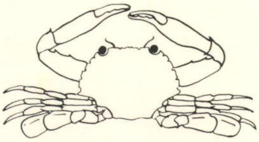
MATTHIJS VAN COUWELAAR

Pelagic faunas in monsoon ruled seas



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ACADEMISCH PROEFSCHRIFT

ter verkrijging van de graad van doctor aan de Universiteit van Amsterdam, op gezag van de Rector Magnificus prof. dr J. J. M. Franse ten overstaan van een door het college voor promoties ingestelde commissie, in het openbaar te verdedigen in de Aula der Universiteit op donderdag 19 november 1998 te 13.00 uur.

door

Matthijs van Couwelaar

geboren te Amsterdam

Promotiecommissie:

Promotor prof. dr S. van der Spoel
Overige leden prof. dr F. R. Schram, Universiteit van Amsterdam
prof. dr J. Ringelberg, Universiteit van Amsterdam
prof. dr P. A. W. J. de Wilde, Rijksuniversiteit Groningen
prof. dr M. V. Angel, University of Southampton, United Kingdom
dr M. A. Baars, Nederlands Instituut voor Onderzoek der Zee, Den Burg
dr P. H. Schalk, Universiteit van Amsterdam

Het onderzoek voor dit proefschrift werd verricht aan het Instituut voor Systematiek en Populatiebiologie van de Faculteit Biologie, Universiteit van Amsterdam. De voltooiing van het proefschrift werd financieel ondersteund door de Stichting ter Bevordering van de Nederlandse Oceanografie (SBNO), Amsterdam.

Gedachten zijn de schaduwen van onze ervaringen — altijd donkerder, leger, simpeler dan deze.

Friedrich Nietzsche

CONTENTS

VOORWOORD

Nu bijna tien jaar geleden deed ik een onderzoek aan zoöplankton in het Noordzeekanaal. In één van de netmonsters zaten heel veel voor mij onbekende kwalletjes. Ik ging er mee naar professor van der Spoel. Het bleek te gaan om een soort die vanuit de Noordzee in het kanaal was gekomen — overigens niet als enige. Deze vondst en deze kennismaking brachten mij niet veel later tot het zoöplanktononderzoek op de Indische Oceaan waarvan dit boekje een resultaat is.

Er is een groot verschil tussen het veldwerk op het Noordzeekanaal en dat op de oceaan, maar de nieuwsgierigheid naar wat er in het net zit, is voor mij wel altijd dezelfde. Of het net van tien meter diep komt zoals op het kanaal, of van duizend meter diep zoals op de oceaan maakt wat dat betreft niet veel uit. De diepzee is een deel van de biosfeer dat moeilijk toegankelijk is en is een omgeving waar een mens zich van nature niet in kan begeven. Het is daarom een voorrecht om er bij te zijn als het net van grote diepte aan dek komt en daarmee het leven in de diepzee iets van z'n geheim laat prijsgeven: ondermeer kwallen en inktvissen, pijlwormen en vleugelslakjes, mosselkreeftjes, roeipootkreeftjes en nog allerlei andere soorten kreeftachtigen, lantaarnvissen, addervissen, enzovoort. De verwondering is groot bij het aanschouwen van al die dieren met zo een verscheidenheid aan vormen, grootte en kleur. Het is ook het enorm grote verschil tussen de menselijke en de oceanische maat dat indruk maakt, waarbij het duidelijk wordt dat oceanische ecosystemen de grootste op aarde zijn.

Eigenlijk zou ik mijzelf als eerste moeten bedanken voor dit boekje, maar zoiets past niet. Stel je voor dat ik zo onbescheiden zou zijn.... Nou, vooruit, toch maar wèl. Matthijs, dankzij jou ligt dit proefschrift daar waar het moet zijn: op het tableau van de wetenschap en onder de ogen van collega-biologen, familie, vrienden en alle andere geïnteresseerden. En dan is daar veel dank voor mijn promotor Siebrecht van der Spoel. Inzicht, geduld en afstand zijn de dimensies waarmee ik onze verhouding wil duiden. Soms was er, aan beide kanten, ook onbegrip, ongeduld en juist geen afstand. Toch heeft dat ook een goede uitwerking gehad op het resultaat. Ik ben erkentelijk voor de ruimte die hij heeft bewaard om het onvermijdelijke te laten gebeuren.

De volgende die ik wil bedanken is Peter Schalk, voor al z'n raad en daad en steun; en in het verlengde daarvan dank ik SBNO voor het genereuze aanbod waardoor dit proefschrift kon worden voltooid. Joke Bleeker heeft enorm geholpen met het uitzoeken van monsters en Lex de Fluiter kon naar hartelust experimenteren met kleuringen, waar ik veel aan heb gehad om bijvoorbeeld de euphausiiden beter te kunnen bekijken.

Al die netvangsten zijn verkregen met twee expedities met de *Tyro*. Aan die naar de noordwestelijke Indische Oceaan heb ik zelf mee gedaan en ik bewaar er goede herinneringen aan. Op deze plaats wil ik Martien Baars noemen, die veel werk verzet heeft voor ons deel van de expeditie en nog altijd nauw en kritisch betrokken is met het onderzoek op de Indische Oceaan. Dank ook aan Mario de Kluijver voor zijn enthousiaste hulp bij de clusteranalyse. De jongens en meisjes van ETI waren nooit te beroerd om mij op een passend moment te helpen met advies, of mij op en met hun geavanceerde apparatuur te laten werken.

Allen van het Instituut die mij op welke wijze dan ook hebben geholpen en allen met wie ik vele avonden heb doorgebracht, wil ik hier ook noemen. We spraken gelukkig niet alleen over ons werk en onderzoek — heel vaak juist niet. Ik moet hier maar geen namen noemen, want het zijn er veel; het is genoeg dat we het met elkaar weten.

De kring van betrokkenen wordt in deze opsomming steeds ruimer en de afstand tot het proefschrift steeds groter, maar de afstand tot mijzelf allerminst. Het zou daarom niet juist zijn om op deze plaats mijn diepe erkentelijkheid te onthouden aan allen die in dit verband van heel dichtbij of iets verder af met mij te maken hebben gehad. Dank.

INTRODUCTION

The oceans cover 70% of the earth's surface and host the world's largest ecosystems. Hidden under a vast area of the sea surface and extending far into the deep, these pelagic ecosystems cover enormous volumes. In the pelagic realm a vertical zonation is present from surface to near-bottom. All strata are interlinked and depend on the primary production generated in the photic zone, roughly in the upper 100 m of the ocean. The human population is putting great stress on oceanic resources, but paradoxically the importance and the vulnerability of oceanic ecosystems are often not recognized. Partially this is because ocean life is concealed in the deep, and the exploration of the ocean requires specialized techniques at high costs. Also, pelagic ecosystems are complex and difficult to comprehend, especially if seasonal changes influence the system, and — as in the tropics — species diversity reaches its peak.

The trade winds dominate the atmospheric circulation over the world oceans between 30°S and 30°N. Generated by the pressure difference between the subtropical high and the intertropical convergence zone low, trade winds blow in the same direction towards the equator throughout the year. Over the northern Indian Ocean and the Indo-Malayan waters, however, trade winds are absent. Here rule the monsoons — winds that reverse direction every half year. There is a strong coupling between the atmospheric and oceanic circulations in these areas, and the monsoonal changes induced in the ocean's pelagic system form the background for the work presented in this thesis.

Monsoon systems are global scaled seasonal cycles in the intertropical atmospheric circulation, driven by the differential heating of sea and land surface. There are two major monsoons: the Indian Monsoon over the northwestern Indian Ocean and the East Asian Monsoon (or Australian-Asian Monsoon) over the Indochina and the Indo-Australian regions (Fig. 1). The Indian monsoon is primarily based on the seasonal cycling in the solar heating of the Asian continent. During the Indian summer, the strong tropospheric Findlater Jet blows over the northwestern Indian Ocean from Somalia to India and forms the core of the southwest monsoon. About 60% of the low-level air transport from the southern to the northern hemisphere takes place through this jet in this period (Findlater, 1971). Average wind speeds over the northwestern Indian Ocean during the SW monsoon (7 to more than 20 m s^{-1}) are twice as high as during the NE monsoon (3 to 11 m s^{-1}). The monsoon is characterized by succeeding dry and wet periods on land, and by reversing winds at sea. These cycles have tremendous importance for both aquatic and terrestrial life. As an example for humans, the monsoon affects the lives of about 60% of the world's population (CLIVAR, 1989). The daily life and the economy — in particular agriculture and fisheries — are tuned to, and depending on, the alternating dry and wet seasons. There is a substantial interannual variability in the Asian summer monsoon that is closely related to the phase of the El Niño/Southern Oscillation (ENSO) (see Rasmusson and Carpenter, 1983; Webster and Yang, 1992). Disruption of the seasonal rhythm has immediate social and economic consequences for the densely populated part of the world affected. In Indonesia for instance, rain forests were on fire over a long period in 1997-98 during a persistent drought that is blamed on the 1997-98 ENSO anomaly (Anon., 1998; WMO, 1998; BoM, 1998).

