Species composition and horizontal distribution of the appendicularian community in waters adjacent to the Kuroshio in winter–early spring

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Abstract: Species composition and horizontal distribution of appendicularians were investigated in waters adjacent to the Kuroshio, south of Honshu in winter–early spring. Twenty-one species belonging to 5 genera were found and the species composition was characterized by a strong dominance of *Oikopleura longicauda* and occasional dense occurrence of *Fritillaria pellucida*. *Oikopleura longicauda* was distributed rather uniformly throughout the study area while *F. pellucida* was usually only sparsely distributed, although it was sometimes found in dense concentrations at the stations close to the Kuroshio axis. Occurrence of *O. dioica*, a well-studied neritic species, was limited to the stations with a relatively shallow bottom and its relative importance in terms of abundance was small. Generally, the appendicularian biomass was less than one tenth of the copepod biomass in carbon. Nevertheless, the role of appendicularians in terms of secondary production was estimated to be smaller but comparable in magnitude to that of copepods, 1.7–202.3 mgC $m^{-2} d^{-1}$ in the former and 30.0–185.2 mgC $m^{-2} d^{-1}$ in the latter, because of their higher somatic growth rates and house production. Clearance rate of appendicularians was also estimated to be comparable to copepods, 3.1–591.3 L $m^{-2} h^{-1}$ in the former and 49.0–462.1 L $m^{-2} h^{-1}$ in the latter, owing to their much higher weight specific clearance rates.

Key words: appendicularian, *Fritillaria*, Kuroshio, *Oikopleura*

Introduction

Appendicularians are famous for their production of "houses", a balloon-like mucous filtering structures, which are one of major sources of sinking particles or marine snow (Alldredge 1977, Hansen et al. 1996, Kiørboe et al. 1996), and high clearance rate of particles from the water column (Alldredge 1981). Their very high ability to concentrate and ingest small food particles ($<5 \mu$m) should be advantageous in oceanic regions where food particles are relatively small and scarce. The role of house production should again be important in oceanic regions where organic carbon is removed from surface layers to the depths as sinking particles (Murray et al. 1994). Previous studies on the appendicularian community have been rather restricted to neritic regions (e.g. Acuña & Anadon 1992, Hopcroft & Roff 1998, Tomita et al. 2003) and knowledge of the oceanic region community is still scarce.

Appendicularians are also important as prey of commercial fish species. Larvae and juveniles of flatfish are often reported to exclusively depend on appendicularians (Shelbourne 1962, Minami 1982, Kuwahara & Suzuki 1983, Gadomski & Boehlert 1984). In the waters adjacent to the Kuroshio, a series of studies have focused on the ecology of commercial pelagic fish (e.g. sardine, anchovy, and saury) and appendicularians were revealed to be one of the common food items of larval/juvenile sardine (e.g. Uotani 1985, Watanabe & Saito 1998). Thus knowledge of appendicularian distribution in oceanic regions is useful in the context of fisheries oceanography as well as of plankton community dynamics and organic material flow.

In this study, species composition and horizontal distribution of appendicularians were investigated in waters adjacent to the Kuroshio, south of Honshu, in winter–early spring, where spawning of the commercial pelagic fish species mentioned above occurs (Watanabe et al. 1995). The importance of appendicularians in terms of biomass, secondary production, and particle clearance rate was discussed in comparison to copepods, which is the most dominant zooplankton group in the study area (Kidachi & Itoh 1979) and important prey for pelagic fish species (Watanabe & Saito 1998).

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Materials and Methods

Samples were collected as a part of the fish egg census program which has been conducted by the Fisheries Research Agency, Japan. In the census, eggs and larvae of pelagic fish as well as zooplankters were collected with a conical net (diameter of 60 cm, mesh size of 0.33 mm) by vertical tows (150 m depth to surface). The volume of water filtered by the net was estimated with a flow meter mounted in the mouth of the net. Each sample was preserved in 5% buffered formalin-seawater solution. Appendicularians were sorted from the entire samples or from aliquot subsamples and identified to species. Trunk length of each specimen was measured to calculate the appendicularian biomass. We included unidentified specimens and damaged appendicularian trunks collected without tails in the quantification, but appendicularian tails without the trunk were not included.

To reveal the horizontal distribution pattern of each species, 6 years were selected to represent patterns of Kuroshio current path; large-meander path (1976, 1977, 1978) and non-large-meander (straight) path (1972, 1982, 1986). Samples collected in meridional transects off Cape Shionomisaki (c.a. 135.5°E, point A in Fig. 1), off Cape Daiozaki (c.a. 137°E, point B), and off Cape Irouzaki (c.a. 139°E, point C) were analyzed for each year. A total of 136 samples were analyzed and we grouped sampling stations into three water types: slope water (75 stations), Kuroshio (32 stations), and subtropical water (29 stations) after Nakata et al. (2001). Briefly, the Kuroshio axis was distinguished by a 15°C isotherm at 200 m depth from the slope water and distinguished by the fast surface current velocity (>2 knots) from subtropical water.

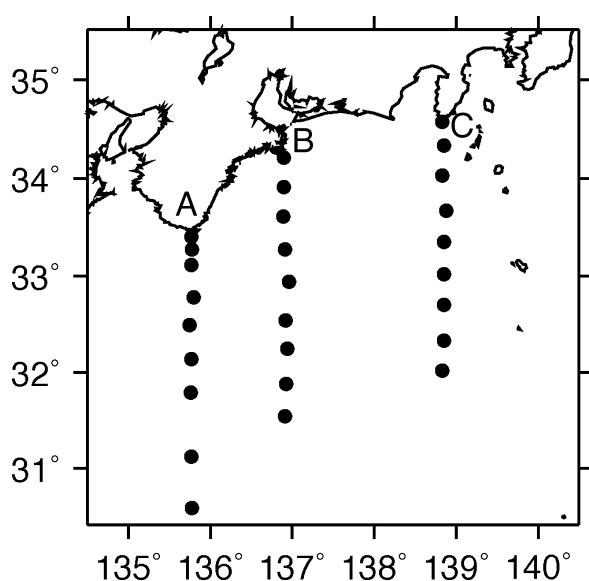Biomass of each appendicularian species was calculated by the size-biomass (in dry weight) relationship based on

Fig. 1. Study area and example of stations. Stations in 1972 are shown.

Hopcroft et al. (1998). The biomass of unidentified specimens was calculated with the size-biomass relationship of *Oikopleura dioica* as $\log DW = 2.51 \log L - 6.54$, where DW is the dry weight (μg) and L is the trunk length (μm) (Hopcroft et al. 1998). Carbon content was assumed to be 46.3% of dry weight after Uye (1982). Somatic production of appendicularians was estimated after Tomita et al. (1999), assuming daily specific growth rate (g) at 20°C was 0.592 and temperature coefficient Q_{10} was 1.68. Clearance rates of appendicularians were calculated after Sato et al. (2005), assuming weight specific clearance rates of 2.8 and 4.5 mL μgC^{-1} h^{-1} for lower and higher estimates, respectively.

