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Metazooplankton distribution across the Southern Indian Ocean with emphasis on the role of Larvaceans

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The abundance and depth distribution of metazoans >20 μm were investigated at seven stations across the Southern Indian Ocean (SIO), October–November 2006. Copepod nauplii, copepodites and larvaceans dominated the metazooplankton community. Copepodites were most abundant within Agulhas Current and Southern Ocean waters, decreasing toward subtropical/tropical areas, whereas larvaceans showed the inverse pattern. The fraction <200 μm contained the majority of the zooplankton enumerated, including 81, 23 and 93% of the larvacean, copepodite and nauplii abundances, respectively. The relative abundance of larvaceans compared with copepodites increased from 7 to 44% from South Africa towards Australia. Peak copepodite biomass was observed off South Africa, while larvacean biomass was <1% of the copepodite biomass there, increasing to 6% in tropical waters. Both copepodite and nauplii biomass were positively correlated to total Chl a ($P < 0.0001$), larvacean biomass was only significantly related to temperature ($P = 0.0213$). Despite their low biomass, larvacean production was estimated to exceed the copepod production up to five times. It appears that the abundance and role of larvaceans in the SIO has been severely underestimated in previous studies; thus future investigations into the fate of organic matter will remain incomplete if this group is not adequately considered.

INTRODUCTION

Compared to other oceans, the Indian Ocean is one of the least studied, and an urgent need for further research efforts has recently been stressed (Hood *et al.*, 2008). Knowledge of the metazooplankton (i.e. multicellular zooplankton combining different size classes with functional differences compared to the protozooplankton; Sieburth *et al.*, 1978) distribution and basin-scale biological oceanography of the Southern part of the Indian Ocean is based on relatively few surveys carried out during the late 19th century, such as Tiefsee Expedition 1898–99, Südpolar Expedition 1901–03 and the International Indian Ocean Expedition IIOE 1960–65 (see Sherman *et al.*, 1998). Historically more attention has been devoted to the northern and continental shelf area around India, the Arabian Sea and Australia as well as the Seychelles (e.g. Rao, 1973; Piontkovski *et al.*, 1995 and references therein). The focus of the early investigations was primarily taxonomic for most groups (e.g. Tiefsee Expedition: Lohmann, 1914, Lohmann, 1931, Südpolar Expedition: Lohmann and Bückmann, 1926, Lohmann, 1931), while abundance and biomass measurements were neglected. Quantification received more attention during

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later periods with the IIOE and work by Russian expeditions that employed primarily 330 μm mesh Indian Ocean Standard Nets (Currie, 1963) and 260 μm mesh nets (Cushing, 1969), respectively.

The Southern Indian Ocean (SIO) is a mixture of water masses from several different origins, consisting of nutrient-rich Agulhas Current and Southern Ocean influenced waters off South Africa, oligotrophic offshore waters in the central areas, with warm and cold eddies mixing in towards tropical waters off Australia (Kostianoy *et al.*, 2003). Metazooplankton communities are shaped by these oceanographic regimes (Legendre *et al.*, 1986), with well-mixed nutrient-rich oceans supporting classical food chains, whereas oligotrophic stratified waters are characterized by small particles with productivity based on microbialy driven food webs.

Traditionally, copepods have been considered the most important metazooplankton group in pelagic food webs (e.g. Verity and Smetacek, 1996; Kiørboe, 1998), although the more fragile larvaceans have been shown to be the second most abundant metazooplankton group when appropriate sampling gear is employed (Fenaux *et al.*, 1998; Gorsky and Fenaux, 1998; Hopcroft and Roff, 1998a). Although similar in size, copepods and larvaceans represent different functional groups with respect to prey size preferences. Copepods primarily graze on microplankton, and to a lesser extent on nanoplankton, since their feeding retention efficiency decreases below 5–10 μm sized particles (Berggreen *et al.*, 1988). In contrast, larvaceans feed on 0.2–2 μm sized particles in addition to nanoplankton (Deibel and Lee, 1992; Flood *et al.*, 1992). Larvacean predator:prey ratios can reach 10 000:1 (Deibel, 1998), while similar sized copepods have a predator:prey ratio of 18:1 (Hansen *et al.*, 1994). Due to their specialized feeding mode, larvaceans are able to utilize directly the picoplankton dominated primary production in oligotrophic ecosystems, where 80% of the algae are <3 μm (Goericke, 1998), while copepods are dependent on protozoans as intermediates to access the primary producers in oligotrophic areas. Therefore, the "larvacean shunt" (Deibel and Lee, 1992) is a more efficient energy transfer to higher trophic levels compared to copepods. Increasingly, the importance of larvaceans is being recognized (Alldredge, 1981; Nakamura *et al.*, 1997; Hopcroft *et al.*, 1998a; Hopcroft and Roff, 1998a; Maar *et al.*, 2004; Scheinberg *et al.*, 2005).

To address this deficiency in knowledge in the Indian Ocean, we investigated the metazooplankton community (including micro-sized components) in high productive cold waters, oligotrophic Open Ocean as well as tropical waters across the SIO during October–November 2006. This investigation focuses on the interaction between hydrographic regimes, food components and the composition of the metazooplankton, with emphasis on the importance of larvaceans in relation to the copepod community.

METHOD

Study area

The investigation of the SIO was conducted during the Danish Galathea3 Expedition (leg 7) from Cape Town, South Africa to Broome, NW Australia, from 17 October to 5 November 2006 (Fig. 1). A detailed description and analysis of the oceanography and the base of the food web are presented in Visser *et al.* (submitted for publication). The oceanography of the SIO covers several frontal systems consisting of the Northern Subtropical Front (NSTF), the Southern Subtropical Front (Subtropical Convergence) (SSTF) and the Agulhas Front (AF), associated with the eastward propagation of the Agulhas Current up to 70°–80° E. The SSTF (Subtropical Convergence) separates warm and saline subtropical Indian Ocean waters from cooler and fresher ones of the Southern Ocean (Kostianoy *et al.*, 2003).

Sampling

To encompass the oceanographic regimes encountered during the cruise, seven stations were sampled across the SIO (Fig. 1). Vertical profiles of salinity and temperature were measured using a Seabird 9/11 CTD on a rosette equipped with twelve 30-L Niskin bottles. At all stations, vertical CTD profiles were repeated thrice to a depth of at least 400 m, starting at 08:00 am, with the downward cast used to describe the water column structure and water samples taken during each upward cast at 400 m, 200 m, 100 m, 60 m, 30 m, 10 m and the depth of maximum fluorescence, if present.

Chlorophyll

Total chlorophyll *a* (Chl *a*) concentrations were determined from the first CTD cast at 8:00 am and measured by filtration of 500 mL seawater onto Whatman GF/F filters. In addition to total Chl *a* (all depths), size-fractionation was applied to samples from the upper 100 m of the water column using 0.2 μm Nucleopore filters (250–500 ml) as well as 10 μm and 50 μm Nitex filters (500–1000 ml). The Chl *a* fraction >0.2 μm was not significantly different from the GF/F fraction and these data are therefore not presented. Measurements of the >50 μm size fraction were not available for the first two stations. Chl *a* was extracted in 5 mL of 96% ethanol

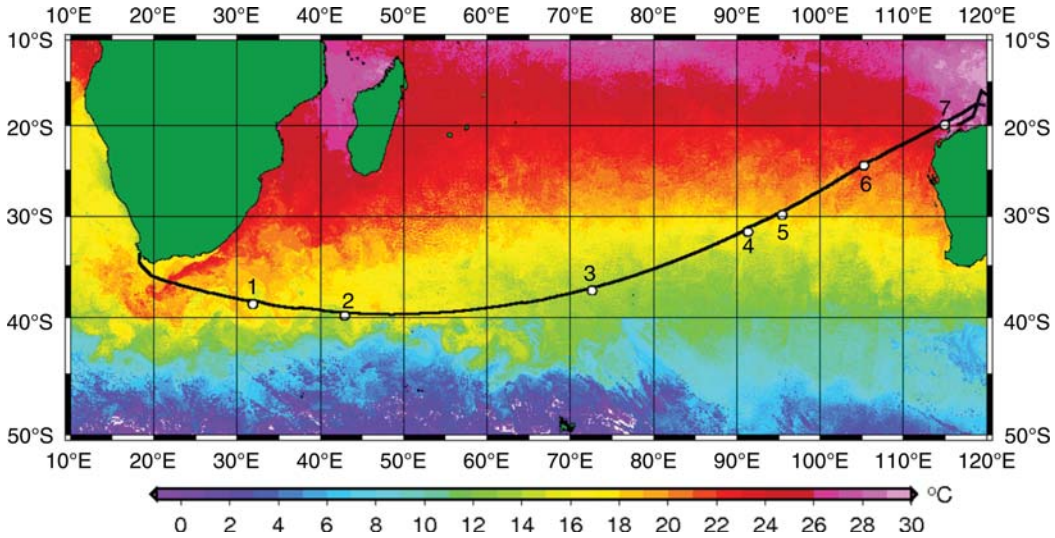

Fig. 1. Sea surface temperatures, cruise track and station locations, illustrating the frontal systems of the Southern Indian Ocean present during October–November 2006 superimposed from Satellite images: ENVISAT, NOAA 17 and 18, MODIS Aqua and AMSR-E. From Visser *et al.* submitted for publication.

for 24 h in darkness at room temperature and measured on a Turner TD-700 Fluorometer before and after acidification (three drops of 1 M HCl) (Jespersen and Christoffersen, 1987). The fluorometer was calibrated against a pure Chl *a* standard, with carbon equivalents estimated using a fixed conversion factor of 50 (Riemann *et al.*, 1989; Aristegui *et al.*, 2004).

