growth rate and production

Seasonal variations in the abundance and biomass of *O.dioica* in the Seto Inland Sea (Fukuyama Harbor) have been previously reported by Uye and Ichino

Table I. Field experiments: changes in the abundance of each planktonic category with and without *Paracalanus* sp.

	Initial abundance (ml^{-1})	Initial biomass (μg C l^{-1})	Final abundance	
			'Control' (ml^{-1})	With copepod (ml^{-1})
Bacteria	6.1×10^6	19.5	$(5.7 \pm 0.6) \times 10^6$	$(5.3 \pm 0.2) \times 10^6$
Picocyanobacteria	9.6×10^5	48.0	$(2.9 \pm 0.2) \times 10^5$	$(2.6 \pm 0.4) \times 10^5$
HNF (2–8 μm)	1.5×10^3	4.8	$(5.1 \pm 0.3) \times 10^3$	$(4.2 \pm 0.2) \times 10^3$
ANP (2–8 μm)	0.2×10^3	0.6	$(0.3 \pm 0.1) \times 10^3$	$(0.3 \pm 0.0) \times 10^3$
HNF (8–20 μm)	7	0.4	18 ± 2	13 ± 2
ANP (8–20 μm)	24	1.2	36 ± 2	22 ± 5
Ciliates (8–20 μm)	1	0.1	2 ± 1	1 ± 1
Favella ehrenbergii	19.2	115	6.7 ± 0.4	2.7 ± 0.2

HNF, heterotrophic nanoflagellates; ANP, autotrophic nanoplankton.
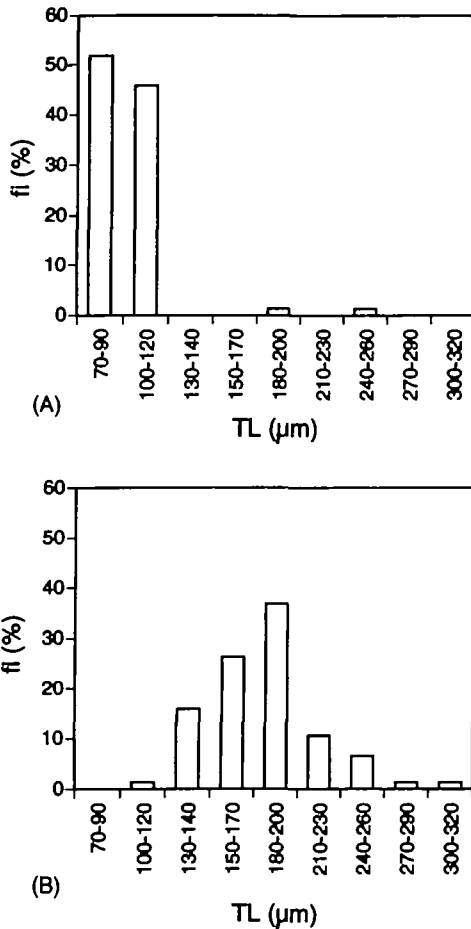
Fig. 8. Changes in the frequency distribution (fi) of *O.dioica* trunk length (TL) in the seawater pre-screened through 100 μm mesh net. (**A**) Initial and (**B**) final (23.5 h).

(1995). During the warm period (May–September), *O.dioica* abundance and biomass reached up to 50 ind. l^{-1} and 12 μg C l^{-1}, and values of 20 ind. l^{-1} and 5 μg C l^{-1}, respectively, were often observed. Thus, the high abundance and biomass of this species obtained in the present study (Figures 6 and 7) are not unusual in the Seto Inland Sea.

There are three previous estimates for the growth rate of *O.dioica* at temperatures >20°C. The values are very high for metazoans, and in the range 0.59–3.18 day^{-1} (Fenaux, 1977; Gorsky and Palazzoli, 1989; Hopcroft and Roff, 1995). Furthermore, the 'theoretical' growth rate of *O.dioica* at 25°C is 2.0 day^{-1} (Uye and Ichino, 1995), which is based on the extrapolation of the time required from hatching to spawning obtained at 6–18°C (Paffenhöfer, 1976). Thus, the growth rate obtained in the present study (1.66 day^{-1}) is comparable to those estimates and a reasonable estimate to calculate the production.
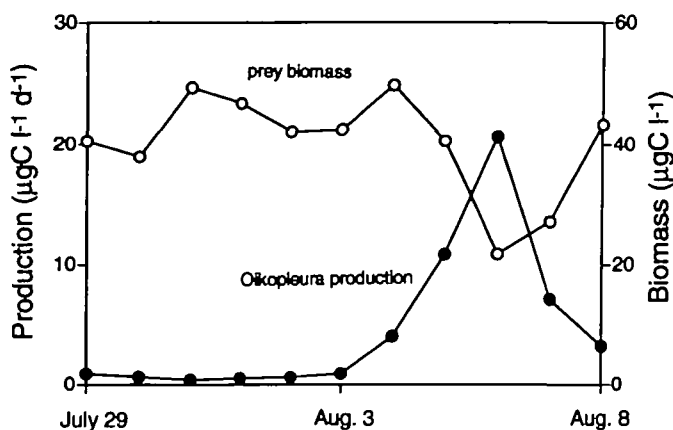
Fig. 9. Temporal changes in the production of *O.dioica* retained in 100 μm net (●) and the biomass of pico- plus nanoplankton (○); average of values for 0 and 10 m.