Life in the seas and oceans is also affected by the monsoons. The major mechanism behind this influence is the strong coupling between the atmospheric and oceanic circulations. The world's

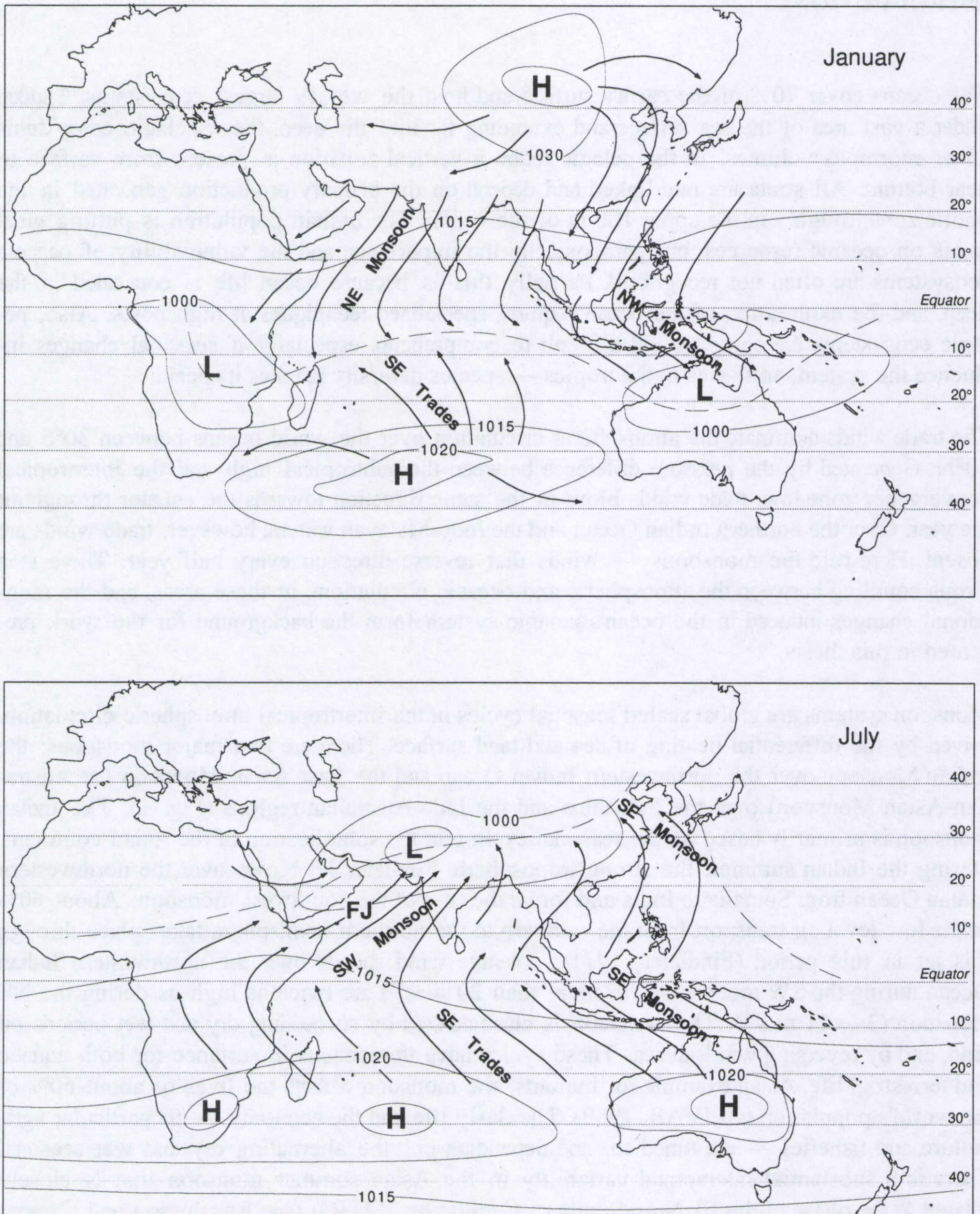

Fig. 1. Schematic overview of surface-level air circulation over the Indo-Western Pacific region between 40°N and 40°S during January (upper panel) and July (lower panel). The two major monsoons indicated with NE/SW monsoon (Indian Monsoon) and NW/SE monsoon (Australian-Asian, or East Asian Monsoon). FJ - Findlater Jet during Indian Summer Monsoon (SW monsoon, lower panel). Surface air pressure in millibar. H - core of high pressure area. L - core of low pressure area. Dashed line - intertropical convergence zone. (Adapted from Times Atlas, 1994)

ocean is divided in three large basins: the Pacific, the Atlantic and the Indian Oceans. The Indian Ocean is the smallest ocean and is unique in that it is landlocked in the north, and moreover, roughly north of 10°S, the circular surface currents reverse every half year with the alternating monsoon winds (*e.g.* Wyrtki, 1973). This seasonal pattern is most manifest in the northwestern sector. Here a clockwise gyre north of 10°S during the SW monsoon (June-September) is forced by the persistent southwestern winds (Fig. 2). The strong, northeast flowing Somali Current is a particular part of this gyre (*e.g.* Molinari *et al.*, 1990; Schott *et al.*, 1990). During the SW monsoon, coastal upwelling occurs off Somalia, Oman and to a lesser extend off SW India, accounting for seasonal enrichment of large parts of the ocean. In addition to this, open-ocean upwelling and even more important, the Omani "off-shore jets" (Keen *et al.*, 1997), are other sources for nutrients and plankton biomass in the open Arabian Sea. Although not simply an anti-clockwise gyre (Swallow, 1991), the northwestern Indian Ocean surface currents generally flow in the opposite direction during the NE monsoon in (*e.g.* Wyrtki, 1973; Molinari *et al.*, 1990) and upwelling is absent along the east African and Arabian coasts.

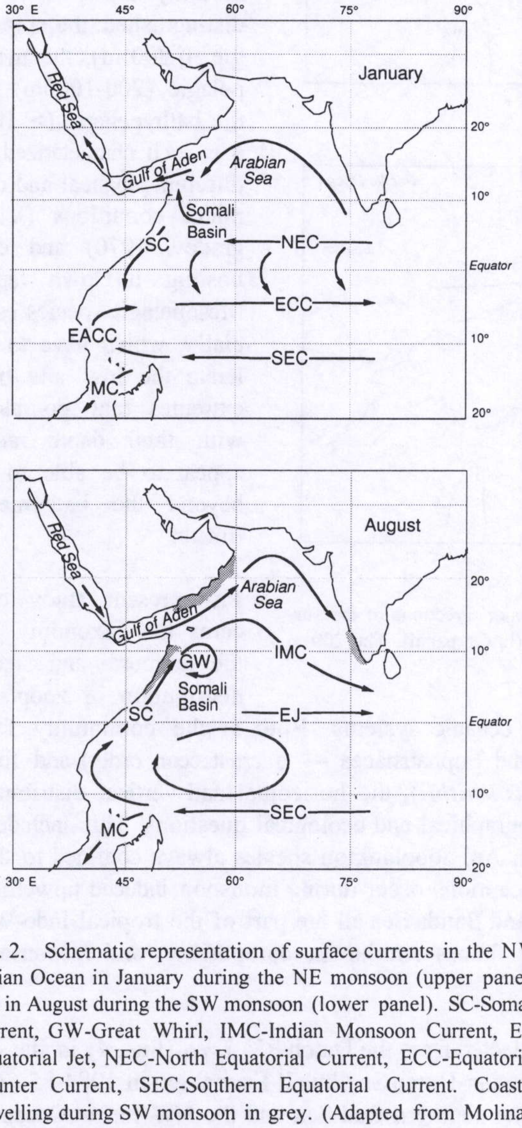

Fig. 2. Schematic representation of surface currents in the NW Indian Ocean in January during the NE monsoon (upper panel) and in August during the SW monsoon (lower panel). SC-Somali Current, GW-Great Whirl, IMC-Indian Monsoon Current, EJ-Equatorial Jet, NEC-North Equatorial Current, ECC-Equatorial Counter Current, SEC-Southern Equatorial Current. Coastal upwelling during SW monsoon in grey. (Adapted from Molinari *et al.*, 1990 and Wyrtki, 1973).

East of the Indian Ocean are the waters of the Indonesian Archipelago (Indo-Malayan region), also subject to a monsoon regime (Fig. 3). Here, however, a circular seasonal pattern is absent, and although the hydrography is very complex, generally the surface currents are westerly during the SE monsoon (May-November) and easterly during the NW monsoon (December-April). In the eastern Banda Sea upwelling induced enrichment of the surface water layers occurs during the SE monsoon (Zijlstra *et al.*, 1990).

Because of their complex dynamics, the northwestern Indian Ocean and the Indo-Malayan region are of great importance to the study of monsoon induced seasonal dynamics of pelagic ecosystems. Given this, the Banda Sea, the Indian Ocean off Somalia, the Gulf of Aden and the adjacent southern Red Sea were chosen as study area during two Dutch multidisciplinary expeditions.

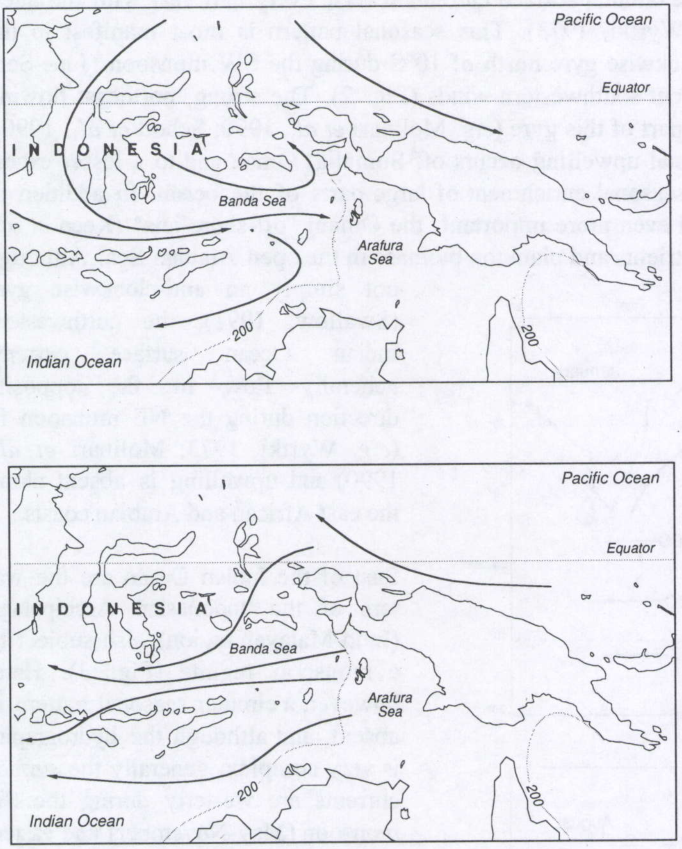

Fig. 3. The Banda Sea and Arafura Sea and the major directions of the surface currents in February (upper panel) and August (lower panel). The 200 m isobath is shown. (Adapted from Wyrtki, 1961).