Nutrients and other measurements

Measurements of nutrient concentrations and bacterial biomass were made from the same CTD cast as fractionated and total Chl *a* (see Visser *et al.*, submitted for publication). Ciliates and heterotrophic flagellates were used to describe the heterotrophic food components of the copepod and larvacean community, but were only sampled at two depths (10–80 m) per station. Values representing other, non-sampled depths were estimated from a linear regression analysis of total Chl *a* concentrations versus ciliate and flagellate biomass, respectively: Ciliate (μg C L^{-1}) = 1.441 × Chl *a* (μg L^{-1}) + 0.037 ($R^2 = 0.85$) and heterotrophic flagellates (μg C L^{-1}) = 21.86 × Chl *a* (μg L^{-1}) + 0.286 ($R^2 = 0.91$) (all protist data, H.H. Jakobsen, Copenhagen, personal communication).

Metazooplankton

Samples for the quantitative metazooplankton analysis were gently concentrated from Niskin bottles immediately after reaching the deck, typically at approximately noon. To obtain a representative sample, an average of 30 L (range 15–65 L) was filtered. Concentration of animals employed a special filtering device (Jaspers, in preparation) which allowed continuous filtering on a permanently submerged, 25 cm diameter, 20 μm Nitex mesh. To reduce the handling pressure on the animals, and to prevent desiccation, the mesh was cleaned by suction instead of rinsing. Samples were preserved in 2% acidified Lugol's solution (final concentration) and stored in a 12°C temperature-controlled room until quantification. Within 24 to 36 h after sampling, copepodites (including adults), copepod nauplii and larvaceans were counted and sized with a Zeiss Binocular microscope at a magnification of 32× using a calibrated ocular scale. Other irregularly occurring metazooplankton such as chaetognaths and doliolids were counted but not included in the quantitative analysis.

For samples at station 7 (30 m), station 5 (60, 100 m), station 3 (10, 30, 100 m) and station 2 (30 m), characteristic dimensions of individual specimens were measured on at least 50% of the homogenized sample for nauplii and copepodites. Larvaceans were analysed within the whole sample. Prosome length or total body length was measured for copepodite stages I–VI, and nauplii, while larvacean sizes were measured as total trunk length. Shrinkage effects due to preservation were taken into account; hence, larvacean and copepod lengths were corrected by 22 and 17%, respectively (Jaspers and Carstensen, submitted for publication).

Carbon estimates

Biomass of metazooplankton was calculated by means of length-to-carbon regressions from the literature, a

Table I: Relationships employed for biomass estimates, where W is computed in AFDW (μg), and C as carbon content (μg)

Taxon	Regression	Reference
Calanoid copepods	ln W (μg) = 2.74 ln L (μm) − 16.41	Chisholm and Roff, 1990
Cyclopoid copepods	ln W (μg) = 1.96 ln L (μm) − 11.64	Chisholm and Roff, 1990
Copepod nauplii	C (ng) = 3.18×10^{-6} BL(μm)$^{3.31}$	Berggreen *et al.*, 1988
Larvacean community	log C (μg) = 2.455 log TL (μm) − 6.96	This study

Copepod measured as prosome length (L, μm), nauplii as total body length (BL, μm) and larvaceans as trunk length (TL, μm). Regressions for copepodites are based on tropical species in a temperature range of 28–29°C, while the regression for the larvacean community from this study represents a mixture of animals across the Southern Indian Ocean.

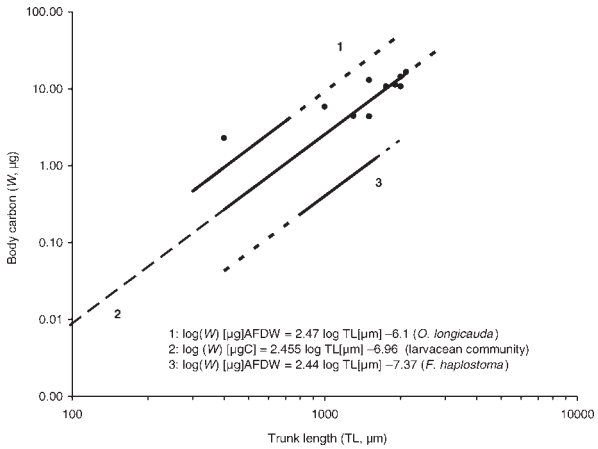

Fig. 2. The relationship between larvacean trunk length (μm) and body carbon (μg C); the Southern Indian Ocean community carbon measurements (dots) are fitted with a fixed average slope from regressions for *Oikopleura longicauda* and *Fritillaria haplostoma* (Hopcroft *et al.*, 1998a). Solid lines represent range of observations, punctuated lines mark extrapolation range.

new carbon regression established for the larvacean community across the SIO (Table I, Fig. 2), and the abundances of the taxa considered. When necessary, we applied a conversion factor from ash-free dry weight (AFDW, μg) to carbon content (μg) of 0.45 for copepods (Båmstedt, 1986) and 0.52 for larvaceans (Alldredge, 1981). Biomass was integrated from 0 to 400 m in units of mg C m^{-2} or expressed as the average per m^{-3} over the investigated water column. For copepodites, specimens in a single sample (maximum copepodite abundance) from each station were separated into calanoids and cyclopoids (including *Oncaea* spp.). The station-specific distribution between the two groups was then assigned to all other samples from that station. Fractions of calanoid and cyclopoid copepodites per size class were used to apply group-specific length-to-biomass regressions (Table I) for calanoid and cyclopoid communities (Chisholm and Roff, 1990). The calanoid and cyclopoid community length-to-carbon relationships gave carbon estimates comparable to those for the calanoid species *Acartia tonsa* (Berggreen *et al.*, 1988) and the cyclopoid species *Oithona similis* (Sabatini and Kiørboe, 1994), respectively. Biomass of copepod nauplii was determined by the length-to-carbon regression obtained for *A. tonsa* (Berggreen *et al.*, 1988), which gives carbon estimates similar to the nauplii regression for the cyclopoid species *O. similis* (Sabatini and Kiørboe, 1994).

To estimate a length-to-carbon relationship, larvaceans were sampled with a hand-towed 45 μm WP2 net with a 1 L non-filtering cod end in the upper 80 m of the water column. Larvaceans were sorted immediately after collection using a wide-mouthed pipette and rinsed several times in 0.2 μm filtered seawater. Individuals of similar shape and size were measured and transferred with tweezers into 0.5 mL pre-combusted aluminium vials (small individuals were pooled) and dried before storage in a freezer at −18°C. Combustion took place at the National Environmental Research Institute, Denmark using a Shimadzu SSM-500A and TOC_{VCPH} for total organic carbon determination.

Larvacean community length-to-carbon regression (Table I) was based on animals collected during the crossing of the SIO, fitted as an intermediate between two literature regressions (Hopcroft *et al.*, 1998a) for representative species of the two most prominent families. Due to the small number of corresponding length and carbon observations ($n = 10$), the slope of the regression on the log–log scale was held fixed as the average slope of those regressions (Hopcroft *et al.*, 1998a), and the intercept on the log–log scale was estimated from our observations (Fig. 2).

Ingestion

The ingestion of the copepod community was estimated from the measured specific copepod faecal pellet production (SPP) rate measured at the same stations across the SIO except for station 1 (Møller *et al.*, in preparation). Grazing rates scale with body size and the same relationship is assumed for the pellet production rate. Therefore, the measured SPP was scaled to the observed sizes of the *in situ* population, differentiated

into copepodites and nauplii (Hansen *et al.*, 1997; Juul-Pedersen *et al.*, 2006). Pellet production was converted to ingestion, assuming that the SPP is equivalent to one-third of the ingestion rate (Kiørboe *et al.*, 1985).

Larvacean grazing was calculated using an equation for total carbon ingestion based on gut content and gut passage time techniques of different species (López-Urrutia *et al.*, 2003), but does not take food adhesion to the mucous house into account (Troedsson *et al.*, 2007). The total carbon ingestion rate (μg C ind.$^{-1}$ day^{-1}) was calculated using the available food concentration (FC, μg C), temperature (T, °C) and body weight (W, μg C ind.$^{-1}$) (López-Urrutia *et al.*, 2003) as follows:

$$\text{Ingestion}(\mu\text{g C ind.}^{-1}\text{day}^{-1}) = \frac{8.27 \times \text{FC} \times \text{e}^{0.0376\times T} \times W^{1.277}}{37.6 + FC} \quad (1)$$

Larvacean food (FC) was here defined as (Chl $a < 10$ μm, in units of carbon), heterotrophic flagellates, ciliates and bacteria.

Average temperatures were calculated from the CTD profiles over the different stratification layers (surface water, thermocline water and intruding water mass). Rates were corrected for temperature differences at each sampling depth using a Q_{10} value of 2.2 for larvaceans, recalculated from literature regressions (López-Urrutia *et al.*, 2003) and 2.8 for copepods (Hansen *et al.*, 1997).

Copepod and larvacean community production rates were estimated using an average cross-taxa metazoan gross growth efficiency (GGE) of about 30% (Kiørboe *et al.*, 1985; Hansen *et al.*, 1997; Straile, 1997). Thus, one-third of the estimated ingestion rates were assumed to represent the productivity of the copepod and larvacean (Nakamura *et al.*, 1997) community, respectively.

Specific growth rates (μ day^{-1}) were calculated to check our assumptions with measured literature specific growth rates and were here calculated as:

$$\mu(\text{day}^{-1}) = \ln(p + b/b) \quad (2)$$

where p is the production of the copepod or larvacean community in mg C m^{-2} day^{-1} and b the community biomass in mg C m^{-2}.

Statistical analysis

Differences between stations and depths were investigated for accompanying variables (salinity, temperature, inorganic nutrients, Chl *a* and biomass of ciliates, bacteria and heterotrophic flagellates) using a two-way analysis of variance (ANOVA) after log-transformation of concentration data. Clusters of stations with equal means were identified with Student Newman–Keuls test. The two-way ANOVA was applied separately to surface waters, thermocline waters and intruding water masses, since these variables were assumed to have stable properties and not to mix.