Results

Species composition

Twenty-one species of appendicularians belonging to 5 genera were found from the samples (Table 1). A summary of the species composition in each oceanic area is shown in Table 2, based on the results of six years (1972, 1976, 1977, 1978, 1982, 1986) to cover the study area evenly. As a dense occurrence of *Fritillaria pellucida* Busch in 1977 (see the next section) strongly influenced the total species composition, five years (1972, 1976, 1978, 1982, 1986) were summarized in Table 2a and all of six years in Table 2b. In Table 2a, *Oikopleura longicauda* (Vogt) was the most dominant species in all of the three regions, representing 48.4–69.2% of the total individuals. The species was most dominant at 86 of 136 stations. At stations where *O. longicauda* was not the most dominant, *F. pellucida* was most dominant in 25 of 50 stations. In the slope water and subtropical water, *F. pellucida* was second most dominant on average. However, the species showed a rather patchy distribution and its median abundance (75.0 indiv. m^{-2}) was much less than the average (260.7 indiv. m^{-2}). *Oikopleura cophocerca* (Gegenbaur), *Oikopleura fusiformis* Fol, *Oikopleura rufescens* Fol were common in the study area and represented 2.6–12.3, 3.6–5.0, 5.9–7.7% of the total individuals, respectively. *Oikopleura dioica* Fol, a well-studied neritic species, accounted for 4.1% of total individuals in the slope water. However, the occurrence of *O. dioica* was limited to 25 of 75 stations and thus the median of observed abundance was zero.

If the result for 1977 were included into the calculation, *F. pellucida* becomes the most dominant on average in the slope water and in the Kuroshio (Table 2b). However, the median abundance of each species was similar between Table 2a (without results for 1977) and Table 2b (all six years), even for *F. pellucida*, which indicates the robustness of the species composition described above which was represented by a strong dominance of *O. longicauda* and occasional dense occurrences of *F. pellucida*.

Table 1. Occurrence of appendicularian species in the present study.

Species	slope water	Oceanic Area Kuroshio	subtropical water
family Oikopleuridae			
Oikopleura albicans (Leuckart)	*	*	*
Oikopleura cophocerca (Gegenbaur)	*	*	*
Oikopleura cornutogastra Aida	*		*
Oikopleura dioica Fol	*	*	*
Oikopleura fusiformis Fol	*	*	*
Oikopleura gracilis Lohmann	*	*	
Oikopleura intermedia Lohmann	*	*	*
Oikopleura longicauda (Vogt)	*	*	*
Oikopleura parva Lohmann	*	*	*
Oikopleura rufescens Fol	*	*	*
Stegosoma magnum (Langerhans)	*	*	
family Fritillaridae			
Appendicularia sicula Fol	*		
Fritillaria aberrans Lohmann	*		
Fritillaria borealis f. *sargassi* Lohmann	*	*	*
Fritillaria charybdae Lohmann	*		
Fritillaria formica Fol	*		*
Fritillaria haplostoma Fol	*	*	*
Fritillaria megachile Lohmann	*		
Fritillaria pellucida Busch	*	*	*
Fritillaria venusta Lohmann	*		
Tectillaria fertilis (Lohmann)	*	*	*

Table 2a. Abundance and species composition of appendicularians collected in the three oceanic areas around the Kuroshio, compilation of five years (1972, 1976, 1978, 1982, 1986).

	slope water (*n*=59)				Kuroshio (*n*=27)				subtropical water (*n*=26)			
	abundance average	(%)	median	maximum	abundance average	(%)	median	maximum	abundance average	(%)	median	maximum
genus *Oikopleura*												
O. longicauda	693.9	(48.4)	464.8	3,919.0	935.9	(54.2)	682.0	4,025.4	1,417.8	(69.2)	177.9	22,745.3
O. dioica	58.9	(4.1)	0.0	655.3	3.7	(0.2)	0.0	61.9	0.4	(0.0)	0.0	10.5
O. fusiformis	64.2	(4.5)	26.1	435.3	62.7	(3.6)	9.1	364.0	101.8	(5.0)	11.1	578.6
O. rufescens	95.2	(6.6)	52.3	485.7	133.2	(7.7)	89.0	570.1	121.6	(5.9)	30.9	1,312.2
O. parva	60.1	(4.2)	18.5	438.2	75.4	(4.4)	15.7	1,299.3	14.5	(0.7)	0.0	129.0
O. cophocerca	76.7	(5.3)	26.1	758.3	211.8	(12.3)	155.8	1,203.5	53.4	(2.6)	37.3	200.8
genus *Fritillaria*												
F. pellucida	260.7	(18.2)	74.7	6,391.0	141.3	(8.2)	27.4	1,264.6	233.1	(11.4)	49.0	1,967.0
others	124.7	(8.7)		673.0	163.3	(9.5)		760.1	107.0	(5.2)		1,312.4
Total	1,434.3 (indiv. m^{-2})	(100.0)	1,085.1 (indiv. m^{-2})	8,125.9	1,727.4 (indiv. m^{-2})	(100.0)	1,592.6 (indiv. m^{-2})	5,596.3	2,049.5 (indiv. m^{-2})	(100.0)	478.2 (indiv. m^{-2})	27,556.7