The vertical dimension is important in the distribution of pelagic organisms in the oceanic realm, as organisms occupy depth zones delimited by biotic (food, predation) and abiotic factors (e.g. light, nutrients, temperature, and oxygen). Generally, three somewhat arbitrary depth zones are distinguished: the epipelagic (0-200 m), the mesopelagic (200-1000m) and the bathypelagic (> 1000 m), each characterized by different physical and chemical conditions (Vinogradov, 1970) and each hosting its own fauna. Mesopelagic species especially, which have to tolerate the low and high extremes that go along with their depth range, appear to be able to go beyond the bathymetric limits.

The present study concerns the taxonomy and the temporal and spatial distribution of zooplankton and micronekton in monsoon-driven oceanic systems. Both at the community level (zooplankton and micronekton biomass, and Euphausiacea — a crustacean order) and for a single taxon (the swimming crab *Charybdis smithii*), the horizontal and vertical distribution patterns were studied with respect to biogeographical and ecological questions. This included a comparison of faunas of the different basins. Are zooplankton species always confined to their depth zone and geographic region, or do exceptions occur during monsoon induced upwelling? The Red Sea, Gulf of Aden, Somali Basin, and Banda Sea all are part of the tropical Indo-West Pacific biogeographic region, but are the faunas similar in composition and response to monsoon influences?

Zooplankton and micronekton data were collected from the Dutch RV *Tyro* (Fig. 4) in the eastern Banda Sea (Indonesia) during the Indonesian-Dutch Snellius II Expedition in 1984-85 (Zijlstra and Baars, 1987; Schalk, 1988) and at the southern Red Sea and the NW Indian Ocean for the Netherlands Indian Ocean Programme (NIOP) in 1992-93 (Baars *et al.*, 1994; Schalk and

Van Couwelaar, 1994). Both expeditions were extensive multidisciplinary enterprises for marine research involving biologists, geologist and hydrographers. These projects involved third parties for partnership: Indonesia in Snellius II, and Kenya and Pakistan in NIOP. For the last decade the Arabian Sea was choosen by several nations for intensive studies, and many opportunities were found to synchronize and to join the seagoing efforts.

Fig. 4. The Dutch R.V. *Tyro* at Port Said awaiting the passage of the Suez Canal, 21 May 1992.

The Snellius II as well as the NIOP expeditions covered two successive monsoon seasons, and each expedition lasted almost a year. In both programmes several research themes were incorporated regarding coastal systems, coral reefs, marine geology, sedimentation, deep-basin ventilation, and the dynamics of pelagic ecosystems. "Theme 3" (Snellius II) and "Theme B" (NIOP) focused on pelagic ecosystems. The sampling and investigating efforts during these themes were the source for the present research. Obviously the zooplankton and micronekton samples provided the core material, but many supporting data originate from hydrographic probes, phytoplankton sampling, primary production experiments, and mesozooplankton sampling.

For sampling of zooplankton and micronekton an Rectangular Midwater Trawl (RMT) 1+8 was used. This gear combines two nets that fish simultaneously (Fig. 5). The RMT1 has a mouth opening of approximately 1 m^2 and mesh size 340 μm, collecting mainly zooplankton, and the RMT8 net has a mouth opening of approximately 8 m^2 and mesh size 4.5 mm, collecting predominantly micronekton. In day and night series, discrete depth layers were sampled systematically, generally from 0-100 m, 100-200 m, 200-300 m, 300-500 (or 600) m, and 500 (600) - 1000 m. Station and haul data can be found in Schalk (1990) for Snellius II, and in Appendix A of this thesis for the NIOP.

Fig. 5. The Rectangular Midwater Trawl 1+8 (RMT) deployed from the *Tyro* during the Netherlands Indian Ocean Programme.

Biomass was chosen to measure the biological response of the zooplankton and micronekton community to the monsoon-induced changes at lower trophic levels irrespective of species composition. The zooplankton biomass in the Banda Sea declined by 40-57% from the SE to NW monsoon and the differences were greatest at the upwelling stations, located in the eastern part of the basin (Schalk, 1987). During the NIOP expedition in 1992-93, zooplankton displacements from vertical net hauls (0-300 m, 200 μm mesh) off Somalia were remarkably higher during the NE monsoon than expected from the classical picture for upwelling areas with an alternating rich period and a poor period. The displacement volumes of the RMT1 (zooplankton) and RMT8 (micronekton) samples were examined for a closer assessment of the response of zooplankton and micronekton to the monsoon induced changes in the Somali Basin, the Gulf of Aden and the southern Red Sea (Chapter 1).

The Euphausiacea were chosen as a group of species that was expected to respond quickly in abundance, species composition, and spatial distribution to the seasonally changing circumstances. Euphausiid species are either herbi-, omni- or carnivorous, and can be divided between epi-, meso-, and bathypelagic distribution; species also display diurnal vertical migration. The euphausiids are a "successful" cosmopolitic group, with a distinct contingent of species from the tropics, many that are common in the Indo-Australian region and the NW Indian Ocean. The monsoonal effects on the vertical distribution including diurnal vertical migration of micronekton were studied in euphausiids from the Banda Sea. With computerized classification, samples and species were ordered in an attempt to reveal spatial and temporal patterns. Filling rates and contents of euphausiid stomachs were studied in relation to vertical distribution in order to study diurnal and seasonal patterns. Special attention was paid to vertical distributions of deep-living species, under the peculiar abiotic circumstances found in this ocean basin, located between the Indian and Pacific Oceans (Chapter 2).

Distribution patterns of planktonic animals were presumed to be bound to water masses and to match surface current patterns, and to show a considerable impact from the seasonal upwelling. The narrow and shallow connection between the Red Sea and the Gulf of Aden was expected to act as a marked (biogeographic) barrier preventing deep-living Indian Ocean species from entering the Red Sea. Spatial and temporal distribution patterns of euphausiids were studied in order to answer the following questions: what are the changes in the euphausiid fauna under seasonally induced enrichment, and how is the vertical distribution influenced on a diurnal and seasonal time basis? Also, what are the differences between the faunas from the Red Sea and the adjacent part of the Indian Ocean? To study similarities between the two monsoon driven systems of the Banda Sea and the NW Indian Ocean, species composition and migratory behaviour of euphausiids from the two areas were compared. Cluster analysis was carried out on all samples together in order to search for patterns in spatial and seasonal distribution of the euphausiids, with an attempt to interpret these in terms of the environmental conditions and biogeographic regions (Chapter 3).

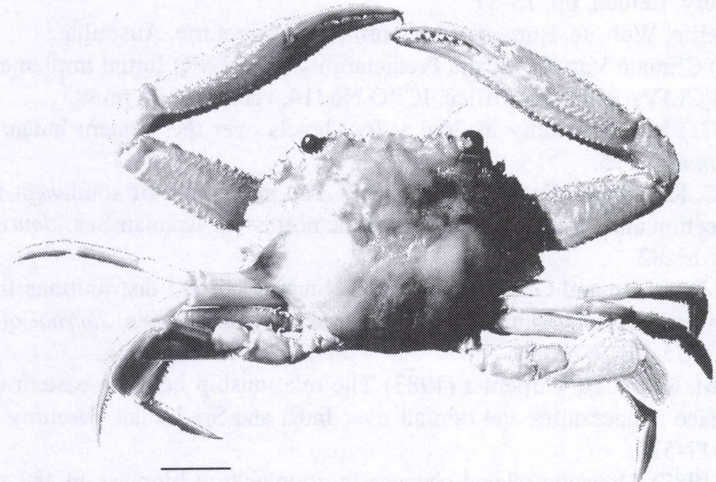

Fig. 6. *Charybdys smithii* McLeay, 1838 (length of horizontal bar equals 1 cm).

The remarkable catch of about 700 swimming crabs *Charybdis smithii* (Fig. 6) from the upper 200 m at one of the first stations during the second cruise with the *Tyro* on the NW Indian Ocean in July 1992, suggested a hitherto unappreciated importance of these animals in the pelagic system. A real pelagic and oceanic occurrence far off-shore is unique amongst crabs, and the vast nightly surface swarms of crabs encountered during the NE monsoon were a striking phenomenon. Since this species is endemic for the western Indian Ocean, it provided an interesting opportunity to study biogeographic patterns in relation to the monsoon. From 1992-1995, dense patches of *C. smithii* were sampled in the Somali Basin and the Arabian Sea with the *Tyro*, the British RRS *Discovery* and the American RV *Malcolm Baldrige* on several cruises during the SW and NE monsoons. The pooled samples taken with the three ships during both monsoons, and supplementary literature data allowed for a reconstruction of the life cycle, distribution pattern and biogeography of this special Indian Ocean pelagic species (Chapter 4).

The collected pelagic materials as presented and elaborated in the Chapters 1 to 4 made it possible to compare open ocean faunas from different basins. A summary and conclusions are given in Chapter 5.