Metazooplankton was assumed to be sufficiently motile to move vertically, so abundance, biomass and size distribution for nauplii, copepodites and larvaceans were analysed using a generic model including all depths

$$Y_{ijk} = \text{station}_i + \text{depth}_j + \text{water mass(depth)}_{k(j)} + \text{e}_{ik(j)} \quad (3)$$

where water mass was nested within depths. The model was analysed using generalized linear models (McCullagh and Nelder, 1989), assuming abundance and biomass to be log-normally distributed. Differences in size distributions were investigated after pooling larvaceans and nauplii into 6 (<100, 100–124, 125–149, 150–174, 175–199 and >200 μm) and copepodites into 7 (<200, 200–249, 250–299, 300–349, 350–399, 400–600 and >600 μm) size classes. These were analysed as multinomial distributions, with ordinal changes between sizes classes modelled as function of station, depth and water mass. For log-normal distributed variables, stations were grouped using Student Newman–Keuls test, whereas a studentized range test was applied for the size distribution analysis. The depth distributions of metazooplankton biomass and abundance were described by means of categorical levels for each sampled depth. However, in order to investigate potential factors that could explain the observed depth distribution, the variables (food items and temperature) were introduced to the model, maintaining the station dependency. A dependency was then suggested if these measured quantities (food variables and temperature) were better than the categorical depth factor at describing variations in metazooplankton biomass and abundance. Further, linear regressions were carried out between integrated biomass and significant variables (total Chl *a* and temperature) as well as station effects on integrated biomass.

The statistical analyses were carried out using the SAS system Proc GLM for two-way ANOVA and Proc GENMOD for generalized linear models with a significance level of 5% and averages ± standard deviations are given in the results.

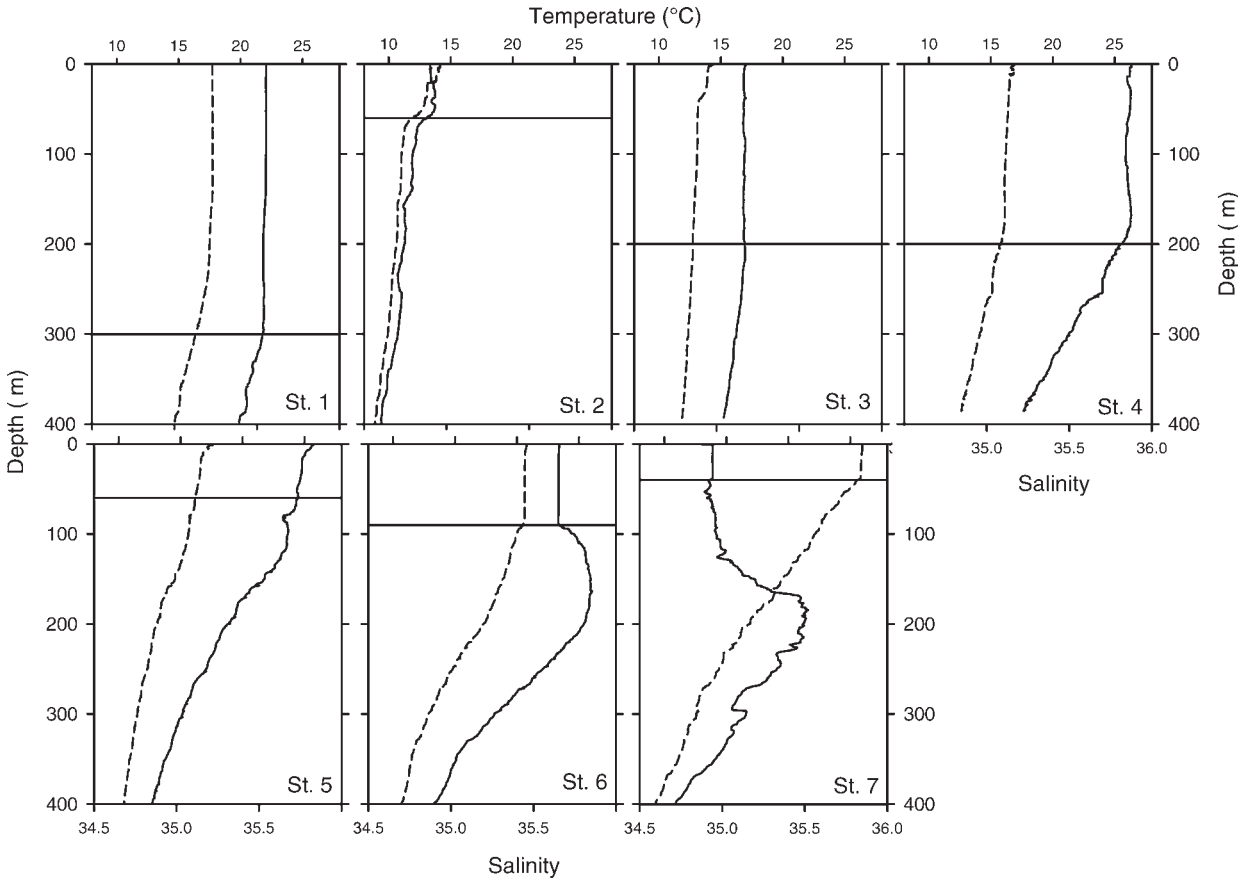

Fig. 3. Profiles of temperature (dashed lines) and salinity (solid lines) in the upper 400 m of the water column of the Southern Indian Ocean during October–November 2006. The mixing depth is indicated with horizontal slash. From Visser *et al.* submitted for publication.

RESULTS

Hydrography

The vertical distribution of salinity and temperature showed distinct and characteristic patterns for the different waters during the crossing of the SIO (Fig. 3). Station 1 was influenced by Agulhas Current water (salinity 35.6). Stations 4 and 5 were influenced by subtropical water, with higher temperatures (16.5–18°C) and higher salinities (35.5–35.8) than observed at stations 2 and 3, which were influenced by colder (11–14°C) and less saline (34.8–35.15) Southern Ocean waters. Stations 6 and 7 can be regarded as tropical sampling sites, with stratified upper water columns of about 90 and 50 m. Furthermore, station 6 showed a pronounced intrusion of high saline water (35.8) at a depth of 90 to 220 m and an intermediate layer formation. Stations 1, 3 and 4 had a very deep surface layer, with mixing of the upper water column down to 300, 200 and 200 m, respectively. The sea-surface temperature reflected large scale eddy formations and ranged from 16.5 to 18°C for the stations 1, 4 and 5, dropped towards 14°C for the Southern Ocean influenced stations, whereas an increase towards 20.8 and 26°C could be observed for stations 6 and 7, respectively.

No significant differences within the thermocline or intermediate water mass were observed ($P > 0.12$), while surface waters significantly differed ($P < 0.0001$) concerning the physical and chemical parameters. Therefore, surface water nitrate concentrations differed significantly between stations but stations 1, 2 and 3 were grouped together with highest mean levels against the other stations. Phosphate showed a similar sequence, while silicate concentrations were lowest at station 2, clustered with lowest mean against all other stations (Supplementary data, Table S1). Notably, station 2 was the only sampling site with diatoms present, accounting for ~12% of the total phytoplankton fraction (L. Schlüter, Copenhagen, personal communication).

Chlorophyll *a*

Total Chl *a* in the surface waters differed significantly between the stations ($P < 0.0001$) (Supplementary

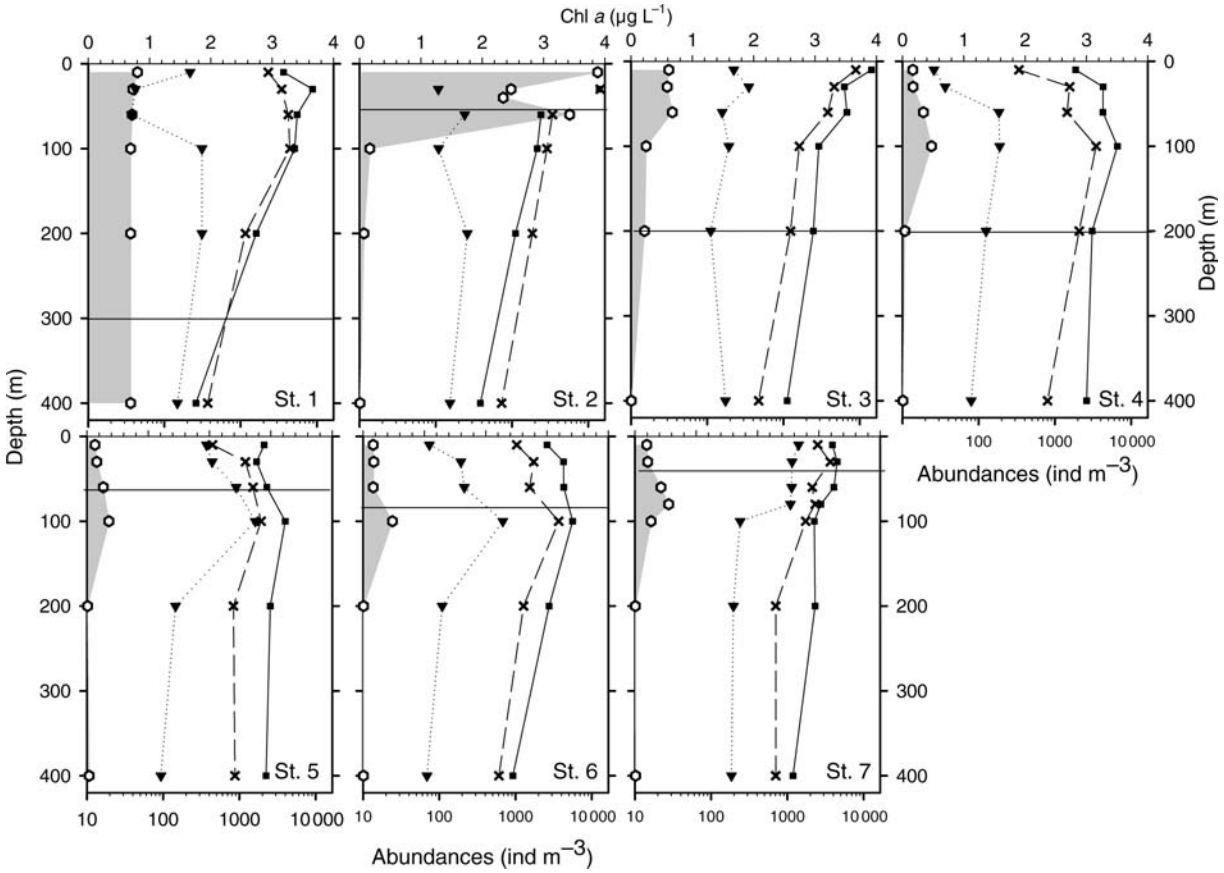

Fig. 4. Metazooplankton distributions across the Southern Indian Ocean, October–November 2006. Abundances are indicated for copepodites inclusive of adults (cross), nauplii (square) and larvaceans (triangle). Total Chl *a* concentrations (μg L^{-1}) are indicated by shaded area and measured at the same depths as the zooplankton.

