



## Biological oceanography across the Southern Indian Ocean – basin scale trends in the zooplankton community

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### ABSTRACT

We present a study on the protozooplankton > 5 µm and copepods larger than 50 µm at a series of contrasting stations across the Southern Indian Ocean (SIO). Numerically, over 80% of the copepod community across the transect was less than 650 µm in size, dominated by nauplii, and smaller copepods, while 80% of the biomass (as mg C m<sup>-3</sup>) was larger than 1300 µm in body length. Predation by the carnivorous copepod *Corycaeus* sp. was estimated to be able to remove up to 2% d<sup>-1</sup> of the copepods < 1000 µm in size. By the help of grazing models we estimated that primary producers were mainly grazed upon by ciliates and heterotrophic dinoflagellates (40–80% d<sup>-1</sup> combined) in temperate waters but appendicularians became increasingly important in the tropical waters grazing about 40% of the biomass per day. Despite their high abundance and biomass, copepods contributed less than 20% of the grazing at most stations. Secondary production was low (carbon specific egg production < 0.14 d<sup>-1</sup>) but typical for food limited oligotrophic oceans.

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### 1. Introduction

Studies on zooplankton communities in the Indian Ocean proper are few and far between. From 1960 to 1965 a major international co-operative effort of mapping the zooplankton composition of the whole Indian Ocean (IO) was carried out during the International Indian Ocean Expedition (IIOE) (Snider, 1961). The results of these plankton sampling efforts were published in a series of plankton atlases (e.g. IOBC, 1970) and in several papers describing the spatial distribution and taxonomy of specific zooplankton genera (see Stephen et al., 1992 and references therein). So far most zooplankton research in the open Indian Ocean has focused almost entirely on the taxonomy and structure of the larger mesozooplankton community (e.g. Timonin, 1971) where most sampling has been conducted with a 330 µm meshed Indian Ocean Standard net (Currie, 1963) or on few occasions with a 243 µm net (Lawson, 1977). Despite their immense value, these studies seriously underestimated the biomasses of smaller zooplankton (e.g. copepod nauplii and cyclopoids), especially in oligotrophic regions (Gallienne and Robins,

2001) where they, together with protists play a potentially important role in ecosystem structuring.

More ecologically focused studies on IO mesozooplankton production and feeding ecology have been carried out in coastal and shelf seas, e.g. off southern South Africa (Huggett and Richardson, 2000), Tanzania (Lugomela et al., 2001) in the Arabian Sea (e.g. Smith, 1982), Andaman Sea (Satapoomin et al., 2004) and off western Australia (McKinnon and Duggan, 2001, 2003). Very few studies have been carried out in the open Indian Ocean. Two publications are available on trophic ecology of krill and bulk copepods from the subtropical convergence zone between 38 and 42°E and 38 and 43°S (Richoux and Froneman, 2009; Richoux, 2011), whereas other studies are from further south of the 50°S in the Sub-Antarctic part of the IO.

During Leg 7 of the Danish 3rd Galathea expedition the southernmost part of the IO was crossed, starting in the Subtropical Convergence Zone and sub-polar waters off Southern Africa transecting through Subtropical Gyre and tropical waters and ending on the North West Australian Shelf. The main aim of this project was twofold; to address the questions regarding the dominating zooplankton size structure in the Indian Ocean, and to investigate the importance of heterotrophic protists and copepods and estimate their potential grazing impact on the autotrophic community at a series of contrasting stations across the Southern Indian Ocean (SIO); from the

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highly productive fronts along its southern periphery to the oligotrophic subtropical gyre.

In the present paper we explore the vertical distribution, abundance, biomass, productivity and potential grazing impact of copepods > 50  $\mu\text{m}$  size and heterotrophic protists from the upper 60 m in the water column. Potential predation pressure on small zooplankton by the carnivorous copepod *Corycaeus* was estimated. In addition to the data presented in this paper, we use the information from two studies conducted on the same leg of the expedition in our estimates of grazing pressure; the one on larvaceans (Jaspers et al., 2009) and the other on the production and fate of copepod fecal pellets (Møller et al., 2011).

## 2. Methods

The present study was conducted on board the Danish Navy surveillance frigate “F359 Vædderen” as a part of the third Danish Galathea expedition; Leg 7 from Cape Town, South Africa, to Broome, NW Australia, from 18 October to 5 November 2006. Seven stations (stations 7-1, 7-8, 7-15, 7-18, 7-23, 7-28 and 7-33) were sampled on the route for chlorophyll, auto- and heterotrophic protists, copepods, vertical distribution and vital rates (Fig. 1).

### 2.1. Hydrography and chlorophyll

The vertical distribution of salinity, temperature, PAR and oxygen was routinely measured down to 400 m using a Seabird SBE 9/11 CTD Sealogger mounted on a rosette sampler with 12  $\times$  30 L Niskin bottles. Water samples from 10, 30, 60, 100, 200 and 400 m were taken at all stations. Chlorophyll *a* (Chl *a*) concentrations were measured on 500 and 1000 mL triplicate samples filtered onto Whatmann GF/F and 11  $\mu\text{m}$  filters, respectively. The filters were extracted overnight in 5 mL 96% ethanol (Jespersen and Christoffersen, 1987) and measured before and after addition of 1 N HCl on a Turner Designs Model 700 Fluorometer calibrated against a pure Chl *a* standard. Integration of Chl *a* with depth was achieved by trapezoidal integration.