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CHAPTER 1

Zooplankton and micronekton biomass off Somalia and in the southern Red Sea during the SW monsoon of 1992 and the NE monsoon of 1993

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Zooplankton and micronekton biomass off Somalia and in the southern Red Sea during the SW monsoon of 1992 and the NE monsoon of 1993

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Abstract—Spatial and seasonal variations in mesozooplankton, macrozooplankton and micronekton biomass distribution were studied in the Somali Basin and the southern Red Sea and Gulf of Aden. Cruises were made in May–June and July–August 1992 during the SW monsoon, and in January–February 1993 during the NE monsoon. Samples were taken in day and night series from stratified layers to depths of 600 or 1000 m, using an RMT1 + 8, combining two nets with mesh size of 0.34 mm and 4.5 mm, respectively. During the SW monsoon the mean zooplankton biomass from RMT1 samples (displacement volume 0–300 m, night) were low in the southern Red Sea and the Gulf of Aden, 14.0–17.5 ml m^{-2}. At 11°N in the Somali Current, where coastal upwelling occurs, the maximum biomass value of 38.0 ml m^{-2} was recorded. Downstream from the upwelling in the Great Whirl, biomass values were lower, ranging from 21.0 to 35.9 ml m^{-2}. In the Somali Basin south of 5°N the mesozooplankton biomass was lower than in the Somali Current and northern areas. During the NE monsoon large phytoplankton blooms occurred in the southern Red Sea and the Gulf of Aden, and the mean zooplankton biomass almost doubled to 23.9–40.2 ml m^{-2} compared with the SW monsoon. Primary production in the northern Somali Basin was much higher during the NE monsoon than recorded during earlier studies, and biomass values for the zooplankton therefore were not as low as might be expected. No statistical significant difference was found in the season's mean biomass values. This is remarkable because in the northern Somali Basin the mean phytoplankton carbon production during the NE monsoon was about two-thirds of the production during the SW monsoon. This seeming paradox is probably due to large mesh sizes that did not retain the small size (herbivorous) zooplankton fraction present during the SW monsoon. The mean macrozooplankton and micronekton biomass from RMT8 samples (0–300 m night) in the southern Red Sea, the Gulf of Aden and the Somali Basin showed no significant seasonal difference. However, biomasses of mesopelagic fish and large crustaceans were high in the southern Red Sea during the SW monsoon, and were high in the Somali Current during the NE monsoon, whereas in the northern Somali Basin biomasses remained about the same. Biomasses of large crustaceans in the Gulf of Aden were higher during the NE monsoon. The pelagic swimming crab *Charybdis smithii* was found during the SW monsoon in the equatorial and northern Somali Basin, attaining high displacements. The species was not found in the Somali upwelling area during this season, whereas during the NE monsoon the highest displacements for *C. smithii* were recorded. Vertical profiles of biomass from RMT1 and RMT8 samples show that zooplankton and micronekton occur in the oxygen minimum zone and that the lowest oxygen concentrations in the sampled depth range (0.1–1 ml l^{-1}) do not seem to hamper diurnal vertical migration. © 1997 Elsevier Science Ltd

INTRODUCTION

Surface circulation in the NW Indian Ocean is characterised by a reversal of current direction induced by the semi-annual shift in monsoon winds. During the NE monsoon in the months January, February and March two counter-rotating gyres extend across the entire basin (Molinari *et al.*, 1990). The southern clockwise gyre has its axis at about 10°S, and is bounded to the south by the Southern Equatorial Current (SEC) and to the north by the Equatorial Counter Current (ECC). The northern, anticlockwise gyre is bounded to the north at about 5°N by the Northern Equatorial Current (NEC) and to the south by the ECC. With the start of the SW monsoon in May, the southern clockwise gyre moves northward. Its axis as a boundary between eastward flow (the ECC, then transformed into the Equatorial Jet) and westward flow (SEC), migrates from 10°S in May to 5°S in June. The anticlockwise northern gyre observed during the NE monsoon dissipates with the disappearance of the NEC, and flow in the eastern Arabian Sea is to the south-east, merging with the Equatorial Counter Current into the eastward flowing Indian Monsoon Current (Molinari *et al.*, 1990).

During the SW monsoon from May to September, the Somali Current, as part of the northern clockwise gyre, flows north-east until the intermonsoon in October–November. Along with the SW monsoon, strong coastal upwelling off Somalia starts in May with a first upwelling centre at 4°N, followed about 1 month later by a second one at 10°N. Together the upwelling centres display a two-wedge pattern separated by the Great Whirl at 5–12°N and 50–55°E, shifting northwards during course of the SW monsoon (Schott *et al.*, 1990). With upwelling large amounts of nutrients are brought in the surface waters, resulting in high chlorophyll concentrations (Krey, 1973; 1989; Yentsch and Phinney, 1992), up to 5 mg m^{-3} in the upwelling wedges off Somalia in July–August (Smith and Codispoti, 1980). During the NE monsoon, the Somali Current flows south-west, until the April intermonsoon (Schott *et al.*, 1990). In contrast to the SW monsoon, nutrient concentrations are lower and chlorophyll concentrations are less than 0.20 mg m^{-3} (Krey, 1973). The monsoon regime affects the surface waters in the southern Red Sea up to 20°N, with a surface outflow into the Gulf of Aden during the SW monsoon and a surface inflow during the NE monsoon. Phytoplankton blooms observed during the NE monsoon in the Red Sea are in seasonal contrast to the blooms in the NW Indian Ocean during the SW monsoon (Halim, 1984).

Monthly average surface chlorophyll concentrations in the NW Indian Ocean (Table 1) were gathered from Coastal Zone Colour Scanner (CZCS) images between 1978 and 1986 (Goddard Space Flight Centre; see Baars *et al.*, 1995). During the SW monsoon, the northern part of the Somali Current (10°N) shows higher chlorophyll concentrations than

Table 1. *Surface chlorophyll concentrations in various areas in the NW Indian Ocean through the year, averaged from monthly CZCS pictures, November* 1978–*June* 1986

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sep.	Oct.	Nov.	Dec.
Red Sea central	–	–	–	–	–	–?	–	–	–	–	–	–
Red Sea, south	+++	++	++	++	x	++?	+++?	++?	++	+++	+++	+++
Gulf of Aden	+	+	–/+	–	–	–	–?	++	–/+	+	+	+
Gulf of Oman	++	++	+++	++	+	–/+	+	++	++	++	++	++
Off Oman	+	+	+	–/+	–	–?	+++?	+++	++(+)	++	+	+
Somali Current, 10°N	+	+	–	–	––	+	++(+)?	++(+)?	++	+	–/+	+
Somali Current, 5°N	+	+	–	––	–	–/+	+	+	+	+	–/+	–/+

x, No data; ?, pictures from only 1 or 2 years; ––, <0.15 mg m^{-3}; –, 0.15–0.3 mg m^{-3}; +, 0.3–0.5 mg m^{-3}; ++, 0.5–1 mg m^{-3}; +++, 1–10 mg m^{-3} [from Baars (1994)].

the southern part (5°N), whereas during the NE monsoon the concentrations in the Somali Current are uniformly low. In the southern Red Sea and the Gulf of Aden, chlorophyll concentrations are higher during the NE monsoon than during the SW monsoon. In contrast to the situation depicted by Halim (1984), the southern Red Sea appears to be productive throughout the year round except for the intermonsoon in May.

Zooplankton data collected during the International Indian Ocean Expedition (IIOE) in 1960–1965 [data summarised by Cushing (1973) and Rao (1973)] and the Indian Ocean Experiment (INDEX) in 1979 (Smith and Lane, 1981; Smith, 1982) unfortunately do not permit a good understanding of the zooplankton biomass dynamics in the NW Indian Ocean, because biomass data are limited to the upper 200 m. The IIOE did not focus on monsoonal differences in particular, therefore Cushing (1973) and Rao (1973) made only a restricted seasonal comparison for zooplankton biomass. Smith (1982) compared the zooplankton species composition in the Somali Current for both monsoons, but presented zooplankton biomass data during the SW monsoon only. Zooplankton biomass from the Red Sea and the Gulf of Aden has been studied during the MESEDA 2 in 1979 (Beckmann, 1984) and the *Meteor* expedition in 1987 (Schneider *et al.*, 1994). However, as these studies took place in March and February–March, respectively, no seasonal comparison was made for either of these areas.

The response of zooplankton in the NW Indian Ocean to the monsoon regime is not well understood. According to Cushing (1973), in the Arabian Sea the difference in the average secondary production during the SW monsoon and NE monsoon is only small, and much smaller than would be expected from the striking difference in primary production between the two periods. However, zooplankton biomass from standard hauls (0–200 m, 330 µm mesh size) during the IIOE in the Somali Current (Rao, 1973) shows an estimated local decrease of 2–4-fold from SW to NE monsoon. Although the primary production values are highest during the SW monsoon, in the Somali upwelling area an extensive production of copepods takes place during the NE monsoon, perhaps because of some time lag for the development of zooplankton populations (Rao, 1979).

One of the aims of Project B Monsoons and Pelagic Systems—part of the multidisciplinary Netherlands Indian Ocean Programme 1992–1993 (NIOP)—is to study seasonal variations in phytoplankton and zooplankton distribution and productivity during the SW monsoon of 1992 and the NE monsoon of 1993 in the southern part of the Red Sea, the Gulf of Aden and in the Somali Basin including the Somali Current (Baars, 1994). This paper presents the horizontal and vertical distribution of meso- and macrozooplankton and micronekton biomass, based on stratified day and night sampling down to depths of 600 or 1000 m during these successive monsoon seasons, and discusses the spatial and temporal variations.

MATERIAL AND METHODS

During Project B with the Dutch R.V. *Tyro* three cruises were made: Cruise B0 from 21 May to 12 June 1992 at the onset of the SW monsoon, cruise B1 from 11 July to 8 August 1992 during the SW monsoon, and cruise B2 from 11 January to 6 February 1993 during the NE monsoon. The Red Sea was visited by the B0 and B2 cruises; the Gulf of Aden and the Somali Basin by the B1 and B2 cruises (Fig. 1).

