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

CORNELIA JASPERS†, TORKEL GISSEL NIELSEN†*, JACOB CARSTENSEN1, RUSSELL R. HOPCROFT2 AND EVA FRIIS MOLLER†

1DEPARTMENT OF MARINE ECOLOGY, NATIONAL ENVIRONMENTAL RESEARCH INSTITUTE, UNIVERSITY OF AARHUS, FREDERIKSBORGVEJ 399, PO BOX 358, 4000 ROSKILDE, DENMARK AND 2INSTITUTE OF MARINE SCIENCE, UNIVERSITY OF ALASKA, FAIRBANKS, AK 99775-7220, USA

†PRESENT ADDRESS: NATIONAL INSTITUTE OF AQUATIC RESOURCES, TECHNICAL UNIVERSITY OF DENMARK, CHARLOTTENLUND SLOT, 2920 CHARLOTTENLUND, DENMARK.
*CORRESPONDING AUTHOR: tgn@dmu.dk

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The abundance and depth distribution of metazoans $>20 \mu m$ 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 $<200 \mu m$ 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
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 microbially 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 nanoplanckton, 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 nanoplanckton (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 picooplankton 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 (Allredge, 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.
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 (\( \mu g\) C L\(^{-1}\)) = 1.441 \times Chl \( a \) (\( \mu g\) L\(^{-1}\)) + 0.037 (\( R^2 = 0.85 \)) and heterotrophic flagellates (\( \mu g\) C L\(^{-1}\)) = 21.86 \times Chl \( a \) (\( \mu g\) 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 \( \mu m \) 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 Lugols 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\( \times \) 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
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.

**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   | In \(W \mu g = 2.74 \ln (L \mu m) - 16.41\) | Chisholm and Roff, 1990              |
| Cyclopod copepods   | In \(W \mu g = 1.96 \ln (L \mu m) - 11.64\) | Chisholm and Roff, 1990              |
| Copepod nauplii     | \(C \mu g = 3.18 \times 10^{-6} BL(\mu m)^{2.31}\) | Berggreen et al., 1988               |
| Larvacean community | \(\log C (\mu g) = 2.455 \log TL (\mu m) - 6.96\) | 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](image-url) **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 (Bämstedt, 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 TOCVCPH 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 copepodes 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:

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

(1)

Larvacean food (FC) was here defined as (Chl \(a < 10 \mu m\), 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:

\[
\mu(\text{day}^{-1}) = \ln (p + b/b)
\]  

(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

\[
F_{p\text{id}} = \text{station}_i + \text{depth}_j + \text{water mass(depth)}_{i(k)} + e_{d(i)}
\]  

(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 copepods 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 size 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.
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
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 $<10 \mu m$. The fraction $>10 \mu m$ 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 $>50 \mu m$, 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 $>20 \mu m$. 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
Larvaceans 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 ±
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 $748 \pm 118$ 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. 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.
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 0.3 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 \( \mu \)m (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 \( \mu \)m mesh nets as advocated by UNESCO.
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 (Paffenhofer, 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 (Paffenhofer 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 Indian 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 Fromeman, 2005; Fielding et al., 2007; Fromeman 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 (Shellbourne, 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 temperature 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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