The production of *O.dioica* retained in the 100 μm net reached up to 20.7 μg C l⁻¹ day⁻¹ (Figure 9). Uye and Ichino (1995) also estimated *O.dioica* production in the Seto Inland Sea, based on the biomass and the 'theoretical' growth rate. Their estimated values are in the range of ≤20 μg C l⁻¹ day⁻¹ during the warm period, comparable to those obtained in our study area. Thus, the production obtained in the present study seems to be in a typical range during the warm season in the Seto Inland Sea.

On 4 August, small individuals of *O.dioica* that passed through the 100 μm mesh net were very abundant (63 l⁻¹) and the production of this fraction was 2.9 μg C l⁻¹ day⁻¹. That of *O.dioica* in the >100 μm fraction was 4.1 μg C l⁻¹ day⁻¹. Thus, the small fraction contributed substantially to the total production in this period. The high abundance and the rapid growth of the small fraction on 4 August seem to be reflected in the rapid increase in the abundance of the >100 μm fraction from 4 to 5 August (Figure 6).

The production of copepods in the Seto Inland Sea during the warm season was estimated by Uye *et al.* (1987), with values of 2–15 μg C l⁻¹ day⁻¹. Thus, the production of *O.dioica* in the Seto Inland Sea during the warm season (Figure 9; Uye and Ichino, 1995) seems to be comparable to or sometimes exceeding that of copepods, indicating that Appendicularia are an important metazoan secondary producer in this area.

Oikopleura dioica as a picoplankton predator

We infer that the ingestion of picoplankton was responsible for the rapid increase in *O.dioica* biomass from 4 to 6 August (Figures 6 and 7) based on the following considerations. First, although we did not measure the size of nano-/picoplankters, the biomass of picoplankton apparently far exceeded that of the nanoplankton from 3 to 5 August (Figure 7). Second, *O.dioica* does not seem to sustain the rapid growth by ingesting nanoplankton alone: on 5 August, the ingestion rate of food

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particles by *O.dioica* was 32 µg C l^{-1} day^{-1} (GGE of 0.33 is assumed), but the biomass of nanoplankton was ~9 µg C l^{-1} (Figure 7). Third, the stomachs of *O.dioica* were filled with picocyanobacteria during this period. Based on these considerations, it is plausible that *O.dioica* developed its population by ingesting picoplankton as the main food source.

The increase in *O.dioica* biomass overlapped with the decrease in picoplankton biomass. Thus, one might consider that the decrease was due to ingestion of picoplankton by *O.dioica*. However, other factors such as ingestion by HNF and viral lysis might have contributed to the decrease. Although there are no cues to assess the viral lysis quantitatively, we compared the production of HNF with *O.dioica* in a semiquantitative manner as follows. The abundance of HNF was relatively constant at around 1.5 × 10^3 ml^{-1} when *O.dioica* developed the population. These values are typical in our study area in summer (Nakamura *et al.*, 1994, 1995) and equivalent to a biomass of ~5 µg C l^{-1}. If we assume that the growth rate of HNF was 2.3 day^{-1} (maximum growth rate of a HNF strain isolated from the study area; Y.Nakamura, unpublished), the production of HNF was ~12 µg C l^{-1} day^{-1}, comparable to that of *O.dioica* from 4 to 6 August. In other words, *O.dioica* played as important role as a picoplankton predator as HNF during this period.

If we assume a GGE of 0.33 for HNF and *O.dioica*, ingestion of picoplankton on 4–5 August by the two groups would be 36 and 21–33 µg C l^{-1} day^{-1}, respectively. Thus, ingestion by both components seemed to play a significant role in the rapid decrease in picoplankton biomass from 4 to 6 August (~16 µg C l^{-1} day^{-1}; Figure 7), although the production of picoplankton was not measured.

Conclusion

Following the picoplankton 'bloom', the abundance and biomass of *O.dioica* increased rapidly by ingesting picoplankton populations. Its production was comparable to that of copepods and HNF during this period, indicating that *O.dioica* played important roles in transporting the picoplankton production to higher trophic levels effectively.

Acknowledgements

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