Meso- and macrozooplankton and micronekton were sampled in day and night series in discrete depth layers, between 0, 100, 200, 300, 400 and 600 m during the B0 and B1 cruises,

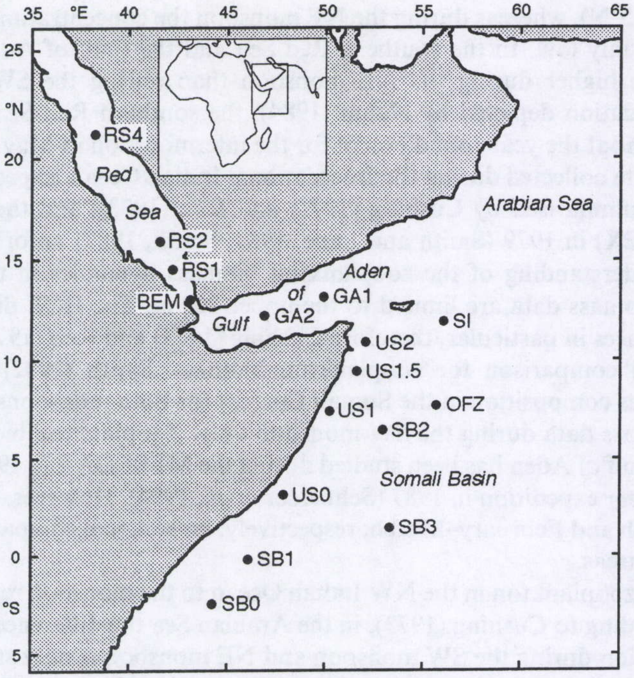

Fig. 1. Position of the RMT1 + 8 stations during the three NIOP cruises. B0 from 21 May to 12 June 1992 during the onset of the SW monsoon (stations RS4, RS2, RS1, BEM, US2), B1 from 11 July to 8 August 1992 during the SW monsoon (stations SB0, SB1, SB2, US0, US1, US1.5, OFZ, SI, GA1, GA2), and B2 from 11 January to 6 February 1993 during the NE monsoon (stations SB3, SB2, US1, US2, SI, GA1, GA2, BEM, RS2, RS1). RS, Red Sea; BEM, Bab-el-Mandab; GA, Gulf of Aden; US, Somali Current; SI, Socotra Island; OFZ, Owen Fracture Zone; SB, Somali Basin.

and 0, 100, 200, 300, 500 and 1000 m during the B2 cruise. Occasional samples to depths of 1000 m (B1) and 1500 m (B2) were made. Sampling was done for each layer in downward oblique hauls with the Rectangular Midwater Trawl RMT1 + 8 (Baker *et al.*, 1973; Roe *et al.*, 1980), an opening and closing net system with two combined nets: the RMT1 (nominal mouth opening 1 m^2, mesh size 320 μm) collecting mesozooplankton, and the RMT8 (nominal mouth opening 8 m^2, mesh size 4.5 mm) collecting macrozooplankton and micronekton. Net speed, measured with a flow meter mounted on the net frame and monitored in real time, was maintained between 1.1 and 3.7 knots (mean 1.9 knots). Filtered volume was calculated in relation to speed and sampling time according to Roe *et al.* (1980). The filtered volume of water per haul was generally between 2000 and 4000 m^3 for the RMT1 and between 20 000 and 40 000 m^3 for the RMT8. Sample locality and date are given in Table 2; further sample data have been given by Schalk and Van Couwelaar (1994).

The displacement volume was established directly after catch. The RMT1 samples consisted of mainly ostracods, copepods, small euphausiids, pteropods and chaetognaths; occasional gelatinous plankton, fish and large crustaceans were removed, and the sample was then vacuum-filtered before measurement. The RMT8 samples were sorted into major groups as fish, decapods, other crustaceans, cephalopods, hydromedusans, heteropods, and a residual group consisting of chaetognaths and gelatinous plankton. After draining for at least 5 min, the displacement volume of each group in the sample was measured. The pelagic

Table 2. *Station data (date and position at the beginning of sampling are given), mixed layer characteristics, depth of the pycnocline/nitracline, primary production, and the oxygen minimum zone for all RMT stations during the legs B0 (start SW monsoon), B1 (SW monsoon) and B2 (NE monsoon)*

		Position			Mixed layer						Oxygen minimum zone	
Station	Date	Latitude (N)	Longitude (E)	Type of water	Temperature (°C)	Nitrate (μM)	Chl (mg m^{-3})	Depth (m)	Pycnocline (m)	Primary production (g cm^{-2} per 24 h)	Depth range (m)	Lowest concentration (μM)
Start SW monsoon (1992)												
RS4	24-05	21°05′	38°08′	oligotrophic	26.7	0.0	0.1	42	42	nd	250–300	25 at 280 m
RS2	26-05	15°58′	41°36′	oligotrophic	30.0	0.0	0.2	10	43	nd	90–> 400	12 at 248 m
RS1	27-05	14°45′	42°16′	oligotrophic	30.1	0.1	0.2	13	59	0.6	90–500	16 at 197 m
BEM	29-05	12°45′	43°14′	oligotrophic	30.2	0.0	0.2	18	32	0.5	(125–> 145)	(56 at 143 m)
US2	02-06	10°00′	50°05′	recent upwelling	25.8	3.2	0.8	35	35	1.7	350–1160	23 at 496 m
US2	04-06	10°47′	51°58′	matured upwelling	26.3	0.0	4.7	24	24	2.8		
SW monsoon (1992)												
SB0	14-07	2°15′S	44°56′	mesotrophic	26.6	0.5	0.4	93	93	nd	(510–> 750)	(52 at 750 m)
SB1	15-07	0°04′S	45°39′	mesotrophic	26.6	0.4	0.4	84	101	0.7	(560–1390)	(46 at 1000 m)
US0	17-07	3°08′	48°17′	mesotrophic	26.4	0.7	0.4	58	96	1.2	1020–1095	41 at 1082 m
US1	19-07	7°02′	49°45′	upwelling	20.8	12.1	0.6	20	0	0.8	220–1160	24 at 598 m
US2	21-07	10°45′	51°53′	recent upwelling	18.8	17.6	0.3	64	0	0.9	200–1300	18 at 749 m
US1.5	29-07	9°27′	51°19′	upwelling	18.1	18.8	0.7	18	0	nd	200–220 + 560–> 705	30 at 701 m
US2	30-07	10°47′	52°00′	matured upwelling	22.2	12.5	2.5	33	0	1.1–2.8		
OFZ	26-07	7°33′	55°59′	downstream upwelling	25.5	3.7	0.4	66	0/169	1.0	200–220 +	23 at 802 m
SB2	27-07	6°45	54°30′	downstream upwelling	25.2	2.9	0.4	37	0/161	1.0	175–210 +	30 at 801 m
SI	31-07	12°01′	56°13′	downstream upwelling	23.2	8.9	0.7	36	0/142	0.8	170–1305	5 at 196 m
GA1	04-08	12°26′	49°48′	oligotrophic	28.9	0.0	0.2	21	48	nd	110–1440	10 at 301 m
GA2	05-08	12°12′	47°01′	oligotrophic	29.7	0.0	0.2	54	54	0.5	80–1415	14 at 125 m
NE monsoon (1993)												
SB3	13-01	1°55′	53°34′	mesotrophic	26.3	0.6	0.3	53	53	1.0	(160–225 + 450–> 750 m)	(49 at 750 m)
SB2	15-01	6°13′	52°27′	mesotrophic	26.8	0.3	0.3	38	38	1.0	600–1230	28 at 699 m

Table 2. *(continued)*

		Position			Mixed layer						Oxygen minimum zone	
Station	Date	Latitude (N)	Longitude (E)	Type of water	Temperature (°C)	Nitrate (µM)	Chl (mg m^{-3})	Depth (m)	Pycnocline (m)	Primary production (g cm^{-2} per 24 h)	Depth range (m)	Lowest concentration (µM)
US1	18-01	7°34′	50°30′	mesotrophic	26.6	0.3	0.3	67	67	0.6	180–1075	24 at 499 m
US2	20-01	10°51′	51°59′	mesotrophic	26.0	1.0	0.3	74	74	0.8	165–1400	20 at 749 m
SI	24-01	12°03′	54°58′	mesotrophic	26.0	0.9	0.3	77	77	0.9	150–1285	9 at 225 m
GA1	27-01	12°50′	50°05′	mesotrophic	25.8	0.5	0.5	92	92	1.3	130–1395	15 at 299 m
GA2	29-01	12°24′	46°58′	mesotrophic	25.2	2.2	0.6	62	62	1.0	120–1500	12 at 200 m
BEM	01-02	12°44′	43°14′	mesotrophic	26.1	0.3	0.4	58	58	nd	(130–> 150)	(78 at 151 m)
RS1	02-02	14°36′	42°20′	mesotrophic	25.6	0.2	1.0	76	76	1.4	95–> 300	13 at 149 m
RS2	03-02	15°55′	41°37′	mesotrophic	25.7	0.9	1.1	56	56	0.6	100–455	17 at 199 m

Hydrographic data averaged from CTD rosette casts (Hiehle and Baars, 1994), 1–6 per station. Primary production according to ^{14}C incubations [adapted from Veldhuis *et al.* (1997)]; nd, not determined. Oxygen minimum zone defined as the zone with oxygen concentrations below 43 µM (1 ml l^{-1}) as determined by the Sensormedics oxygen sensor on the CTD. (Note that casts sometimes were not deep enough to determine the lower limit.) Values were averaged for down- and upcasts to compensate for the lagging behind the sensor; if values were always greater than 43 µM, the zone less than 86 µM is given in parentheses. Lowest oxygen value originates from photometric Winkler titration on descrete samples during upcast.

swimming crab *Charybdis smithii* McLeay, 1838 often was found in large numbers and sometimes made up 50–90% of the displacement in the RMT8 catch. In this paper, biomass values from RMT8 samples include this swimming crab, but in the RMT8 data *C. smithii* is treated separately to avoid a bias in the crustacean biomass figures.

The weighed mean depth (WMD) of the zooplankton biomass in the sampled water column is calculated with

$$\mathrm{WMD} = \sum d_i v_i / V$$

where d_i is the depth of a sampled layer i (i.e. the mean of the upper and lower limit of the stratum), v_i is the displacement (ml m^{-2}) in this layer, and V is the total displacement in the sampled water column (after Roe *et al.*, 1984). Vertical shift of RMT8 biomass is assumed to be the result of diurnal vertical migration of pelagic organisms.