### 2.2. Auto- and heterotrophic protists

Water from 10 and 60 m depths was carefully tapped from the Niskin bottles. Immediately after sampling, 200 mL aliquots were fixed in 2% final concentration Lugol's solution in brown glass bottles and stored at 5 °C in the dark. Within 3 months after sampling, cells were counted and identified to genera or species if possible after settling for 24 h in 100 mL Utermöhl settling

chambers. Cells less than 20  $\mu\text{m}$  in size were counted under an inverted microscope using 400  $\times$  magnification, while larger cells were counted at a 100  $\times$  magnification. Cell sizes were measured by the use of calibrated ocular micrometers. Only protists larger than 5  $\mu\text{m}$  were considered and their volume estimated using appropriate equations based on their shape. Depending on the abundance of the species/taxon under consideration either a fraction or the entire sample was counted, with 100 cells being the count limit. Although mixotrophy does occur among ciliates, all known ciliate species include phagotrophy and we therefore considered all ciliates as heterotrophs. Due to the fixative, detailed ciliate identification was generally difficult, while most of the thecate dinoflagellates were identified to genera. The athecate dinoflagellates presented a challenging taxonomical problem with only one strict heterotrophic species, *Gymnodinium spirale*, identified. However, pigment analyses conducted on the same sub-samples as analyzed in the current study concluded that autotrophic dinoflagellate pigment concentrations were very low at all stations except at station 7-8 (Schlüter et al., 2011). We therefore assume that unidentified athecate dinoflagellates were heterotrophic at the remaining stations. Ciliates were grouped into sizes as outlined above and their biomasses were estimated, but are presented here as larger or smaller than 30  $\mu\text{m}$  ESD. Cellular carbon content of protists was estimated from taxon specific ESD:carbon relationships (Menden-Deuer and Lessard, 2000). Depth integrated (100 m) protist biomass ( $\mu\text{g C m}^{-2}$ ) was calculated on cells > 5  $\mu\text{m}$  as the average of the two sampling depths multiplied by 100.

### 2.3. Copepod sampling

Copepods were sampled by a midi Hydro-Bios Multinet equipped with five 50  $\mu\text{m}$  mesh nets. The depth strata sampled were 0–50, 50–100, 100–200, 200–300 and 300–400 m, with the exception of Station 7-33 where only the two upper most strata were sampled due to instrument failure. Sampling at all stations was conducted between 0930 and 1200 h local time, so the phase of the likely diel vertical migration of zooplankton is comparable between stations. Samples were fixed in 4% borax buffered formaldehyde. Before enumeration of major copepod genera, samples were filtered through 1-mm nylon mesh. All copepods retained on the mesh were counted as were 1/8 of the copepods that passed through the net. In addition, a total of about 100 nauplii and 200 copepodites were measured for length. Total length was measured for nauplii and harpacticoids while prosome length was measured for the remaining copepods. Copepod carbon was calculated by converting length to ash free dry weight (afdw) using the regression of Chisholm and Roff (1990) and applying a conversion factor of 0.45  $\mu\text{g C afdw}^{-1}$  (Båmstedt, 1986). Naupliar carbon was calculated from their total length after Berggren et al. (1988). The conversion factors are given in detail in Jaspers et al. (2009).

### 2.4. Copepod egg production rates

#### 2.4.1. Calanoids

At each station, with the exception of Station 7-8, live copepods were collected with a 200  $\mu\text{m}$  WP2 net with a large (10 L) non-filtering cod end towed vertically from 100 m depth to the surface. Immediately after collection the sample was diluted with surface water in a 25 L insulated box. Adult females of the most abundant calanoid copepod species were sorted within 1 h of sampling and incubated in 600 mL polycarbonate bottles containing 50  $\mu\text{m}$  screened surface water. The number of females and replicates differed between stations, but generally 2–5 *Acartia* sp. were incubated per bottle in 8–10 replicates, 1–4 *Mecynocera* sp. per bottle in five replicates, and one *Neocalanus gracilis* per bottle in 12–20 replicates.

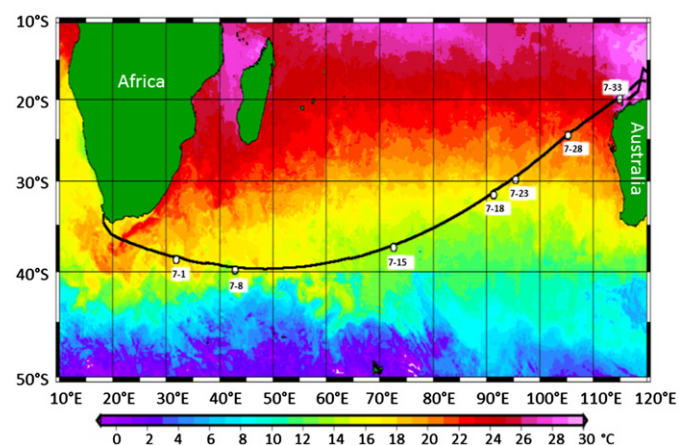


Fig. 1. The cruise track and station locations of leg 7 of the Galathea 3 expedition.

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