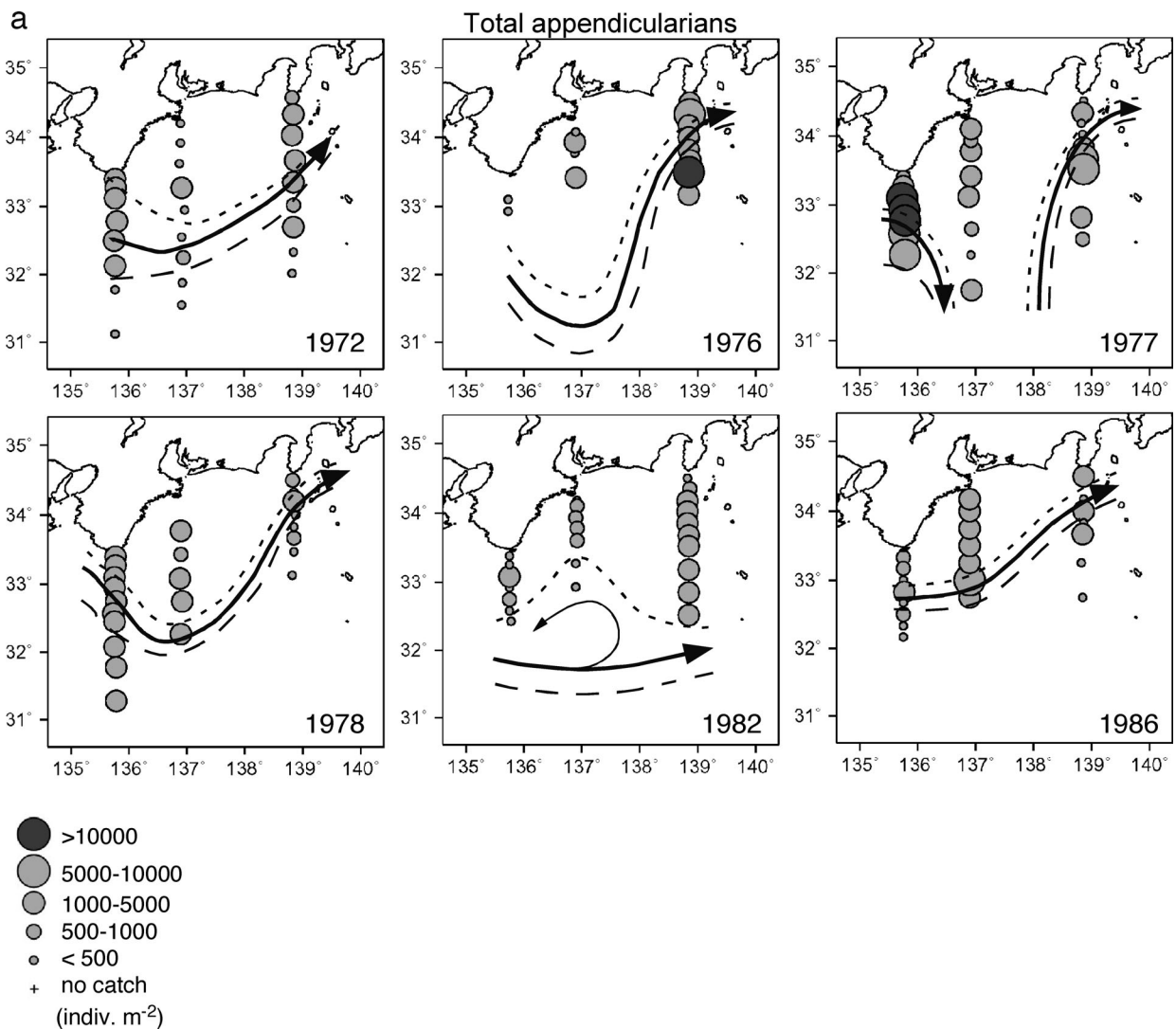*n*=number of stations

Horizontal distribution

Horizontal distribution of the total appendicularian abundance, for the most dominant two species (*Oikopleura longicauda* and *Fritillaria pellucida*), and *O. dioica* are shown in Fig. 2. There was no statistical difference in the total ap-
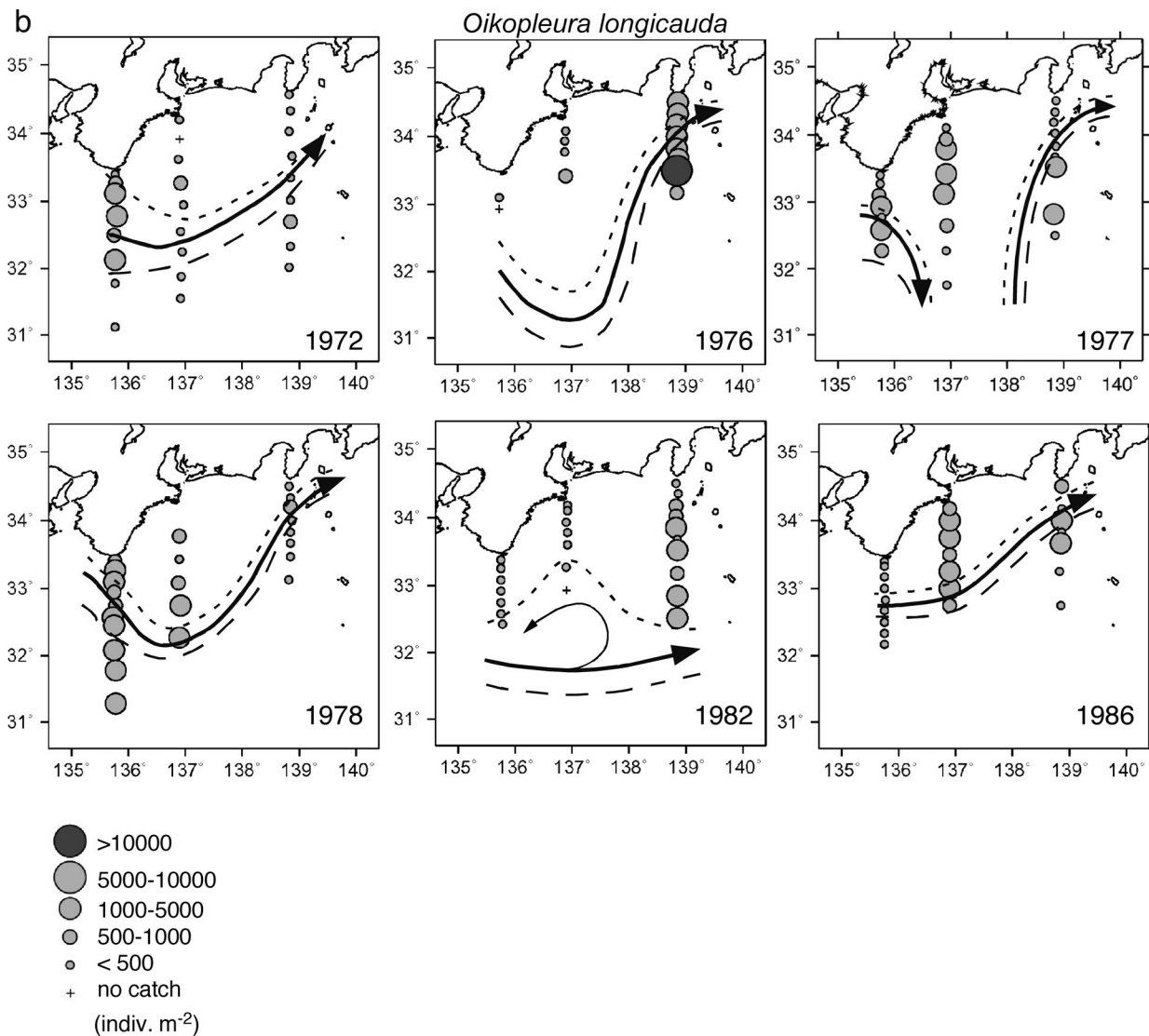
pendicularian abundance among the three oceanographic regions (Kruskal-Wallis test, $p>0.05$) for all of the six years. However, high total abundance sometimes occurred around the Kuroshio axis (Fig. 2a). This distributional pattern of the total appendicularian abundance reflected that of the two dominant species, *O. longicauda* and *F. pellucida*,

Table 2b. Abundance and species composition of appendicularians collected in the three oceanic areas around the Kuroshio, compilation of six years (1972, 1976, 1977, 1978, 1982, 1986).