The B0 and B1 cruises together sampled 16 stations (Fig. 1), of which five had both the day and night series (RS2, RS1, GA2, US1 and US0); because of heavy weather and rough sea state during the SW monsoon (B1 cruise), sampling was hampered at some stations and no complete series could be made. The B2 cruise sampled ten stations, of which eight had complete day and night series (RS2, RS1, GA2, GA1, SI, SB2, US2 and US1). Stations where only one or two hauls were made (SB0, SB3, US1.5, OFZ) were omitted in the comparison of vertical distribution of biomass. Based on the similarity in hydrographic conditions encountered (Table 2), the following regions could be distinguished: the central and southern Red Sea (RS4, and RS1 and RS2, respectively), Bab-el-Mandab (BEM), the Gulf of Aden (GA1 and GA2), the northern Somali Basin (SI, OFZ, and SB2), the equatorial Somali Basin (SB0, SB1, SB3, and US0), and the Somali Current (US1, US1.5, and US2). It should be noted that Somali Current station US0 was assigned to the equatorial part of the Somali Basin. Average biomass values for the southern Red Sea, the Gulf of Aden, the northern and equatorial Somali Basin, and the Somali Current were calculated for pooled stations. Because of low sample numbers, the non-parametric Mann–Whitney U-test was used to test the difference in the biomass means. To study spatial and seasonal variation, only night samples were used, as most of the zooplankton are present at night in the upper layers, and underestimation because of net avoidance is less than during daytime.

RESULTS

General hydrography

Basic information on sampling locality and date, and hydrographic conditions at each station during the three cruises are given in Table 2. Oligotrophic conditions in the mixed layer, with temperatures of 26–30°C and low nitrate and chlorophyll concentrations were seen in the southern Red Sea at the onset of the SW monsoon in May, and in the Gulf of Aden during the SW monsoon in August. At the onset of the SW monsoon in early June during the B0 cruise, in the Somali Current upwelling conditions prevailed at about 10°N, 50°E (US2) and near 4°N, 49°E in (the vicinity of station US0). At the height of the SW monsoon in the second half of July during the B1 cruise, the upwelling at US0 had ceased and had migrated northwards. From 7° to 11°N the isotherms sloped up and surface temperatures dropped below 20°C. The strong upwelling conditions in the Somali Current led to high nutrient concentrations, but the primary production remained low because of a short residence time of the water. In areas outside the main axis of the Somali Current, the residence time was sufficiently long to allow the phytoplankton to bloom. At US2, maximum primary production was found. At the oceanic stations SI, OFZ and SB2 downstream from the upwelling located in the Great Whirl, primary production was also high, although nitrate concentrations were lower than at the stations in the Somali Current.

During the B2 cruise in January and February during the NE monsoon, mesotrophic conditions were seen in the mixed layer in all parts of the study area. In the southern Red Sea and the Gulf of Aden mixed-layer temperatures were 4–5°C lower than during the SW monsoon. At RS1, GA1 and GA2, strong local phytoplankton blooms developed in response to nutrient entrainment from the thermocline by winter cooling (Baars *et al.*, 1995), leading to a high primary production (Table 2). In the Somali Basin outside the Somali Current, nutrient and chlorophyll concentrations remained sufficiently high to lead to primary production rates about equal to or even higher than those of the preceding SW monsoon. In the Somali Current, however, the primary production was lower during the NE monsoon.

Throughout the study area an oxygen minimum zone (OMZ) was present during both monsoon seasons (Table 2). Except for the southern Somali Basin (SB0 and SB1) and at Bab-el-Mandab (BEM), the lowest values in the OMZ were generally well below 1 ml l^{-1}. In both the depth range of the OMZ and the value and depth of the minimal oxygen concentration, no important seasonal differences were seen.

Zooplankton biomass from RMT1 samples in the Somali Basin

In July 1992 in the equatorial part of the Somali Basin at SB0 and SB1, under mesotrophic conditions (Table 2), zooplankton biomass values from RMT1 samples over 0–300 m were moderate, 12.9 and 15.9 ml m^{-2} during daytime and 19.3 ml m^{-2} during night, respectively (Table 3). At US0 in the southernmost part of the Somali Current, a similar value was found during the night, whereas the daytime value was much greater because of a great amount of zooplankton in the upper 100 m (Table 3). At the height of the SW monsoon, upwelling conditions in the Somali Current were attained (Table 2), with high zooplankton displacements from RMT1 samples. At US1, US1.5 and US2, high biomass values were established, with a maximum of 38.0 ml m^{-2} in the 0–300 m layer by night at US2 (Table 3). Notably, the 0–100 m samples at these stations made a large contribution to the total zooplankton biomass. Because of patchiness in the distribution of the plankton, even higher biomasses occasionally were found, as at US2 in the 0–300 m daytime layer (Table 3). Downstream from the upwelling at SI, OFZ and SB2 located in the Great Whirl, the average zooplankton biomass in the 0–300 m layer by night was somewhat lower than in the upwelling area (28.5 vs 33.3 ml m^{-2}, Table 3). At these stations the vertical distribution of the zooplankton in the upper 300 m was less biased than at the upwelling stations US1 and US2, where the zooplankton concentration during night in the 0–100 m layer was much greater than in the 100–300 m layer (Fig. 2).

During the NE monsoon in the Somali Basin, zooplankton biomass values in the 0–100 m layer were lower than during the SW monsoon. In particular, at the stations in the Current area (US1 and US2) the biomass dropped by half. However, high biomass values in the upper layer both during day and night at SB2 during the NE monsoon contributed to a mean zooplankton biomass for the northern Somali Basin (SB2, SI, US2 and US1 pooled, Table 3) that was not significantly lower than during the SW monsoon.

Table 3. Zooplankton stock (displacement ml m^{-2}*) from RMT1 samples (*320 µm *mesh size) during SW and NE monsoons in* 0–100, 100–300, 300–(5)600 *and* 500–1000 m *depth layers for night (N) and in* 0–300 m *column for night and day (D)*

	SW monsoon May–June(B0) and July–Aug. (B1) 1992					NE monsoon Jan.–Feb. 1993 (B2)					
	N	N	N	N	D	N	N	N	N	N	D
	0–1	1–3	3–6	0–3	0–3	0–1	1–3	3–5	5–10	0–3	0–3
Red Sea, central											
RS4	3.2^{a}		4.1^{b}	7.3^{c}	–					x	x
Red Sea, south											
RS2	6.1	7.3^{d}	7.4^{e}	13.4^{f}	14.4	12.3	12.1	5.4	5.5	24.4	17.7
RS1	7.5	7.1^{d}	3.7^{e}	14.6^{f}	15.3	16.9	6.5	–	–	23.4	21.7
Mean	6.8			14.0	14.9	14.6				23.9	19.7
Bab-el-Mandab											
BEM				–	16.7^{g}					–	62.1^{h}
Gulf of Aden											
GA2	7.1	9.2	4.4	16.3	15.8	24.0	18.7	10.8	6.8	42.7	24.4
GA1	9.1	9.5	–	18.6	–	27.1	10.7	7.5	6.0	37.8	31.1
Mean	8.1			17.5		25.6				40.2	27.7
Somali Basin, north											
SB2	12.7	8.3	–	21.0	7.7^{i}	29.3	6.0	4.7	12.7	35.3	22.6
SI	13.9	22.0	5.4	35.9	14.0^{i}	8.1	5.8	6.6	12.4	13.9	9.5
OFZ				–	16.6^{i}					x	x
Mean	13.3			28.5	12.8	18.7				24.6	16.1
Somali Basin, current											
US2	37.3	0.7	–	38.0	61.6	11.1	18.5	11.2	7.6	29.6	16.6
US1.5	17.7	–	–		–					x	x
US1	23.0	5.5	9.2	28.5	6.7	15.2	5.5	5.7	7.3	20.7	11.8
Mean	26.0			33.3	34.2	13.1				25.1	14.2
Somali Basin, equator											
US0	7.9	8.8	2.5	16.7	27.2					x	x
SB3				x	x	9.2					–
SB1	17.0	2.3	6.0	19.3	12.9					x	x
SB0				–	15.9					x	x
Mean	12.5	5.6	4.3	18.0	18.7						
Southern Red Sea and Gulf of Aden											
Mean				15.7						32.1	
SD				2.3						9.7	
n				4						4	
Northern Somali Basin (north + current)											
Mean				30.8†						24.9†	
SD				7.7						9.5	
n				4						4	

*Depth (× 100 m).

†No significant difference at the 2.5% level (Mann–Whitney U-test) between season's means for pooled stations US1, US2, SI and SB2 in the northern Somali Basin and stations RS2, RS1, GA2 and GA1 in the southern Red Sea and the Gulf of Aden.

Deviating depths: ^{a}0–200 m, ^{b}200–500 m, ^{c}0–500 m, ^{d}100–400 m, ^{e}400–600 m, ^{f}0–400 m, ^{g}0–160 m, ^{h}0–170 m, ^{i}0–100 m. x, Station not occupied; –, layer not sampled.