data, Table S1 and Fig. 4). Station 2 had the highest mean and formed a single station cluster, while stations 1 and 3 were clustered together, showing second highest mean levels compared to all other stations, with 6 having the lowest rank (Supplementary data, Table S1). Hence, high total Chl *a* concentrations were found at nutrient rich stations off South Africa and decreased towards Australia. The largest fraction of total Chl *a* was <10 μm. The fraction >10 μm was significantly different between all stations ($P < 0.0001$), and accounted for 1–9% of total Chl *a* except station 2, where it averaged 40% of the total Chl *a*. Size fraction >50 μm, only available for stations 3–7, did not show significant difference between stations ($P = 0.1007$) and contributed 0.3 to 2.2% and 4% of the total Chl *a* for stations 3–7. In absolute values, the highest Chl *a* concentration in surface waters was observed at station 2 (3.03 ± 0.75 mg Chl *a* m^{-3}), whereas stations 4, 5 and 6 showed the lowest values, ranging from 0.23 ± 0.10 to 0.29 ± 0.15 mg Chl *a* m^{-3}.

Metazooplankton abundances

Copepod nauplii, copepodites and larvaceans dominated the metazooplankton community >20 μm. Chaetognaths and doliolids were occasionally present with low abundances (data not shown). Massive thaliacean blooms in the surface water were observed off NW Australia, but are not reflected in our data due to the small volume processed. For all stations, nauplii (max. 26 432 ind. m^{-3}, st. 2, 30 m) and copepodites (max. 15 946 ind. m^{-3}, st. 2, 30 m) dominated the metazooplankton community and nauplii were always more abundant than copepodites except for 60–100 m samples at station 2 (Fig. 4). No significant differences were found in nauplii ($P > 0.5$) and copepodite ($P > 0.3$) abundances between stations and water masses, whereas their abundances differed significantly with depth ($P = 0.0042$ and $P = 0.0083$) (Table II). Total Chl *a* showed a positive relationship to nauplii ($P < 0.0001$) and copepodite ($P < 0.0001$) abundances (Table III). Within the copepods, abundances of calanoids decreased from 70% at

Table II: Relationships between metazooplankton biological and spatial variables across the Southern Indian Ocean, October/November 2006

	Distribution	*P* (station) (*df* = 6)	*P* (depth) (*df* = 6)	*P* (water mass) (*df* = 5)	Station difference
Larvaceans					
Abundance	LN	0.0461	0.4792	0.8356	4 1 6 3 2 5 7
Biomass	LN	0.4834	0.8365	0.6417	4 1 6 3 2 5 7
Size distribution	MN	0.4375	**0.0053**	0.2070	4 6 5 1 7 2 3
Nauplii					
Abundance	LN	0.6823	**0.0042**	0.9860	5 7 6 4 2 3 1
Biomass	LN	0.6969	**0.0023**	0.9169	5 6 7 1 4 3 2
Size distribution	MN	**0.0001**	**0.0059**	**0.0258**	5 1 4 6 3 2 7
Copepodites					
Abundance	LN	0.3507	**0.0083**	0.9401	5 4 6 7 3 1 2
Biomass	LN	0.2470	**0.0086**	0.9920	6 5 4 7 1 2 3
Size distribution	MN	**<0.0001**	**<0.0001**	**0.0264**	6 7 4 3 5 1 2

Distributions: LN, lognormal; MN, multinomial. Significant variations ($P < 0.05$) for station, depth and water masses are highlighted in bold. Stations are ranked by increasing order and clusters of stations having equal means are shown within boxes.

Table III: Relationships between metazooplankton biomass and abundances with respect to fractionated food components and temperature across the Southern Indian Ocean, Oct./Nov. 2006

	Covariate	*P* (covariate)	*P* (station)
Larvaceans			
Biomass	Temperature	**0.0213**	0.0614
Abundance	Temperature	**0.0031**	**0.0031**
	Chl a	**0.0042**	**0.0010**
Nauplii			
Biomass	Chl a	**<0.0001**	0.8353
Abundance	Chl a	**<0.0001**	0.8775
Copepodites			
Biomass	Chl a	**<0.0001**	0.7143
Abundance	Chl a	**<0.0001**	0.6211

Only significant relationships are shown and ($P < 0.05$) are emphasized in bold.

station 1, to 40% at station 2 and 20% for station 3, while the proportion between calanoids and cyclopoids was similar at the remaining stations consisting of 50% each.

Larvacean abundances ranged from 26 to 1611 ind. m^{-3}. Larvaceans represented 7–9% of the copepodite abundances for stations 1–4, while their proportion increased to 44, 13 and 32% for stations 5–7. In contrast to copepodites and nauplii, their abundances differed significantly between the stations ($P = 0.0461$), and increased towards Australia (Fig. 4). Lowest overall abundances were found at station 4 with 107 ± 71 ind. m^{-3}, and highest abundances at station 7 (772 ± 538 ind. m^{-3}). Further, station 5 had the second highest overall larvacean abundance, while copepodites and nauplii had the lowest values observed over all stations. Larvacean abundances showed a positive relationship to temperature ($P = 0.0031$) and total Chl *a* ($P = 0.0042$) (Table III).

Metazooplankton sizes

Nauplii sizes differed significantly between stations ($P = 0.0001$), depths ($P = 0.0059$) and water masses ($P = 0.0258$) (Table II). Average body sizes ranged between 104 and 163 μm (Supplementary data, Table SII). The largest nauplii were observed at station 7 and smallest at station 5, while larger individuals tended to be present in the surface samples and smaller in the deeper parts. Mean copepodite prosome lengths ranged from 190 to 523 μm (Supplementary data, Table SII), with large variability between stations, depths (both $P < 0.0001$) and water masses ($P = 0.0264$). Largest individuals were found at station 2, while smallest were found at station 6. Concerning the size depth distribution, the largest individuals were observed in the surface samples (10 m), tended to decrease with depth, and smallest individuals occurred at 400 m. Copepodite individuals >1 mm were present at all stations and accounted for about 1%, except at station 3 where they formed 7% of the total copepodite community (Fig. 5).

Larvacean sizes were homogeneously distributed across stations ($P = 0.4375$) and water masses ($P = 0.2070$), but differed significantly with depth ($P = 0.0053$) (Table II). In general, the smallest larvaceans were found in the surface samples (10 m). Very large individuals (>1.7 mm) were uncommon and represented 0.5–5.8% of the larvacean community at only three stations (Fig. 5).

Metazooplankton biomass

Nauplii biomass differed significantly ($P = 0.0023$) with regard to depth (Table II) and total Chl *a* concentrations ($P < 0.0001$) (Table III). In terms of integrated biomass per station, nauplii biomass averaged $71 \pm$