	slope water (*n*=75)				Kuroshio (*n*=32)				subtropical water (*n*=29)			
	abundance average	(%)	median	maximum	abundance average	(%)	median	maximum	abundance average	(%)	median	maximum
genus *Oikopleura*												
O. longicauda	701.1	(31.6)	460.4	3,919.0	906.2	(36.9)	674.0	4,025.4	1,434.0	(68.0)	204.9	22,745.3
O. dioica	48.3	(2.2)	0.0	655.3	4.9	(0.2)	0.0	61.9	0.3	(0.0)	0.0	10.5
O. fusiformis	65.5	(3.0)	26.1	435.3	68.6	(2.8)	4.6	502.9	113.3	(5.4)	14.8	578.6
O. rufescens	81.9	(3.7)	46.3	485.7	112.4	(4.6)	46.4	570.1	109.4	(5.2)	24.1	1,312.2
O. parva	58.7	(2.6)	28.4	438.2	63.9	(2.6)	4.1	1,299.3	13.0	(0.6)	0.0	129.0
O. cophocerca	78.2	(3.5)	27.3	758.3	195.2	(8.0)	132.2	1,203.5	50.1	(2.4)	36.5	200.8
genus *Fritillaria*												
F. pellucida	1,038.6	(46.8)	68.7	41,029.3	960.8	(39.1)	42.0	14,599.2	282.9	(13.4)	66.9	1,967.0
others	146.6	(6.6)		2,735.8	142.3	(5.8)		760.1	105.8	(5.0)		1,312.4
Total	2,218.9 (indiv. m^{-2})	(100.0)	1,085.1 (indiv. m^{-2})	45,077.5	2,454.3 (indiv. m^{-2})	(100.0)	1,667.2 (indiv. m^{-2})	14,850.4	2,108.8 (indiv. m^{-2})	(100.0)	568.2 (indiv. m^{-2})	27,556.7

n=number of stations

b   *Oikopleura longicauda*

1972 1976 1977 1978 1982 1986

>10000
5000-10000
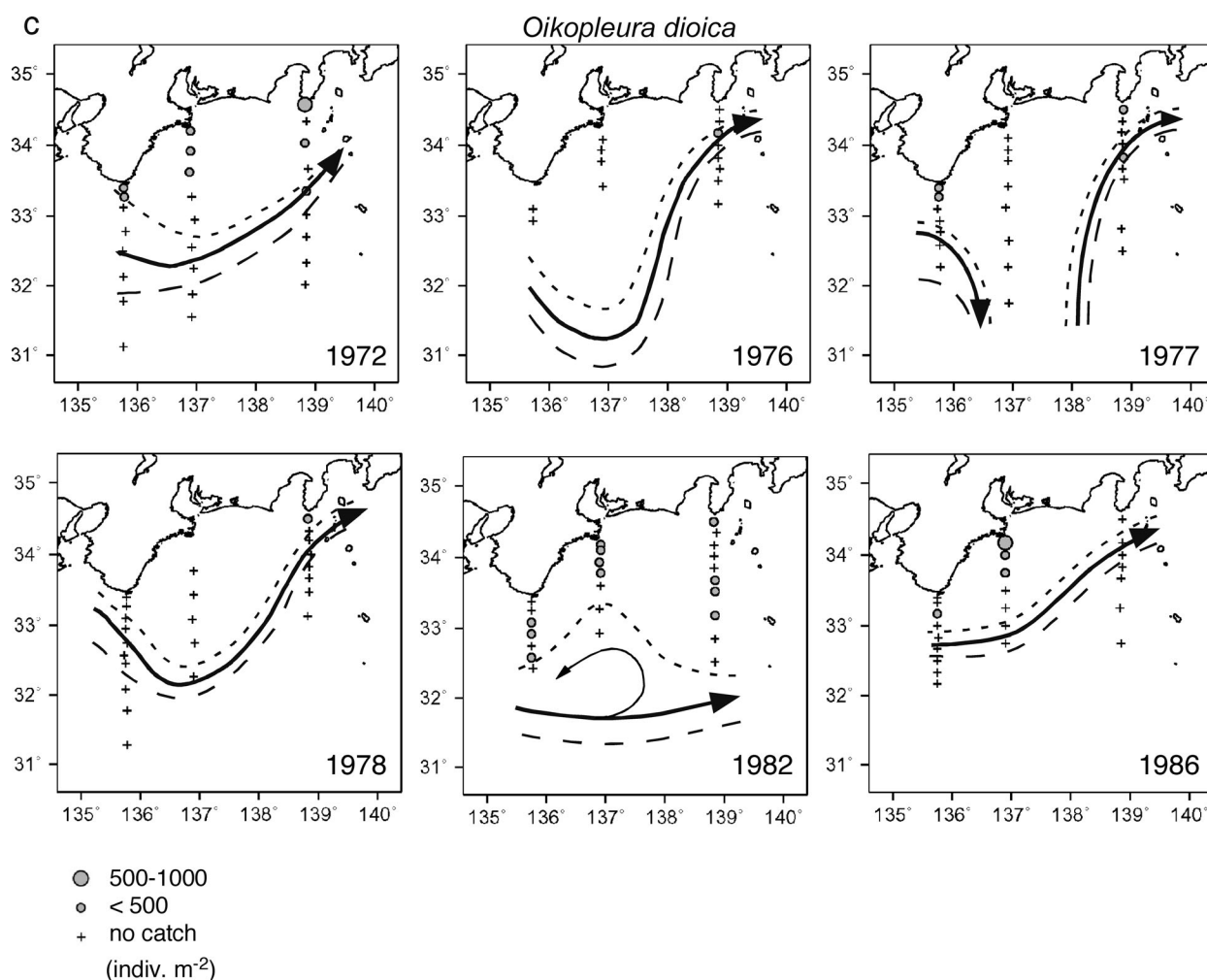1000-5000
500-1000
< 500
+   no catch
(indiv. m⁻²)

both of which had characteristic distribution patterns.

Oikopleura longicauda was distributed rather uniformly throughout the study area and sometimes occurred at abundances $>1,000$ indiv. m^{-2} (Fig. 2b). Such high abundances were not restricted to any oceanic region, which can be seen typically in 1976 and 1978. In contrast, *F. pellucida* was usually distributed sparsely (75.0 indiv. m^{-2} median), but high abundances ($> 1,000$ indiv. m^{-2}, sometimes $>10,000$ indiv. m^{-2}) were found mainly at stations close to the Kuroshio (Fig. 2d). Occurrence of *O. dioica* was limited to the slope water and maximum density was 655.3 indiv. m^{-2}, which was much less than that of either *O. longicauda* (3,919.0 indiv. m^{-2}) or *F. pellucida* (41,029.3 indiv. m^{-2}) (Fig. 2c).

Relationship between sea surface temperature and appendicularian abundance

The relationship between sea surface temperature (SST) and abundance of appendicularians is shown in Fig. 3. The range of SST at the stations in the present study was 14.4–20.4°C. High abundances of *Oikopleura longicauda* ($>2,000$ indiv. m^{-2}) were observed in the SST range of 17–20.4°C (Fig. 3b). It should be noted that even at stations where SST was <17°C, *O. longicauda* often occurred in abundances of $>1,000$ indiv. m^{-2} and was the most dominant species. Occurrence of *O. dioica* was restricted to the slope water, as mentioned above, with SST <18°C and mainly 15–17°C (Fig. 3c). *Oikopleura fusiformis* occurred in an SST range of 15–20°C, with a low abundance at stations with 17–18°C SST (Fig. 3d). *Oikopleura rufescens* exhibited a pattern similar to *O. fusiformis*, but the abundance of *O. rufescens* was low at stations with 16–17°C SST (Fig. 3e). *Oikopleura parva* was distributed rather uniformly in an SST range of 15–20°C and its abundance was higher in the slope water than in other regions (Fig. 3f). *Oikopleura cophocerca* exhibited a unimodal distribution in the range of SST, with a peak abundance at 18.2°C (Fig. 3g). *Fritillaria pellucida* occurred in a similar temperature range to *O. longicauda*, but occurrences of $>1,000$ indiv.

c *Oikopleura dioica*

500-1000
< 500
no catch
(indiv. m⁻²)

m⁻² were restricted to the stations with an SST of 18–20°C except for at one station with an SST of 16.4°C (Fig. 3h).