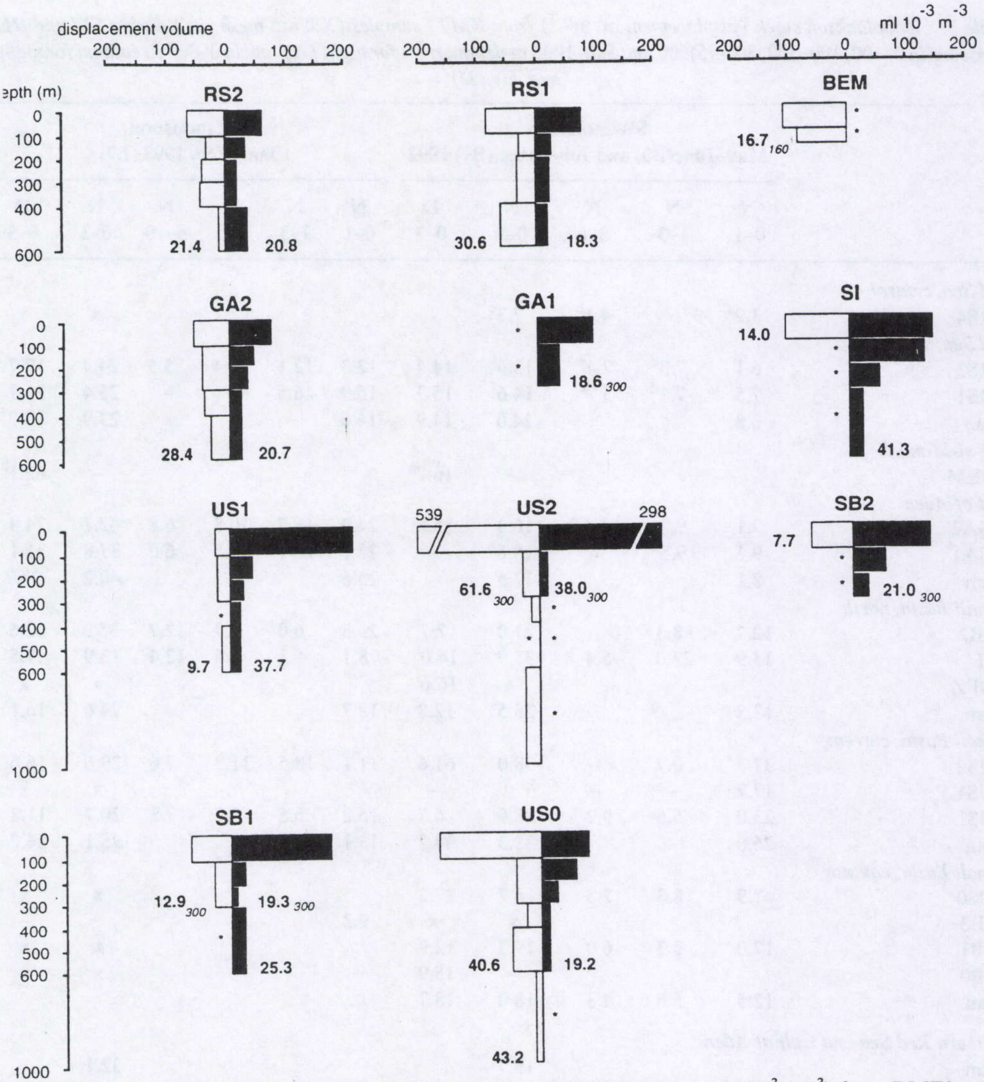

Fig. 2. Vertical distribution of zooplankton biomass (displacement ml 10^{-3} m^{-3}) from RMT1 hauls (320 μm mesh) during the SW monsoon (B0 and B1 cruise combined) for day (open bars) and night (solid bars). Vertical axes represent length of sampled water column. Numbers in bold indicate biomass (displacement ml m^{-2}) in 0–600 m water column, unless otherwise indicated with suffix; *, more than one sample missing, no calculations made.

Zooplankton biomass from RMT1 samples in the southern Red Sea and the Gulf of Aden

In the period May–August 1992 during the SW monsoon, the zooplankton biomass in RMT1 samples during night from 0–300 m (Table 3) increased from the central Red Sea (7.3 ml m^{-2}) to the southern Red Sea (mean 14.0 ml m^{-2}) and the Gulf of Aden (mean 17.5 ml m^{-2}). In both these areas, where oligotrophic conditions prevailed in the mixed layer (Table 2), regional variance in biomass appeared to be low, as a result of similarity in biomass values from comparable layers. The vertical distribution of the zooplankton (Fig.

2) showed a normal pattern with high concentrations in the upper layers and low concentrations deeper in the water column during night as well as during day. At BEM the RMT1 daytime catches consisted mainly of large numbers of chaetognaths, and the biomass concentration decreased with depth (Fig. 2).

In January–February 1993 during the NE monsoon, in the Red Sea and the Gulf of Aden under mesotrophic mixed layer conditions (Table 2), zooplankton displacements in the upper 100 m were doubled and even tripled compared with the SW monsoon. The mean zooplankton biomass in the 0–300 m layer by night increased to 23.9 ml m^{-2} in the southern Red Sea, and to 40.2 ml m^{-2} in the Gulf of Aden (Table 3). The vertical distribution of the zooplankton at RS1, RS2, GA1 and GA2 (Fig. 3) showed again the normal pattern, with high biomass concentrations in the upper layers and decreasing with depth. Samples below 500 m made only a small contribution to the total zooplankton biomass. At BEM very high biomass values were established, particularly in the lower, near-bottom stratum where the concentration was almost three times higher than in the 0–100 m layer (Fig. 3). Here the zooplankton in the RMT1 samples mainly consisted of hydromedusans. Compared with the first cruise in May, the zooplankton biomass at this station has almost quadrupled (Table 3). By pooling of the stations in the Red Sea and the Gulf of Aden, mean zooplankton biomass during the NE monsoon was about twice as high as during the SW monsoon (Table 3).

Macrozooplankton and micronekton biomass from RMT8 samples

During the SW monsoon, biomass from RMT8 samples showed low values (4.5 ml m^{-2}) for the 0–300 m layer at night (Table 4) in the central Red Sea and increased towards the south, with mean values somewhat higher in the southern Red Sea (9.0 ml m^{-2}) than in the Bab-el-Mandab (8.0 ml m^{-2}) and the Gulf of Aden (7.0 ml m^{-2}). Biomass was rather similar throughout the Somali Basin, with mean values for the 0–300 m layer ranging from 6.3 to 7.3 ml m^{-2}. Particularly high biomasses in the upper 100 m were found in the Somali Current at US1.5 and US2 and downstream from the upwelling at SI. During the NE monsoon, macrozooplankton and micronekton biomass from 0 to 300 m at night in the southern Red Sea were lower than at the onset of the SW monsoon, whereas at BEM and in the Gulf of Aden higher values were found (Table 4). In the Somali Current in this season the biomass was somewhat higher than during the SW monsoon. Only at the oceanic stations SI and SB2 during the NE monsoon were lower biomass values recorded. After pooling of stations in the southern Red Sea and the Gulf of Aden there was no significant difference in the mean biomass of macrozooplankton and micronekton during the SW and the NE monsoons. In the northern Somali Basin also, no significant seasonal difference in macrozooplankton and micronekton biomass was found (Table 4).

Biomass of fish and crustaceans from the RMT8 samples

In the southern Red Sea the average biomasses (0–300 m night) of mesopelagic fish and crustaceans dropped considerably from the SW to the NE monsoon (Table 5). In the Gulf of Aden only a small seasonal difference was found in the fish biomass, but the crustacean biomass more than doubled. In the Somali Current higher values for both groups were found during the NE monsoon, whereas in the northern part of the Somali Basin average biomasses remained similar. During the SW monsoon the pelagic swimming crab *C. smithii* was found

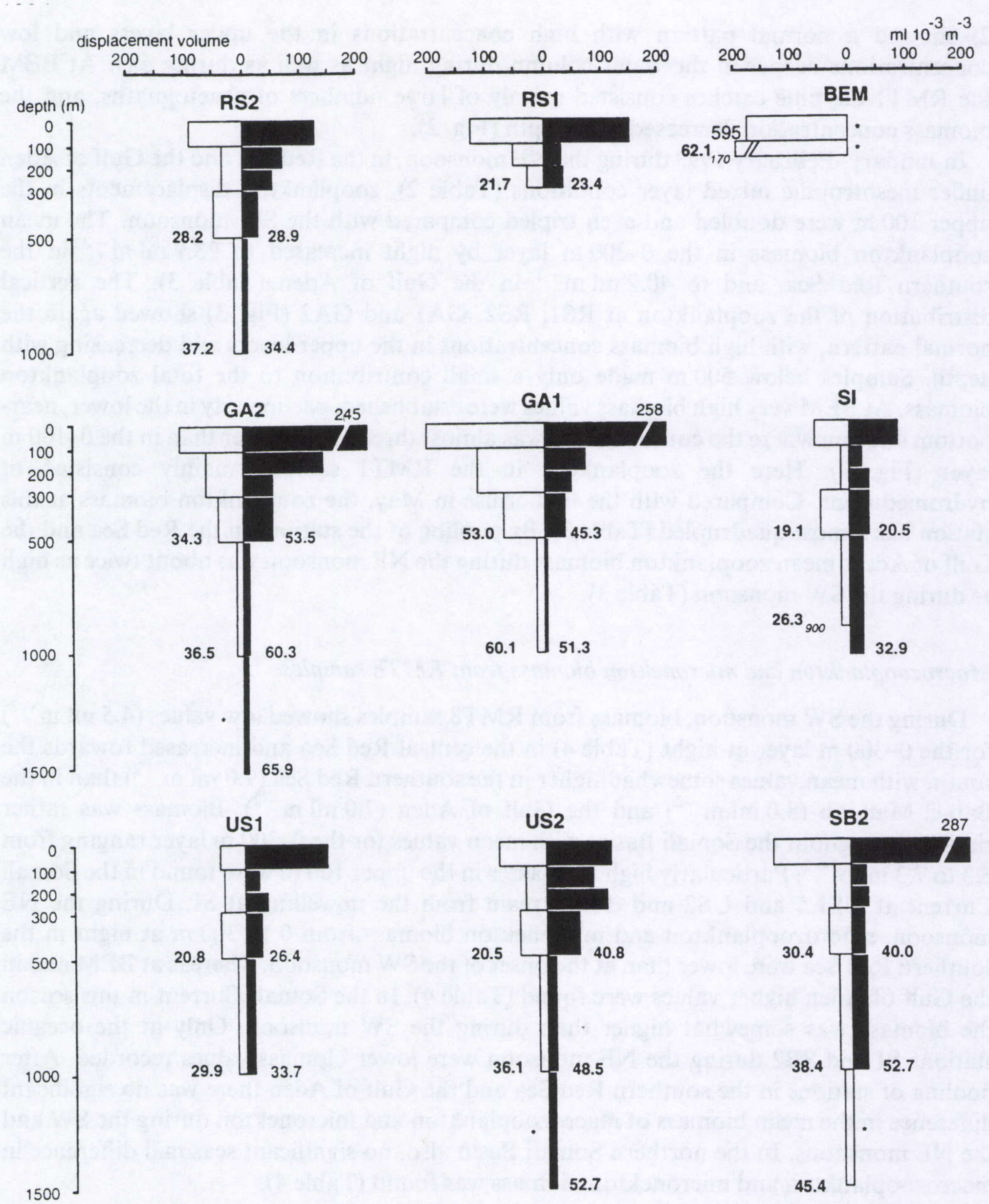

Fig. 3. Vertical distribution of zooplankton biomass (displacement ml 10^{-3} m^{-3}) from RMT1 hauls (320 µm mesh) during the NE monsoon (B2 cruise) for day (open bars) and night (solid bars). Vertical axes represent length of sampled water column. Numbers in bold indicate biomass (displacement ml m^{-2}) in 0–500 m, 0–1000 m and 0–1500 m water column, unless otherwise indicated with suffix; *, more than one sample missing, no calculations made.