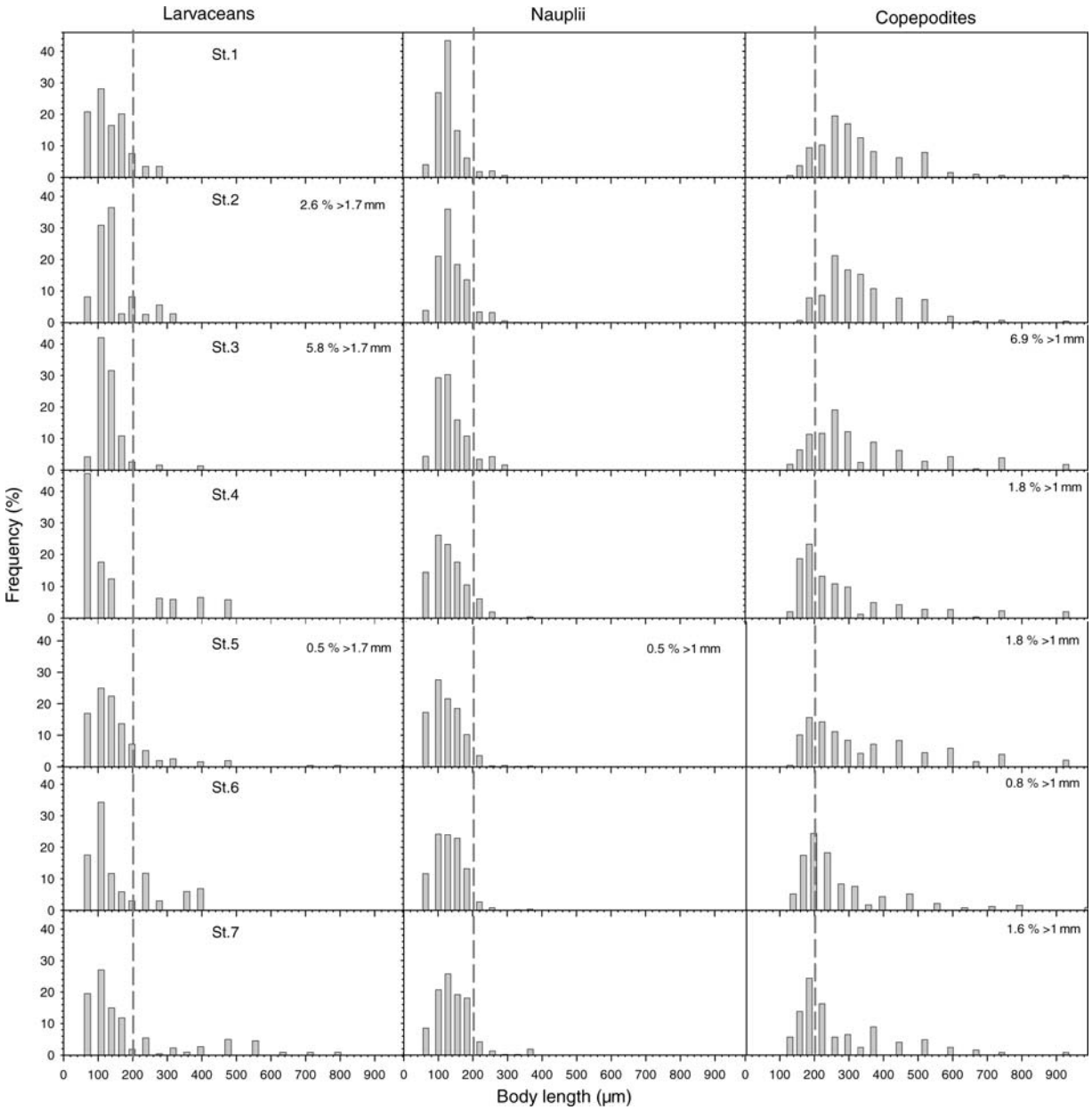

Fig. 5. Metazooplankton size (µm) distribution across the Southern Indian Ocean, October–November 2006; measured as total trunk length for larvaceans, prosome length for copepodites including adults and total body length for nauplii. The <200 µm fraction is indicated by the dashed line. Contribution by large individuals (>1.7 mm for larvaceans and >1 mm for copepods) are stated as per cent of total when present.

22 mg C m^{-2} (Fig. 6A), and was positively related to total Chl *a* concentrations ($R^2 = 0.49$; $P = 0.02$), with no effect of temperature ($R^2 = 0.30$; $P = 0.26$). Copepodite biomass did not show a significant difference between stations ($P = 0.2470$) but with regard to depth ($P = 0.0086$) (Table II) and total Chl *a* ($P < 0.0001$) (Table III). Temperature had no significant effect on biomass ($P = 0.8188$). In terms of integrated biomass, copepodites showed a significant decrease with station ($R^2 = 0.80$; $P < 0.01$), averaged 748 ± 118 mg C m^{-2} at stations 1–3 and were reduced to one-third for stations 4–7 (Fig. 6A). Further, total Chl *a* and integrated biomass of copepodites were positive related ($R^2 = 0.72$; $P = 0.02$). Calanoid copepodites dominated from a biomass point of view throughout the SIO and contributed on average 80% of the total copepodite biomass (Fig. 6A).

Larvacean biomass was two orders of magnitude lower than copepod biomass. There was no significant relationship with total Chl *a* concentrations ($P = 0.3041$),

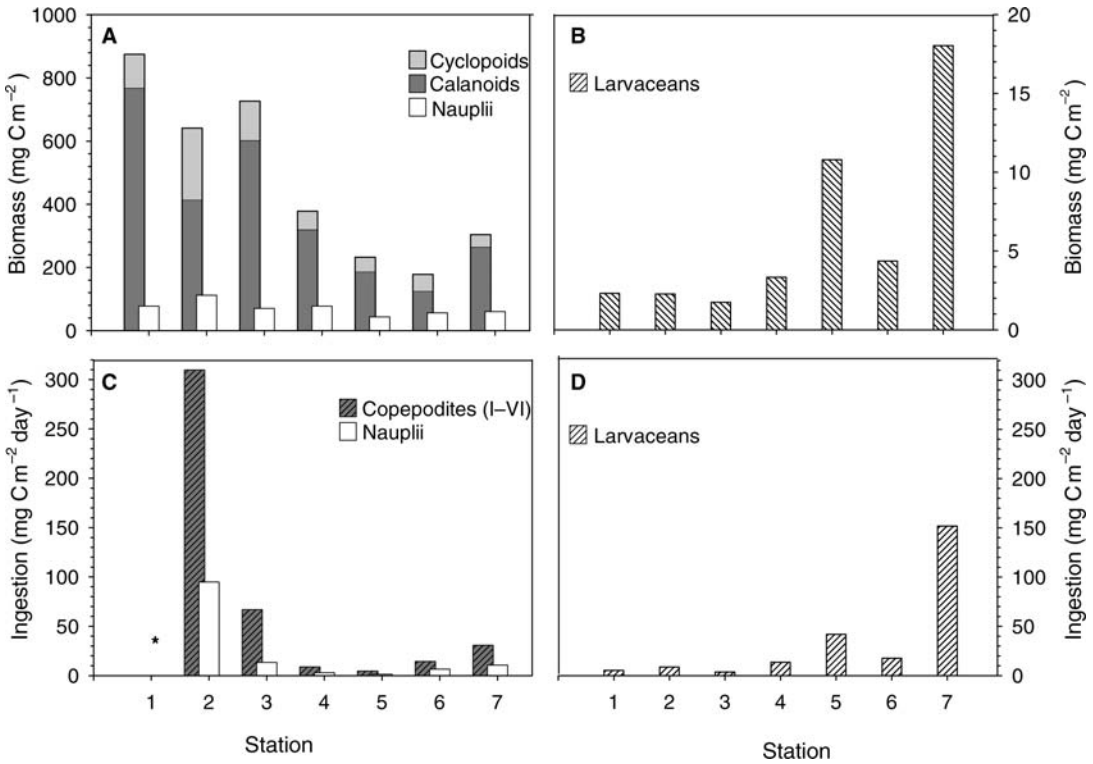

Fig. 6. Integrated biomass distribution across the Southern Indian Ocean, October–November 2006; for (**A**) the copepod community differentiated in calanoid and cyclopoid copepodites (stages I–VI), nauplii and (**B**) larvaceans, integrated over the upper 400 m. Ingestion estimates from measured (**C**) specific faecal pellet production (SPP) rate and (**D**) larvacean community ingestion (López-Urrutia *et al.*, 2003). *No measurements available.

whereas biomass showed a positive correlation to temperature ($P = 0.0213$) (Table III). Integrated biomass per station significantly increased ($R^2 = 0.58$; $P = 0.05$) towards subtropical, tropical stations off NW Australia (Fig. 6B) and showed a positive relationship to temperature ($R^2 = 0.49$; $P = 0.05$), whereas total Chl *a* remained insignificant ($R^2 = 0.39$; $P = 0.08$).

Ingestion

At station 2, which showed the highest community ingestion rate (Fig. 6C), the copepodite community ingested 53% of their standing stock in units of carbon per day.

Integrated larvacean community ingestion rates (Fig. 6D) showed the same pattern as biomass and increased from South Africa to Australia.

Production and growth

Calculated copepodite and nauplii production was highest at stations 1–3, while estimated larvacean production peaked at stations 5–7 (Fig. 7A). At stations 1–3, larvacean production was <5% of copepod community productivity, while it was equal at station 4 and 6, and four to five times higher at stations 5 and 7. Estimated larvacean specific growth rates (average 0.8 day^{-1}) were higher than those of copepods (average 0.04 day^{-1}) and nauplii (average 0.07 day^{-1}) across the entire SIO (Fig. 7B).

DISCUSSION

Although copepods dominated the abundance and biomass of the zooplankton community at all stations, larvaceans were present throughout all the different oceanic regimes across the SIO. The major part of the larvacean and the copepod community were <200 μm (Fig. 5, Supplementary data, Table SII). Hence, we stress the need for use of fine-meshed nets to collect the smallest size fractions of the metazooplankton, especially larvaceans, to adequately assess the food web structure (Hopcroft *et al.*, 1998a; Hopcroft and Roff, 1998a; Hopcroft *et al.*, 2001).

Mesh size

Traditionally zooplankton investigations have used 200 μm mesh nets as advocated by UNESCO

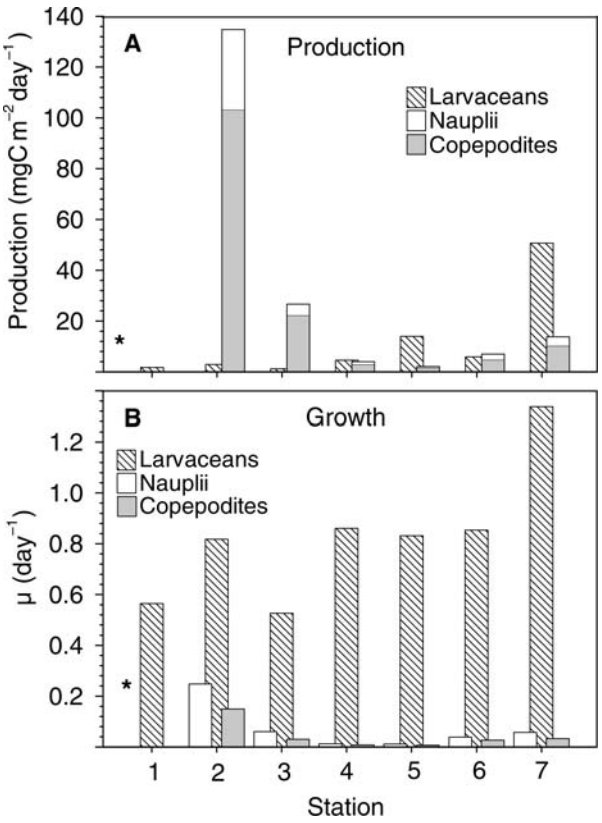

Fig. 7. (**A**) Station-specific estimated metazooplankton production assuming a GGE of one third of the ingested material and (**B**) growth rates estimated by the production to biomass ratio; across the Southern Indian Ocean, October–November 2006.

zooplankton sampling procedures (Tranter and Fraser, 1979). More recently, it has been shown that substantial parts of the metazooplankton consist of micro-sized stages as well as species, and therefore investigations including this fraction are necessary to understand the composition and functioning of the system (Paffenhöfer, 1998). Overall, it has been shown that 200 μm mesh nets capture <10% of the metazooplankton community from an abundance point of view, underestimate the biomass by one-third and the secondary production by two thirds (Gallienne and Robins, 2001). Further, 200 μm nets in oligotrophic offshore regions near Bermuda (Paffenhöfer and Mazzocchi, 2003) and Jamaica (Hopcroft *et al.*, 2001) have been shown to capture one order of magnitude less than 63 μm mesh nets.