Effect of the Kuroshio flow path

Figure 4 shows the relationship between SST and the abundance of appendicularians in the non-large-meander (straight) path (1972, 1982, 1986) and in the large-meander (meander) path (1976, 1977, 1978) of the Kuroshio (cf. Fig. 2). The effect of the Kuroshio path on SST was apparent in the slope water and the Kuroshio, where SST had a relatively broader range in years of the meander path (Fig. 4b,d). In years of the straight path, the SST in the slope water was <17°C at 34 of 39 stations (21 of 36 stations in years of the meander path) and the SST range in the Kuroshio area was 18.5–20.0°C (16.4–19.7°C in years of the meander path), if we exclude three stations with an SST of 15–16°C (Fig. 4a,c). The appendicularian abundance in the slope water in years of the straight path, 1209.9 indiv. m⁻² in average and 990.3 indiv. m⁻² in median, was lower than in that during the meander path, 3,312.0 indiv. m⁻² and 1,233.3 indiv. m⁻². High abundances of *F. pellucida*, >5,000 indiv. m⁻², occurred in years of the meander path

(Fig. 2d).

Appendicularian biomass, metabolic rates and their relative importance in comparison to copepods

Biomass, somatic growth production and clearance rates of appendicularians and copepods in the study area are shown in Table 3. Copepod biomass data were derived from the data set of Nakata et al. (2001). Somatic production of copepods was estimated after Huntley & Lopez (1992), where daily specific growth rate (g) was expressed as: $g = 0.0445 \, e^{0.111T}$, where T is the water temperature. Clearance rate of copepods was calculated after Sato et al. (2005), assuming a weight specific clearance rate of 0.6 mL $\mu g C^{-1} h^{-1}$.

Appendicularian biomass in terms of carbon in the study area was 7.4 mg m⁻² on average with a median of 3.0 mg m⁻² in the slope water, 8.1 and 4.0 mg m⁻² (average and median) in the Kuroshio and 7.9 and 1.1 mg m⁻² (average and median) in the subtropical water (Table 3). Figure 5 shows the relative importance of appendicularians to copepods in terms of biomass in the study area. The frequency distribution of the carbon biomass ratio of appendicularians
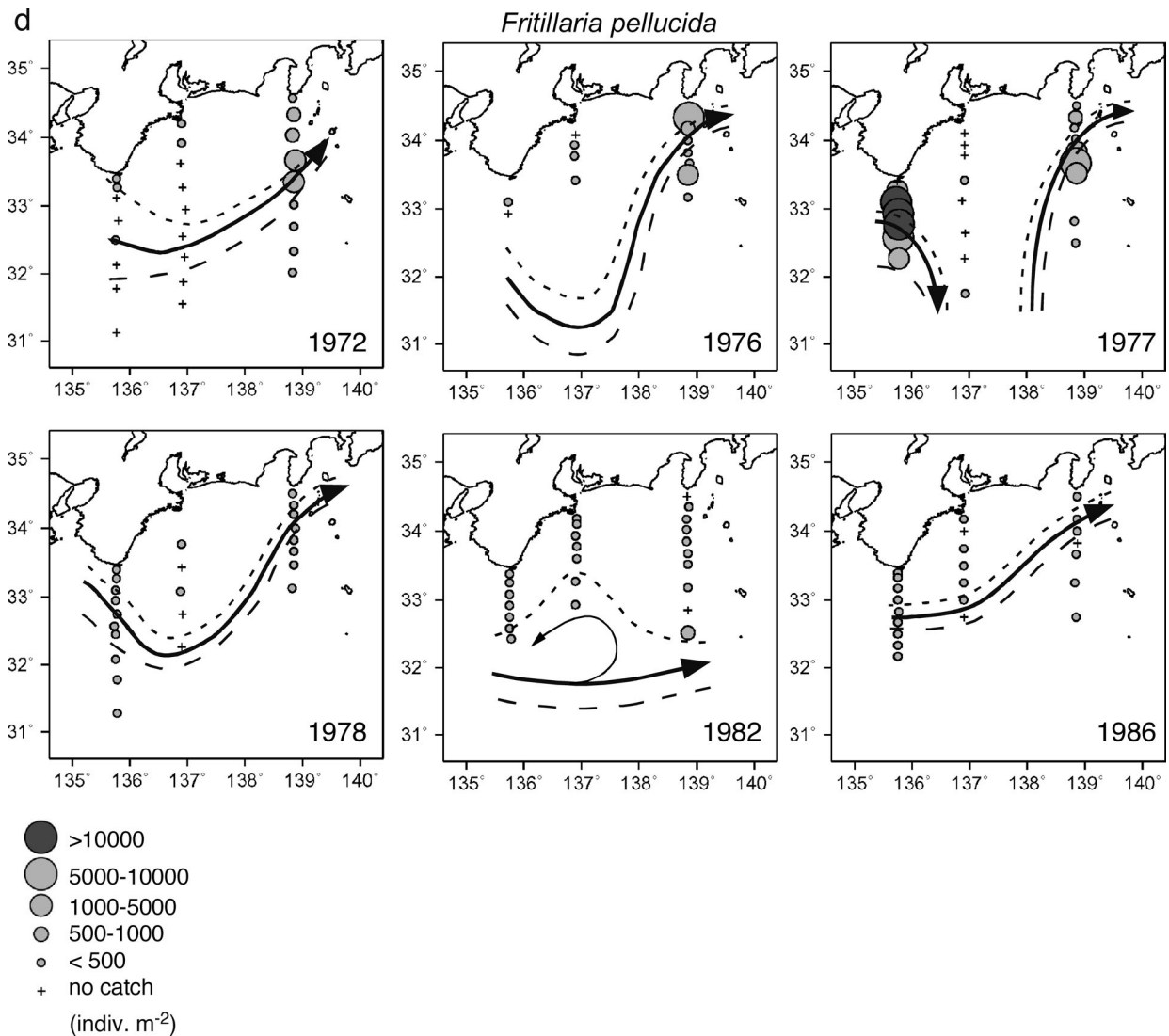
Fig. 2. Horizontal distributions of abundance of total appendicularians and representative species. The solid curve in each figure shows the main stream and bifurcation of the Kuroshio flowpath. The short dashed curve indicates the boundary of the slope water and the Kuroshio water. The long dashed curve indicates the boundary of the Kuroshio water and the subtropical water. a: Total appendicularians. b: *Oikopleura longicauda*. c: *O. dioica*. d: *Fritillaria pellucida*.

to copepods are shown as a histogram. The modal class in the histogram was $-1.5 < x < -1.0$, which corresponds to a biomass ratio (appendicularians/copepods, in carbon) of 0.03 to 0.10. The average and median of the ratio was 0.025 (average) and 0.037 (median) in the slope water, 0.028 and 0.036 in the Kuroshio, 0.021 and 0.015 in the subtropical water, and 0.025 and 0.032 over all stations. Appendicularian biomass did not exceed the copepod biomass except for at 2 out of 142 stations.