Investigations along two longitudinal transects in the central Indian Ocean during the International Indian Ocean Expedition, based on 330 μm mesh Indian Ocean Standard Nets (Currie, 1963), showed that larvacean abundances ranged between 0.005 and 3 ind. m^{-3} (Fenaux, 1973). Similarly, Ward *et al.* (Ward *et al.*, 2006) found 6–50 larvaceans m^{-3} in the Southern Ocean using 200 μm mesh nets. In more recent studies from the SIO and Indian sector of the Southern Ocean using 200 μm mesh nets with smaller water volumes processed, larvaceans were not a reported component of the zooplankton community (Bernard and Froneman, 2005; Fielding *et al.*, 2007; Froneman *et al.*, 2007). In comparison, the abundances obtained by whole-water filtration onto 20 μm sieves in the present study ranged from 107 to 772 ind. m^{-3}. In support of our findings, other studies using small mesh nets off Zanzibar (50 μm) (Lugomela *et al.*, 2001) and at the Mascarene Plateau and Basin, south-western Indian Ocean (125 μm nets) (Gallienne *et al.*, 2004), found that larvaceans are the second most abundant component of the zooplankton community from oligotrophic to upwelling induced eutrophic areas with an average range of 100–160 ind. m^{-3} for the Mascarene Plateau and Basin.

Larvaceans span a wide size range from the smallest species, *Appendicularia sicula*, with a trunk length of 45 μm for newly hatched specimens (Hopcroft *et al.*, 1998a) to mesopelagic giant larvaceans of 60 mm in trunk length (Robison *et al.*, 2005). Most knowledge of larvaceans is based on large individuals (500–1700 μm trunk lengths). Studies considering smaller individuals (Uye and Ichino, 1995; Dagg *et al.*, 1996; Nakamura *et al.*, 1997; Nakamura, 1998; Hopcroft and Roff, 1998a; Tomita *et al.*, 1999; López-Urrutia *et al.*, 2005) showed that a substantial part of the community is within the micro size fraction and on average only 4% of the larvacean community is represented by adults during the course of a year (Tomita *et al.*, 1999).

Thus, the abundance of larvaceans reported is greatly influenced by use of different sized meshes in sampling gear, and community estimates are heavily biased, which makes it difficult to compare across studies and properly assess the role of micro-sized metazoans, especially larvaceans in the plankton community.

Metazooplankton community

Numerically, copepod nauplii dominated the metazooplankton. Nauplii abundances significantly followed the total Chl *a*. The average nauplii biomass was 16% of the total copepod biomass (Fig. 6A). A similar high contribution of nauplii was found off Jamaica where nauplii stages contributed ~11% of the whole copepod community biomass along a tropical eutrophication gradient from coastal to offshore areas (Hopcroft *et al.*, 1998b).

Copepodite abundances followed the total Chl *a* and were significantly lower east of productive stations 1–3.

Biomass estimates obtained in this study ranged from 0.45 to 2.2 mg C m^{-3} as calculated from integrated values, but reached levels of 5–20 mg C m^{-3} for chl *a* maximum strata off South Africa. In another study, the coastal copepod biomass off Australia was between 0.1 and 5 mg C m^{-3}, calculated from integrated biomass (McKinnon and Duggan, 2003), and tropical yearly average of the copepod community including the micro fraction off Jamaica was 10 mg C m^{-3} (Hopcroft *et al.*, 1998b). Further, in Australian waters copepod community biomass of 24–90 mg C m^{-3} has been described (McKinnon *et al.*, 2005; McKinnon *et al.*, 2008). Generally, when taking small copepodite size fractions into account, their biomass in tropical waters equals or exceeds the biomass fraction in temperate areas (Hopcroft *et al.*, 1998b), although later works suggest a less clear pattern (Hopcroft *et al.*, 2001), with perhaps only central Arctic waters having a low importance of smaller copepodites (Hopcroft *et al.*, 2001). Even though small size classes have been included in our investigation, their biomass was significantly higher in cold waters compared to tropical stations.

The present study shows that larvaceans are an important part of the plankton community of the SIO. Highest densities were linked to subtropical and tropical warm water areas. The significant relationship between larvacean abundance and temperature is in line with a strong temperature dependency of larvaceans found in temperate areas (e.g. López-Urrutia *et al.*, 2003; López-Urrutia *et al.*, 2005). At the tropical coastal station 7 off Australia, abundances averaged 1200 ± 140 ind. m^{-3} for the upper 80 m (range 1094–1400) which is one-third of the yearly average of 3607 ind. m^{-3} (range 0–16 910) found for shallow tropical Kingston Harbour, Jamaica (Hopcroft and Roff, 1998a), whereas on the nearby shelf in the same area, Clarke and Roff (Clarke and Roff, 1990) found average annual abundances of 440 ind. m^{-3}. Even though the present abundance data are in the range previously reported, our biomass estimates are low, ranging between 0.01 and 0.2 mg C m^{-3}, averaged over stations. The average annual biomass on the nearby shelf in Jamaica was reported to be 0.19 mg C m^{-3} (Clarke and Roff, 1990). The depth-integrated larvacean biomass increased by nearly 10 times from stations 1–3 to station 7. Comparing the surface biomass of tropical sampling site 7 with the Jamaica study of outer Kingston Harbour, our study represented 15% of the yearly averaged larvacean community biomass of 1.2 mg C m^{-3} (Hopcroft and Roff, 1998a). Other investigations including small size classes in Japanese waters show that biomass ranged between 0.1–8 mg C m^{-3} (Nakamura, 1998) and 0.21–11.4 mg C m^{-3} (Uye and Ichino, 1995). The comparable low biomass but medium to high larvacean abundance data reported in this study shows that the larvacean community even at peak abundances is dominated by small size classes. Large individuals which contribute a major proportion of the biomass were nearly absent from our investigation which may be due to the small amount of water processed. Nevertheless, this study shows that small size classes are present throughout all systems investigated and that their contribution to the population is larger than previously recognized.

In our study, no significant relationship to any size fractions of Chl *a*, nor heterotrophic food items, such as ciliates, heterotrophic flagellates or bacteria, could be found for the larvacean biomass. Similarly, Hopcroft and Roff (Hopcroft and Roff, 1998a) found no relationship between larvacean biomass and any Chl *a* size fraction in their tropical study area, leading them to the conclusion that the observed high yearly abundance fluctuations have to be explained by predation.

The lack of response in biomass to increasing food availability as shown in this study indicates that other factors are crucial in influencing or even controlling the larvacean population such as predation (Hopcroft and Roff, 1995; Båmstedt *et al.*, 2005; Purcell *et al.*, 2005; Hoover *et al.*, 2006), or temperature acting as regulating factor through lower productivity at lower temperatures. Fish larvae have been reported to depend on larvaceans as primary food items in the North Sea and that the availability of larvaceans is crucial in recruitment success of plaice and sand eel (Shelbourne, 1962; Ryland, 1964). Furthermore, it is interesting to note that station 5 had high larvacean biomass but lowest copepod biomass, which might suggest a negative coupling between copepods and larvaceans (e.g. Sommer *et al.*, 2003; López-Urrutia *et al.*, 2004) although the mechanisms are not well understood.

Role of larvaceans in the food web

Larvaceans can utilize a broad prey size spectrum and are therefore assumed to be of special importance in oligotrophic environments as the most competitive metazooplankton group to survive and live at low food concentrations (Gorsky and Fenaux, 1998; Fenaux *et al.*, 1998; Acuña, 2001).

We showed that the estimated larvacean ingestion rate increases towards warm tropical areas with a reverse pattern for the copepod community. This can be explained by the confounding effect of dominating pico-sized autotrophs and temperature leading to an increased ingestion rate by up to 26-fold. Larvaceans can utilize parts of the bacterioplankton and in

subtropical areas *Oikopleura fusiformis* ingested bacteria equivalent to 8% of their daily diet (Scheinberg and Landry, 2005). Thus, the abundance of 2 ind. L^{-1} as observed off Australia in this study is sufficient to remove 16% of the bacteria standing stock per day. Copepods showed a significant relationship to total Chl *a*, even though the majority was too small to be ingested directly, while protozoans showed no significant relationship. The more pronounced coupling to Chl *a* can be explained by trophic cascades (reduced grazing pressure of protozoans on algae due to copepod grazing on protozoans) even though these interactions are difficult to observe from single station measurements.