Somatic growth production of appendicularians (average and median) was $0.6–4.5\,mgC\,m^{-2}\,d^{-1}$ and was one order lower than that of copepods. However, the maximum values of appendicularian somatic production, $24.4–70.9\,mgC\,m^{-2}\,d^{-1}$, were comparable in magnitude to those of copepods. The clearance rate of appendicularians was $20.8–36.5\,L\,m^{-2}\,h^{-1}$ on average, with a median of $3.1–18.1\,L\,m^{-2}\,h^{-1}$,

and a maximum of $124.6–591.3\,L\,m^{-2}\,h^{-1}$ (Table 3). These values were comparable to those of copepods in each oceanic area, except for the median values in the subtropical water.

Discussion

The dominance of *Oikopleura longicauda* and *Fritillaria pellucida*

All of the appendicularian species that occurred in the study area have been reported previously from the western Pacific Ocean (Tokioka 1955, Itoh 1990). The strong dominance of *Oikopleura longicauda* and occasional occurrence of *Fritillaria pellucida* (relatively large average abundance and smaller median) were common to the three regions, i.e.
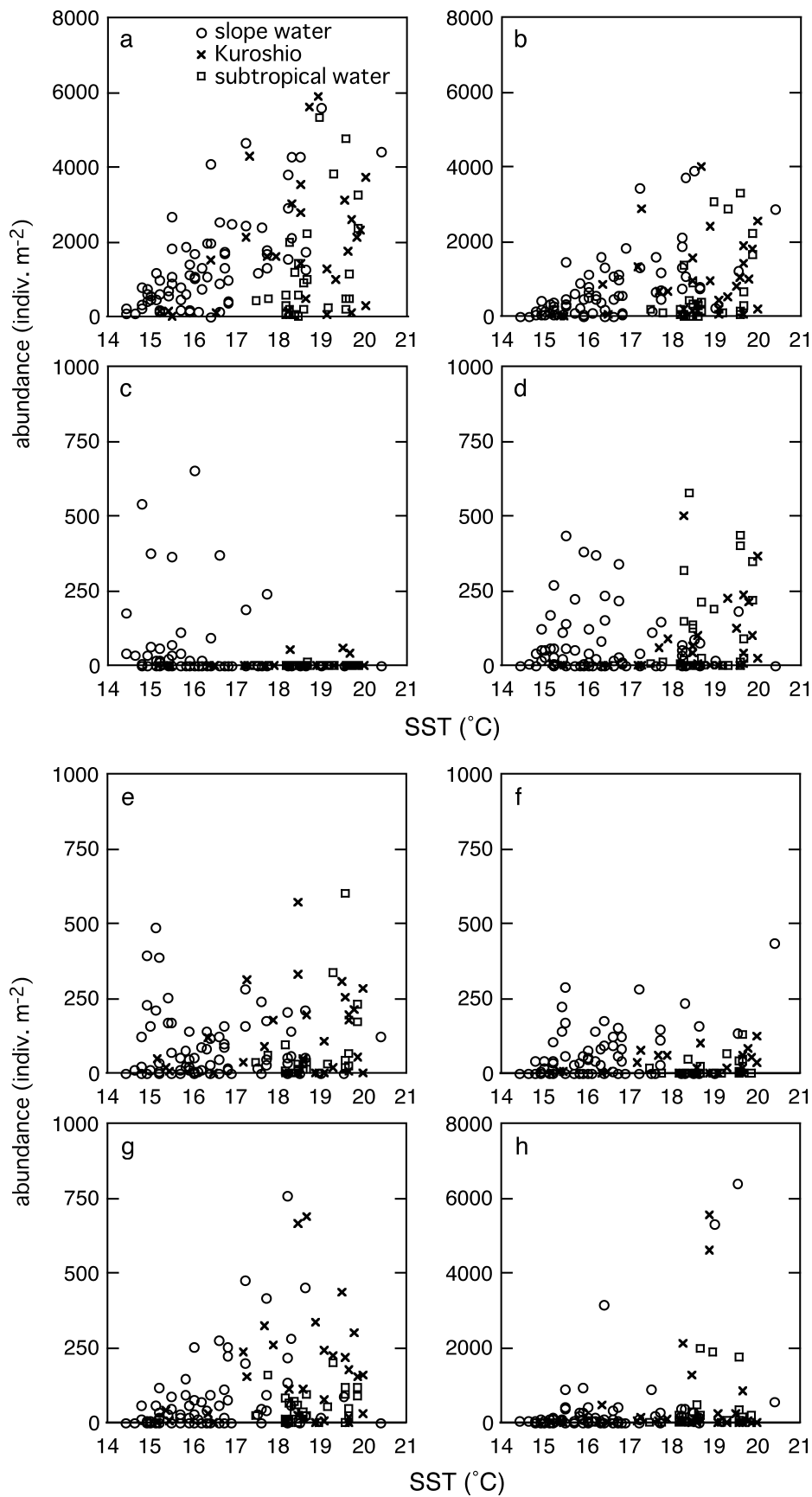
Fig. 3. Relationship between sea surface temperature (SST) and abundance of total appendicularians and dominant species. a: Total appendicularians. b: *Oikopleura longicauda*. c: *O. dioica*. d: *O. fusiformis*. e: *O. rufescens*. f: O. parva. g: *O. cophocerca*. h: *Fritillaria pellucida*.
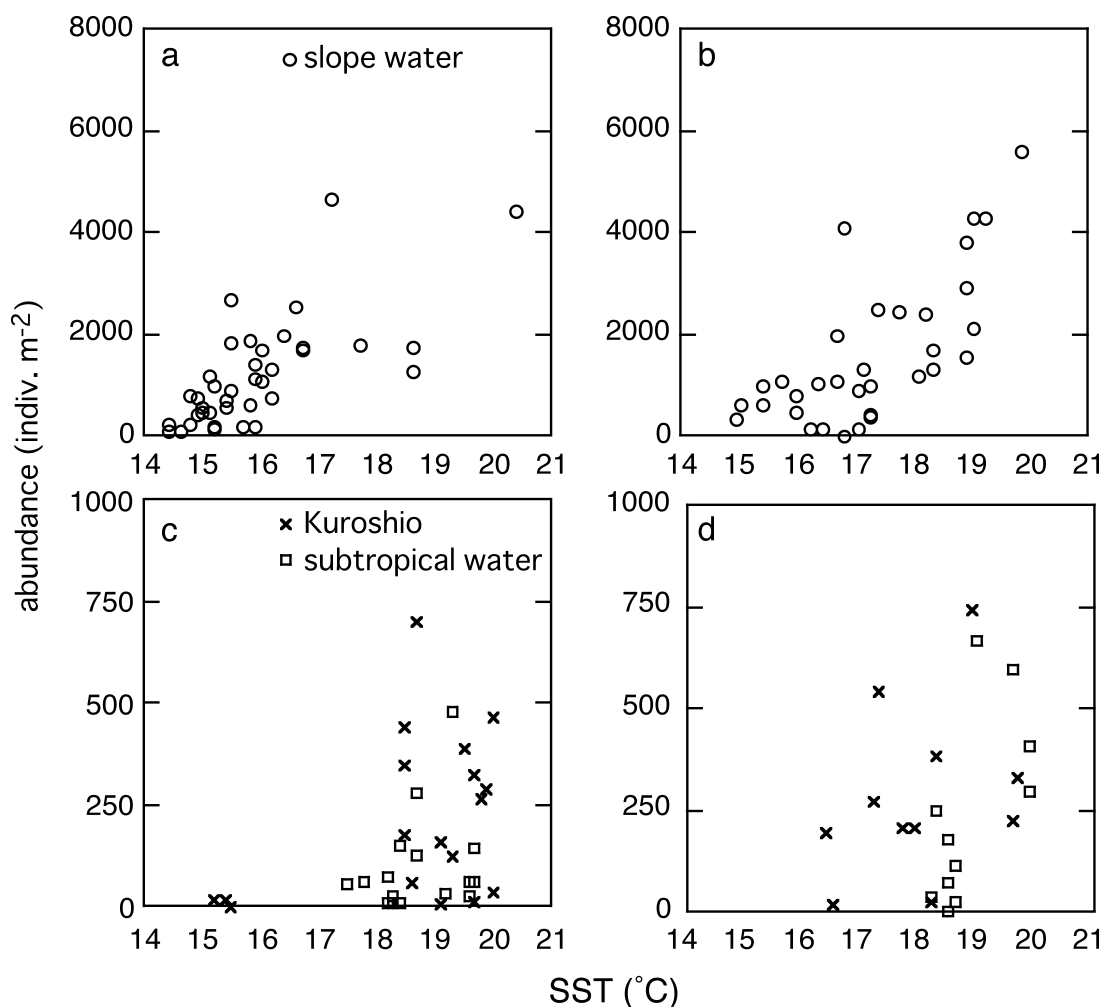
Fig. 4. Relationship between sea surface temperature (SST) and total appendicularian abundance in the straight paths (1972, 1982, 1986) and in the meander-type path (1976, 1977, 1978) of the Kuroshio. a: appendicularian abundance in the slope water, straight path. b: the slope water, meander-type path. c: the Kuroshio water and the subtropical water, straight path. d: the Kuroshio water and the subtropical water, meander-type path.