From observed biomass and calculated ingestion rates, we extrapolated to the production level which showed that even though larvaceans represented up to 6% (at station 7) of the copepod community biomass, their calculated production was up to five times higher than the estimated copepod production. The copepod production estimates for tropical station 7 of 10.25 mg C m^{-2} day^{-1} is comparable to measurements in the NW Australian continental shelf break area of 10.3 ± 2.9 mg C m^{-2} day^{-1} (McKinnon and Duggan, 2003). Our daily larvacean production estimate for the surface water at station 7 was 1.5 mg C m^{-3}, which lies in the same range as data for eutrophic waters off Japan of 2.6 mg C m^{-3} day^{-1} (calculated from Uye and Ichino, 1995). Other studies have found that even though larvacean biomass is lower than copepod biomass, their production is >30 to 100% of the latter in coastal temperate and tropical areas, and occasionally even exceeds copepod production (Nakamura *et al.*, 1997; Hopcroft and Roff, 1998a; Vargas and González, 2004). This shows that larvacean production can be of considerable importance despite abundance and biomass estimates suggesting otherwise and that larvaceans are important secondary producers (Hopcroft and Roff, 1998a; Sato *et al.*, 2008).

The specific growth rates calculated from ingestion were in range of earlier reports. Copepod specific growth rates are reported to range between 0.04 and 0.26 day^{-1} for different species for tropical oligotrophic, mesotrophic and eutrophic regions (Hopcroft and Roff, 1998b), which is in the same range as our observations of 0.01–0.15 day^{-1}. For the larvacean community, our estimated specific growth rates ranged from 0.5 day^{-1} at station 3 to 1.3 day^{-1} at station 7. Tomita *et al.* (Tomita *et al.*, 1999) found growth rates of 0.4 day^{-1} in their temperate area study and 0.7 to 3.3 day^{-1} were found for several tropical studies (e.g. Clarke and Roff, 1990; Hopcroft and Roff, 1998b). It has been shown that growth rates of larvaceans compared to copepods can exceed the latter by factor 10 or more (Hopcroft and Roff, 1995).

In conclusion, the micro-sized portion of the metazooplankton is of key importance throughout the different oceanographic regimes of the SIO. We demonstrate that former studies under-sampled the smallest components of the larvacean and copepod community due to the use of coarse-mesh nets. Even though the larvacean biomass is low, their grazing impact and their production are high, exceeding that of the copepod community in the tropical part of the SIO. It is therefore critical that larvaceans are fully considered in any future research or modelling efforts exploring the fate of organic matter in this region, and oceanic areas in general.

SUPPLEMENTARY DATA

Supplementary data can be found online at http://plankt.oxfordjournals.org.

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REFERENCES

Acuña, J. L. (2001) Pelagic tunicates: why gelatinous? *Am. Nat.*, **158**, 100–107.

Alldredge, A. L. (1981) The impact of appendicularian grazing on natural food concentrations *in situ*. *Limnol. Oceanogr.*, **26**, 247–257.

Aristegui, J., Barton, E. D., Tett, P. *et al.* (2004) Variability in plankton community structure, metabolism, and vertical carbon fluxes along an upwelling filament (Cape Juby, NW Africa). *Progr. Oceanogr.*, **62**, 95–113.

Båmstedt, U. (1986) Chemical composition and energy content. In Corner, E. D. S. and ÓHara, S. C. M. (eds), *The Biological Chemistry of Marine Copepods*. Oxford University Press, New York, pp. 1–58.

Båmstedt, U., Fyhn, H. J., Martinussen, M. B. *et al.* (2005) Seasonal distribution, diversity and biochemical composition of Appendicularians in Norwegian Fjords. In Gorsky, G., Youngbluth, M. J. and Deibel, D. (eds), *Response of Marine Ecosystems to Global Change—Ecological Impact of Appendicularians*. Contemporary Publishing International, Paris, pp. 227–254.

Berggreen, U., Hansen, B. and Kiørboe, T. (1988) Food Size Spectra, Ingestion and Growth of the Copepod *Acartia tonsa* during development—implications for determination of copepod production. *Mar. Biol.*, **99**, 341–352.

Bernard, K. S. and Froneman, P. W. (2005) Trophodynamics of selected mesozooplankton in the west-Indian sector of the Polar Frontal Zone, Southern Ocean. *Polar Biol.*, **28**, 594–606.

Chisholm, L. A. and Roff, J. C. (1990) Size-weight relationships and biomass of tropical neritic copepods off Kingston, Jamaica. *Mar. Biol.*, **106**, 71–77.

Clarke, C. and Roff, J. C. (1990) Abundance and biomass of herbivorous zooplankton off Kingston, Jamaica, with estimates of their annual production. *Estuarine Coastal Shelf Sci.*, **31**, 423–437.

Currie, R. I. (1963) The Indian Ocean standard net. *Deep-Sea Res.*, **10**, 27–32.

Cushing, D. H. (eds) (1969) *Upwelling and Fish Production*. Food and Agriculture organization of the United Nations, Rome.

Dagg, M. J., Green, E. P., Mckee, B. A. *et al.* (1996) Biological removal of fine-grained lithogenic particles from a large river plume. *J. Mar. Res.*, **54**, 149–160.

Deibel, D. (1998) Feeding and Metabolism of Appendicularia. In Bone, Q.(ed.), *The Biology of pelagic Tunicates*. Oxford University Press, pp. 139–149.

Deibel, D. and Lee, S. H. (1992) Retention efficiency of submicrometer particles by the pharyngeal filter of the pelagic tunicate *Oikopleura vanhoeffeni*. *Mar. Ecol. Prog Ser.*, **81**, 25–30.

Fenaux, R. (1973) Appendicularia from the Indian Ocean, the Red Sea and the Persian Gulf. In Zeitzschel, B.(ed.), *The Biology of the Indian Ocean*, 3rd edn. Springer Verlag, Berlin, pp. 409–414.

Fenaux, R., Bone, Q. and Deibel, D. (1998) Appendicularia distribution and zoogeography. In Bone, Q.(ed.), *The Biology of Pelagic Tunicates*. Oxford University Press, New York, pp. 251–264.

Fielding, S., Ward, P., Pollard, R. T. *et al.* (2007) Community structure and grazing impact of mesozooplankton during late spring/early summer 2004/2005 in the vicinity of the Crozet Islands (Southern Ocean). *Deep-Sea Res. Pt. II*, **54**, 2106–2125.

Flood, P. R., Deibel, D. and Morris, C. C. (1992) Filtration of colloidal melanin from sea-water by planktonic tunicates. *Nature*, **355**, 630–632.

Froneman, P. W., Ansorge, I. J., Richoux, N. *et al.* (2007) Physical and biological processes at the subtropical convergence in the south-west Indian Ocean. *S. Afr. J. Sci.*, **103**, 193–195.

Gallienne, C. P. and Robins, D. B. (2001) Is *Oithona* the most important copepod in the world's oceans? *J. Plankton Res.*, **23**, 1421–1432.

Gallienne, C. P., Conway, D. V. P., Robinson, J. *et al.* (2004) Epipelagic mesozooplankton distribution and abundance over the Mascarene Plateau and Basin, south-western Indian Ocean. *J. Mar. Biol. Assoc. UK*, **84**, 1–8.

Goericke, R. (1998) Response of phytoplankton community structure and taxon-specific growth rates to seasonally varying physical forcing in the Sargasso Sea off Bermuda. *Limnol. Oceanogr.*, **43**, 921–935.

Gorsky, G. and Fenaux, R. (1998) The role of appendicularians in marine food webs. In Bone, Q.(ed.), *The Biology of Pelagic Tunicates*. Oxford University Press, New York, pp. 161–170.

Hansen, B., Bjornsen, P. K. and Hansen, P. J. (1994) The size ratio between planktonic predators and their prey. *Limnol. Oceanogr.*, **39**, 395–403.

Hansen, P. J., Bjornsen, P. K. and Hansen, B. W. (1997) Zooplankton grazing and growth: Scaling within the 2-2,000-mu m body size range. *Limnol. Oceanogr.*, **42**, 687–704.

Hood, R., Naqvi, W., Wiggert, J. D. *et al.* (2008) Research opportunities and challenges in the Indian Ocean. *EOS*, **89**, 125–126.

Hoover, R. S., Hoover, D., Miller, M. *et al.* (2006) Zooplankton response to storm runoff in a tropical estuary: bottom-up and top-down controls. *Mar. Ecol. Prog. Ser.*, **318**, 187–201.

Hopcroft, R. R. and Roff, J. C. (1995) Zooplankton growth-rates—extraordinary production by the larvacean *Oikopleura dioica* in tropical waters. *J. Plankton Res.*, **17**, 205–220.

Hopcroft, R. R. and Roff, J. C. (1998a) Production of tropical larvaceans in Kingston Harbour, Jamaica: are we ignoring an important secondary producer? *J. Plankton Res.*, **20**, 557–569.

Hopcroft, R. R. and Roff, J. C. (1998b) Zooplankton growth rates: the influence of female size and resources on egg production of tropical marine copepods. *Mar. Biol.*, **132**, 79–86.

Hopcroft, R. R., Roff, J. C. and Bouman, H. A. (1998a) Zooplankton growth rates: the larvaceans Appendicularia, Fritillaria and Oikopleura in tropical waters. *J. Plankton Res.*, **20**, 539–555.

Hopcroft, R. R., Roff, J. C. and Lombard, D. (1998b) Production of tropical copepods in Kingston Harbour, Jamaica: the importance of small species. *Mar. Biol.*, **130**, 593–604.

Hopcroft, R. R., Roff, J. C. and Chavez, F. P. (2001) Size paradigms in copepod communities: a re-examination. *Hydrobiologia*, **453**, 133–141.

Jespersen, A. M. and Christoffersen, K. (1987) Measurements of chlorophyll-A from phytoplankton using ethanol as extraction solvent. *Arch. Hydrobiol.*, **109**, 445–454.

Juul-Pedersen, T., Nielsen, T. G., Michel, C. *et al.* (2006) Sedimentation following the spring bloom in Disko Bay, West Greenland, with special emphasis on the role of copepods. *Mar. Ecol. Prog Ser.*, **314**, 239–255.

Kiørboe, T. (1998) Population regulation and role of mesozooplankton in shaping marine pelagic food webs. *Hydrobiologia*, **363**, 13–27.

Kiørboe, T., Mohlenberg, F. and Hamburger, K. (1985) Bioenergetics of the planktonic copepod *Acartia tonsa*—relation between feeding, egg-production and respiration, and composition of specific dynamic action. *Mar. Ecol. Prog Ser.*, **26**, 85–97.

Kostianoy, A. G., Ginzburg, A. I., Lebedev, S. A. *et al.* (2003) Fronts and mesoscale variability in the southern Indian Ocean as inferred from the TOPEX/POSEIDON and ERS-2 altimetry data. *Oceanology*, **43**, 632–642.

Legendre, L., Demers, S. and Lefaivre, D. (1986) Biological production at marine ergoclines. In Nihoul, J. C. J.(ed.), *Marine Interfaces Ecohydrodynamics*. Elsevier, Amsterdam, pp. 1–29.

Lohmann, H. (1914) Die Appendicularien der Valdivia-Expedition. *Verhandlungen der Deutschen zoologischen Gesellschaft*, **24**, 157–192.

Lohmann, H. (1931) Die Appendicularian der Deutschen Tiefsee-Expedition. *Wissenschaftliche Ergebnisse der Deutschen Tiefsee-Expedition auf dem Dampfer "Valdivia" 1898-1899*, **21**, 1–158.

Lohmann, H. and Bückmann, A. (1926) Die Appendicularien der deutschen Südpolar-Expedition 1901–1903. *Zoologie*, **18**, 63–231.

López-Urrutia, A., Acuña, J. L., Irigoien, X. *et al.* (2003) Food limitation and growth in temperate epipelagic appendicularians (Tunicata). *Mar. Ecol. Progr. Ser.*, **252**, 143–157.

López-Urrutia, A., Harris, R. P. and Smith, T. (2004) Predation by calanoid copepods on the appendicularian *Oikopleura dioica*. *Limnol. Oceanogr.*, **49**, 303–307.

López-Urrutia, A., Harris, R. P., Acuña, J. L. *et al.* (2005) A comparison of appendicularian seasonal cycles in four distinct European Coastal environments. In Gorsky, G., Youngbluth, M. J. and Deibel, D. (eds), *Response of Marine Ecosystems to Global Change—Ecological Impact of Appendicularians*. Contemporary Publishing International, Paris, pp. 255–276.

Lugomela, C., Wallberg, P. and Nielsen, T. G. (2001) Plankton composition and cycling of carbon during the rainy season in a tropical coastal ecosystem, Zanzibar, Tanzania. *J. Plankton Res.*, **23**, 1121–1136.

Maar, M., Nielsen, T. G., Gooding, S. *et al.* (2004) Trophodynamic function of copepods, appendicularians and protozooplankton in the late summer zooplankton community in the Skagerrak. *Mar. Biol.*, **144**, 917–933.

McCullagh, P. and Nelder, J. A. (eds) (1989) *Generalized Linear Models*. Vol. 2. Chapman and Hall, New York.

McKinnon, A. D. and Duggan, S. (2003) Summer copepod production in subtropical waters adjacent to Australia's North West Cape. *Mar. Biol.*, **143**, 897–907.

McKinnon, A. D., Duggan, S. and De'ath, G. (2005) Mesozooplankton dynamics in nearshore waters of the Great Barrier Reef. *Estuarine Coastal Shelf Sci.*, **63**, 497–511.

McKinnon, A. D., Duggan, S., Carleton, J. H. *et al.* (2008) Summer planktonic copepod communities of Australia's North West Cape (Indian Ocean) during the 1997-99 El Nino/La Nina. *J. Plankton Res.*, **30**, 839–855.

Nakamura, Y. (1998) Blooms of tunicates *Oikopleura* spp. and *Dolioletta gegenbauri* in the Seto Inland Sea, Japan, during summer. *Hydrobiologia*, **385**, 183–192.

Nakamura, Y., Suzuki, K., Suzuki, S. *et al.* (1997) Production of *Oikopleura dioica* (Appendicularia) following a picoplankton 'bloom' in a eutrophic coastal area. *J. Plankton Res.*, **19**, 113–124.

Paffenhöfer, G. A. (1998) Heterotrophic protozoa and small metazoa: feeding rates and prey-consumer interactions. *J. Plankton Res.*, **20**, 121–133.

Paffenhöfer, G. A. and Mazzocchi, M. G. (2003) Vertical distribution of subtropical epiplanktonic copepods. *J. Plankton Res.*, **25**, 1139–1156.

Piontkovski, S. A., Williams, R. and Melnik, T. A. (1995) Spatial heterogeneity, biomass and size structure of plankton of the Indian-Ocean—some general trends. *Mar. Ecol. Prog. Ser.*, **117**, 219–227.

Purcell, J. E., Sturdevant, M. V. and Galt, C. P. (2005) A review of appendicularians as prey of invertebrate and fish predators. In Gorsky, G., Youngbluth, M. J. and Deibel, D. (eds), *Response of Marine Ecosystems to Global Change—Ecological Impact of Appendicularians*. Contemporary Publishing International, Paris, pp. 359–434.

Rao, T. S. S. (1973) Zooplankton studies in the Indian Ocean. In Zeitzschel, B.(ed.), *The Biology of the Indian Ocean*, 3rd edn. Springer Verlag, Berlin, pp. 243–255.

Riemann, B., Simonsen, P. and Stensgaard, L. (1989) The carbon and chlorophyll content of phytoplankton from various nutrient regimes. *J. Plankton Res.*, **11**, 1037–1045.

Robison, B. H., Reisenbichler, K. R. and Sherlock, R. E. (2005) Giant larvacean houses: rapid carbon transport to the deep sea floor. *Science*, **308**, 1609–1611.

Ryland, J. S. (1964) Feeding of plaice+sandeel larvae in southern North Sea. *J. Mar. Biol. Assoc. UK*, **44**, 343–352.

Sabatini, M. and Kiørboe, T. (1994) Egg-production, growth and development of the cyclopoid copepod *Oithona similis*. *J. Plankton Res.*, **16**, 1329–1351.

Sato, R., Ishibashi, Y., Tanaka, Y. *et al.* (2008) Productivity and grazing impact of *Oikopleura dioica* (Tunicata, Appendicularia) in Tokyo Bay. *J. Plankton Res.*, **30**, 299–309.

Scheinberg, R. D. and Landry, M. R. (2005) Clearance rates and efficiencies of *Oikopleura fusiformis* on the natural prey assemblage of a subtropical coastal ecosystem. In Gorsky, G., Youngbluth, M. J. and Deibel, D. (eds), *Response of Marine Ecosystems to Global Change—Ecological Impact of Appendicularians*. Contemporary Publishing International, Paris, pp. 207–223.

Scheinberg, R. D., Landry, M. R. and Calbet, A. (2005) Grazing of two common appendicularians on the natural prey assemblage of a tropical coastal ecosystem. *Mar. Ecol. Prog. Ser.*, **294**, 201–212.

Shelbourne, J. E. (1962) Predator–prey size relationship for plaice larvae feeding on Oikopleura. *J. Mar. Biol. Assoc. UK*, **42**, 243–255.

Sherman, K., Okemwa, E. N. and Ntiba, M. J. (eds) (1998) *Large Marine Ecosystems of the Indian Ocean: Assessment, Sustainability and Management*. Vol. 1. Blackwell Publishing, UK.

Sieburth, J. M., Smetacek, V. and Lenz, J. (1978) Pelagic ecosystem structure—heterotrophic compartments of plankton and their relationship to plankton size fractions—comment. *Limnol. Oceanogr.*, **23**, 1256–1263.

Sommer, F., Hansen, T., Feuchtmayr, H. *et al.* (2003) Do calanoid copepods suppress appendicularians in the coastal ocean? *J. Plankton Res.*, **25**, 869–871.

Straile, D. (1997) Gross growth efficiencies of protozoan and metazoan zooplankton and their dependence on food concentration, predator–prey weight ratio, and taxonomic group. *Limnol. Oceanogr.*, **42**, 1375–1385.

Tomita, M., Ikeda, T. and Shiga, N. (1999) Production of *Oikopleura longicauda* (Tunicata: Appendicularia) in Toyama bay, southern Japan Sea. *J. Plankton Res.*, **21**, 2421–2430.

Tranter, D. J. and Fraser, J. H. (eds) (1979) *Zooplankton Sampling Monogr. on Oceanographic Methodology*. UNESCO-Press, Paris.

Troedsson, C., Frischer, M. E., Nejstgaard, J. C. *et al.* (2007) Molecular quantification of differential ingestion and particle trapping rates by the appendicularian Oikopleura dioica as a function of prey size and shape. *Limnol. Oceanogr.*, **52**, 416–427.

Uye, S. and Ichino, S. (1995) Seasonal-variations in abundance, size composition, biomass and production-rate of *Oikopleura dioica* (Fol)

(Tunicata, Appendicularia) in a temperate eutrophic inlet. *J. Exp. Mar. Biol. Ecol.*, **189**, 1–11.

Vargas, C. A. and González, H. E. (2004) Plankton community structure and carbon cycling in a coastal upwelling system. I. Bacteria, microprotozoans and phytoplankton in the diet of copepods and appendicularians. *Aquat. Microb. Ecol.*, **34**, 151–164.

Verity, P. G. and Smetacek, V. (1996) Organism life cycles, predation, and the structure of marine pelagic ecosystems. *Mar. Ecol. Prog. Ser.*, **130**, 277–293.

Ward, P., Shreeve, R., Atkinson, A. *et al*. (2006) Plankton community structure and variability in the Scotia Sea: austral summer 2003. *Mar. Ecol. Prog. Ser.*, **309**, 75–91.