slope water, Kuroshio, and subtropical water.

Oikopleura longicauda has been reported to occur in neritic waters in cases where the sites have been affected by warm oceanic currents (Itoh 1990, Tomita et al. 2003). The slope water area in the present study was like this and thus *O. longicauda* was the dominant species from the slope water to subtropical water (Tables 2a,b). *Oikopleura longicauda* has a house without inlet filters and has the potential to ingest larger food particles (e.g. diatoms) that other appendicularian species cannot utilize as food (Alldredge 1977). The dominance of *O. longicauda* throughout the study area, from the continental slope to outside the Kuroshio, could also be a consequence of the ability of this species to utilize a broad size range of food particles.

Fritillaria pellucida was concentrated around the Kuroshio axis (Fig. 2d), which can be seen clearly in the relationship between its abundance and distance from the Kuroshio axis (Fig. 7). In general, planktonic organisms show dense distributions around oceanic fronts, because of

mechanical accumulation and higher biological production associated with the fronts (e.g. Fernandez et al. 1993, Lima et al. 2002). The observed dense distribution of *F. pellucida* is not thought to be due only to passive accumulation, because other oceanic appendicularian species did not occur in such high concentrations as *F. pellucida*. Physical and/or biological conditions around the Kuroshio front, e.g. water stratification and/or composition of food particles, is thought to have benefited the reproduction and/or survival of this species.

Occurrence pattern of *Oikopleura dioica* in the study area

Oikopleura dioica has been reported to occur as the most dominant appendicularian species in neritic water at high abundances, e.g. ca. 6,000 indiv. m^{-2} from 7–8 m to the surface (Uye & Ichino 1995) or 60,000 indiv. m^{-2} from 10 m to the surface (Nakamura et al. 1997). In this study, abun-

Table 3. Biomass, somatic growth produciton and clearance rates of appendicularians and copepods in the upper 150 m in the three oceanic areas around the Kuroshio.

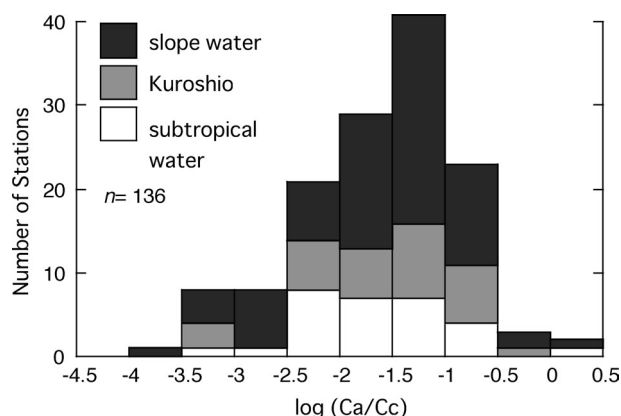|	slope water ($n=75$)			Kuroshio ($n=32$)			subtropical water ($n=29$)		
	average	median	maximum	average	median	maximum	average	median	maximum
biomass (mgC m^{-2})									
Appendicularians	7.4	3.0	131.4	8.1	4.0	44.5	7.9	1.1	115.9
Copepods	148.5	110.4	770.2	121.4	81.6	388.2	93.8	87.6	267.0
secondary production (mgC m^{-2} d^{-1})									
Appendicularians									
somatic production	3.9	1.4	70.9	4.5	2.2	24.4	4.5	0.6	67.2
somatic production +house production	11.3	4.4	202.3	12.6	6.2	68.9	12.5	1.7	183.1
Copepods	40.5	30.0	185.2	42.0	31.5	131.7	34.3	31.5	105.8
clearance rate (L m^{-2} h^{-1})									
Appendicularians									
lower estimate	20.8	8.4	367.9	22.7	11.2	124.6	22.2	3.1	324.6
higher estimate	33.4	13.4	591.3	36.5	18.1	200.3	35.7	5.0	521.6
Copepods	89.1	66.2	462.1	72.8	49.0	232.9	56.3	52.6	160.2

$n=$ number of stations

Fig. 5. The frequency distribution of biomass ratio of appendicularians to copepods. Ca: appendicularian biomass in carbon, Cc: copepod biomass in carbon. Copepod biomass data was derived from the data set used in Nakata et al. (2001).

Fig. 6. Relationship between bottom depth and abundance of *Oikopleura dioica*.

dance of *O. dioica* was generally lower than in these two previous reports even in the slope water (<655.3 indiv. m^{-2} for 0–150 m depth for 75 stations). The appendicularian community was generally dominated by *O. longicauda*, and *O. dioica* was less important than the other oceanic species, e.g. *O. rufescens* or *O. cophocerca* (Tables 2a, b). Figure 6 shows the relationship between bottom depth and abundance of *O. dioica* and it can be seen that occurrence of *O. dioica* at >100 indiv. m^{-2} was restricted to the area with a bottom depth of less than 1,000 m except for at one station where bottom depth was 2,120 m. *Oikopleura dioica* occurring in the slope water area would be advected from the nearshore zone to the offshore zone of the slope water by
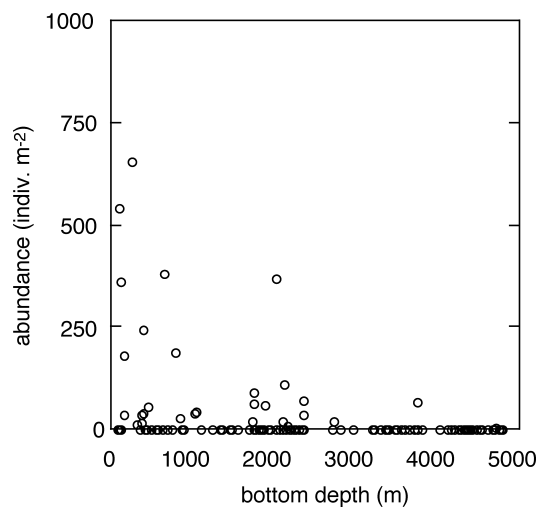
the Kuroshio or its bifurcation current (Kim & Onbé 1989, Ogawa & Wakabayashi 1992) but was most probably unable to adapt to the physical and/or biological environment well enough to become dominant.

SST and abundance

In the present study, the relationships between SST and abundances of *Oikopleura longicauda*, *O. dioica*, and *Fritillaria pellucida* were reflected clearly in the horizontal distribution patterns described above. *Oikopleura dioica* was distributed in neritic waters of low SST (Fig. 3c) and dense occurrences of *F. pellucida* were restricted to around the
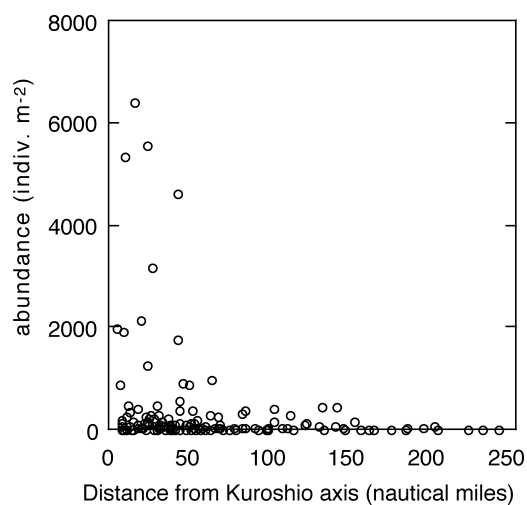
Fig. 7. Relationship between distance from the Kuroshio axis and abundance of *Fritillaria pellucida*.

Kuroshio with a narrower temperature range than in *O. longicauda* (Fig. 3b, h). Among the other species examined, the bi-modal distributional patterns seen in *O. fusiformis* and *O. rufescens* should be discussed. Sato (2000) suggested two genetic types for each of the two species based on the optimal temperature range for reproduction and morphological differences in their houses. For *O. rufescens*, Sato (2000) reported two types, one can live and mature at 20–23°C and one at >23°C. For *O. fusiformis*, one type which can mature at 23–26°C and another at 20–23°C were reported (Sato 2000). In the present study, however, the boundary of SST in the distributional range of the two populations was 16–17°C in *O. rufescens* and 17–18°C in *O. fusiformis* (Fig. 3d, e). Though the populations observed in our results were not identical with Sato's types, they could reflect other intraspecific populations, especially in *O. fusiformis* for which several morphological types have been suggested (Tokioka 1940).

The temperature range in the present study overlapped with the optimal temperature range (OTR) of each species reported by Itoh (1990), in which the abundance of each appendicularian species exceeded the averages in the study. The SST-abundance relationship of *O. longicauda* reflected its OTR, 17.8–26.8°C, with higher abundances at >17°C. Abundances of *O. dioica* and *F. pellucida*, with OTRs of 12.5–21.4°C and 15.0–18.8°C respectively, should not have reflected SST distributions but instead be determined by oceanographic structure as discussed above. In *O. fusiformis*, the OTR (14.8–21.4°C) matched the SST range well in the present study and this range corresponded to two assumed populations as above. In *O. rufescens*, the reported OTR of 17.8–26.8°C would correspond to one of the two assumed populations in the present study, the one that occurred at >17°C. Occurrence of *O. cophocerca* in Itoh (1990), in Suruga Bay, was limited to the period from September to January and the unimodal SST-abundance rela-

tionship of the species in Februaly–March, with peak abundance at 18.2°C, was first observed in the present study.

Effect of the type of Kuroshio flow path

The broader SST distribution in the slope water and the Kuroshio area (Fig. 4) in years of the meander-type path of the Kuroshio were most likely brought about by expansion of warm water from the Kuroshio, probably by bifurcation currents (Ogawa & Wakabayashi 1992). Then the relatively higher SST in the slope water should have favored the dominant species in the study area, *Oikopleura longicauda*, and lead to higher appendicularian abundances in years of the meander-type path (Fig. 2a,b, Fig. 3a,b, Fig. 4a,b). We cannot fully explain the high abundances of *Fritillaria pellucida* in years of the meander-type path (Fig. 2d), but the specific oceanic structure around the Kuroshio axis in those years presumably benefited the reproduction and/or survival of the species as discussed above.

Appendicularian biomass and their ecological importance

Appendicularian biomass in the study area was one order lower than copepod biomass, with a modal biomass ratio of 0.03 to 0.10 (Fig. 5). However, the estimated clearance rate of appendicularians in the study area was >20% of that of copepods in all estimates except the estimate in the slope water with a median biomass and lower weight specific clearance rate, and the estimates in the subtropical water with median biomass (Table 3). Thus the importance of appendicularians in terms of the consumption of food particles are roughly comparable in magnitude to those of copepods, owing to the high weight specific clearance rate of appendicularians. As shown and discussed in previous sections, appendicularians in the study area were dominated by *Oikopleura longicauda*, which has the potential to consume food particles over a broad size range. Thus appendicularians in the study area might not be strictly preying only on pico-plankton (<2 μm), but be a competitor of copepods through also consuming particles of nano-(2–20 μm) and micro-size (20–200 μm) classes.

Somatic growth production of appendicularians in terms of the average and median was 0.6–4.5 mgC m^{-2} d^{-1} and was one order lower than that of copepods, while the maximum values, 24.4–70.9 mgC m^{-2} d^{-1}, were comparable in magnitude to those of copepods. It should be pointed out that the secondary production of appendicularians is not restricted to growth of their body and/or reproduction. They produce a number of houses daily (e.g. 13–24 houses d^{-1} in *O. longicauda*) and the house production corresponds to 45–258% of their body growth in carbon (Sato et al. 2003). *Oikopleura longicauda*, the dominant species in the present study, has a daily biological production of houses corresponding to 112% of their body biomass (Sato et al. 2005) and 43–249% as body growth (Fenaux & Gorsky 1983). If we tentatively estimate daily house production rate as 100%

of the body biomass, total secondary production of appendicularians amounts to 1.7–202.3 mgC m^{-2} d^{-1}, smaller than but comparable in magnitude to that of copepods.

Besides secondary production or particle consumption, the role of appendicularians in the pelagic food web should be more complex if we regard that the discarded houses can serve as food particles (Ohtsuka et al. 1996), sinking particles (Hansen et al. 1996), and substrates for small organisms (Alldredge 1976). The total role of appendicularians in the ocean, in the various contexts described above, should be investigated and compiled in future studies.

Acknowledgements

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