Table 4. Macrozooplankton and micronekton stock (displacement ml m^{-2}*) from RMT8 samples (4.5 mm mesh size) during SW and NE monsoons in 0–100, 100–300, 300–(5)600 and 500–1000 m depth layers during night (N) and in 0–300 m column for night and day (D)*

	SW monsoon May–June (B0) and July–Aug. (B1) 1992					NE monsoon Jan–Feb. 1993 (B2)					
	N	N	N	N	D	N	N	N	N	N	D
	0–1*	1–3	3–6	0–3	0–3	0–1	1–3	3–5	5–10	0–3	0–3
Red Sea, central											
RS4	1.9[a]		2.6[b]	4.5[c]						x	
Red Sea, south											
RS2	4.5	5.6[d]	2.1[e]	10.1[f]		2.3	3.3	1.1	2.2	5.7	
RS1	2.0	5.9[d]	1.2[e]	7.9[f]		6.2	0.8	–	–	7.0	
Mean	3.3			9.0		4.3				6.4	
Bab-el-Mandab											
BEM				–	8.0[g]					–	12.2[h]
Gulf of Aden											
GA2	2.1	5.0	2.6	7.1		3.9	6.3	6.6	10.3	10.3	
GA1	2.4	4.5	–	6.9		4.7	3.3	5.1	8.7	8.0	
Mean	2.3			7.0		4.3				9.1	
Somali Basin, north											
SB2	2.5	4.6	–	7.1		2.7	1.8	2.0	7.3	4.4	
SI	4.0	3.5	2.5	7.5		1.6	3.3	2.1	5.6	4.9	
OFZ				–						x	
Mean	3.2			7.3		2.2				4.6	
Somali Basin, current											
US2	4.1	3.2	–	7.3		1.6	5.5	5.7	4.4	7.2	
US1.5	5.9	–	–							x	
US1	2.3	2.9	5.3	5.2		2.5	4.1	3.1	3.4	6.6	
Mean	4.1			6.3		2.1				6.9	
Somali Basin, equator											
US0	2.0	3.4	2.3	5.4						x	
SB3				x		2.3					
SB1	3.6	3.9	6.0	7.5						x	
SB0				–						x	
Mean	2.8			6.5							
Southern Red Sea and Gulf of Aden											
Mean				6.8†						5.8†	
SD				1.1						1.3	
n				4						4	
Northern SomaliI Basin (north + current)											
Mean				8.0†						7.8†	
SD				1.5						1.9	
n				4						4	

*Depth (× 100 m).

†No significant difference at the 2.5% level (Mann–Whitney U-test) between season's means for pooled stations US1, US2, SI and SB2 in the northern Somali Basin and stations RS2, RS1, GA2 and GA1 in the southern Red Sea and the Gulf of Aden.

Deviating depths: [a]0–200 m, [b]200–500 m, [c]0–500 m, [d]100–400 m, [e]400–600 m, [f]0–400 m, [g]0–160 m, [h]0–170 m, x, Station not occupied; –, layer not sampled. By consequence of diurnal vertical migration and probable net avoidance, daytime depth distributions are not considered, except at BEM.

Table 5. Average biomass (displacement ml m^{-2}*) of major macrozooplankton and micronekton groups in 0–300 m depth layer (0–400 m at RS1 and RS2) at night during SW monsoon (cruises B0 and B1) and NE monsoon (cruise B2) in the southern Red Sea, Bab-el-Mandab, Gulf of Aden and the Somali Basin*

	Small mesopelagic fish	Crustaceans	*Charybdis smithii*	Rest
Southern Red Sea (RS1, RS2)	1.6/0.2	5.4/1.9	–/–	2.0/4.2
Bab-el-Mandab (BEM)	0.1/<0.1	0.1/–	–/–	7.3/12.2
Gulf of Aden (GA1, GA2)	2.0/1.4	1.5/3.2	<0.1/0.6	3.6/3.9
Somali Basin				
current (US1, US2)	1.5/2.5	0.8/1.2	–/1.8	3.3/1.4
north (SI, SB2)	1.6/1.6	1.1/0.9	2.1/0.9	2.1/1.3
equator (US0, SB1)	1.0/x	1.1/x	3.4/x	0.5/x
Northern Somali Basin	1.4/1.9	1.0/1.2	1.1/1.1	2.8/1.4
Southern Red Sea and Gulf of Aden	1.8/0.8	3.5/2.6	<0.1/0.3	2.8/4.1

'Crustaceans' are predominantly Decapoda and Euphausiacea; *Charybdis smithii* is a swimming crab species (family Portunidae); 'rest' consists mainly of Hydromedusae, Chaetognatha and Tunicata. –, Group not present; x, stations not occupied. Values for B0 and B1 cruises left of slash, values for B2 cruise right of slash.

south in the Somali Basin and downstream in the Somali Current, but was absent from the upwelling area. The animals were small (mean carapace width 25 mm) and occurred in high densities in the upper 200 m at night. At SB1, US0, SI and SB2 this species made up over 50% of the RMT8 displacement volume (see also Table 5). During the NE monsoon *C. smithii* also occurred in the Gulf of Aden, the northern Somali Basin (SI and SB2) and the Somali Current (US1 and US2). The animals were larger than in the preceding season (mean carapace width 52 mm), though densities were considerably lower, and the mean biomass in the northern Somali Basin was as large as during the SW monsoon (Table 5).

The vertical distribution of the zooplankton and micronekton

During both monsoons the concentration of the zooplankton from RMT1 samples was high in the upper layers during day and night, and decreased with depth (Figs 2 and 3). The weighed mean depth (WMD) of the biomass over 0–600 m during the SW monsoon (Table 6) ranged from 162 to 199 m during night in the Somali Basin and from 204 to 282 m in the Gulf of Aden and the Red Sea. On average, the WMD during the day was 47 m lower than during night. The mean WMD at night was shallower during the NE monsoon, mainly because the shallower WMD in the Red Sea and the Gulf of Aden. However, the day–night difference over either 0–500 m or 0–1000 m was similar to that during the SW monsoon (Table 6). The WMD of the biomass (Table 6) and the vertical profiles of the zooplankton (Figs 2 and 3) in the Red Sea, the Gulf of Aden and the Somali Basin indicated that a large part of the zooplankton community occurred in the OMZ (Table 2) during day as well as during night both during the SW and NE monsoons.

The vertical distribution of the macrozooplankton and micronekton biomass from RMT8 samples during both monsoons showed a normal pattern, with high concentrations in the upper layers at night and high concentrations deeper in the water column during the day (Figs 4 and 5), because of diel vertical migration. The average day–night difference of the WMD of the biomass over 0–5(6)00 m (Table 7) was greater during the SW monsoon (128 m) than during the NE monsoon (67 m), and the WMD for both day and night also was shallower during the NE monsoon. The macrozooplankton and micronekton could well

Table 6. Weighed mean depth (in m) of mesozooplankton biomass (RMT1 samples) during day (D) and night (N) and the day–night difference (Δ)

	SW monsoon May–June (B0) and July–Aug. (B1) 1992 (0–600 m)			NE monsoon Jan.–Feb. (B2) 1993 (0–500 m)			NE monsoon Jan.–Feb. (B2) 1993 (0–1000 m)		
Station	D	N	Δ	D	N	Δ	D	N	Δ
RS2	225	282	−57	223	165	+58	352	258	+94
RS1	296	218	+78	107*	93*	+14*			
GA2	273	204	+69	211	166	+45	243	232	+11
GA1	—	145*		179	143	+36	248	215	+33
US2	73*	65*	+8*	245	215	+30	355	300	+55
US1	258	199	+59	256	162	+94	408	291	+117
US0	250	162	+88	x	x	x	x		
SB1	118*	63*	+55*	x	x	x	x		
SB2	–	110*		201	96	+105	296	266	+30
SI	–	175		254	209	+45	377	416	−39
Mean	260	213	47	224	165	59	325	282	43
	n=5	*n*=5		*n*=7	*n*=7		*n*=7	*n*=7	

Data from standard columns at ten stations during SW monsoon (B0 and B1 cruises: 0–600 m) and NE monsoon (B2 cruise: 0–500 m and 0–1000 m) except for *0–300 m column. —, Layer not sampled; –, one or more samples missing; x, station not occupied. For calculation of the mean WMD only complete day and night sets are used.

stay in the OMZ (Table 2) both during the day and night, as indicated by the vertical profiles (Figs 4 and 5) and the WMD (Table 7) of the biomass.

DISCUSSION

Pooled data from the IIOE 1959–1965 in the area between 5°–15°N and 45°–55°E (see Cushing, 1973: Figs 1 and 2) and data from the INDEX 1979 (see Smith and Codispoti, 1980) indicate that primary productivity in the northern Somali Basin during the NE monsoon is about 25–30% of the productivity during the SW monsoon (Fig. 6). The general idea for the ecosystem in the northern Somali Basin is that the SW monsoon is the rich period and the NE monsoon the poor period. However, the present study showed that the primary production rates during the NE monsoon were much higher than expected, close to those during the SW monsoon. At least, the rather small seasonal difference was due to the high production at US2, SI and SB2 during the NE monsoon, which was almost as high as during the SW monsoon (Table 2). Enrichment of the mixed layer by winter cooling could be the reason for the subsequent high primary productivity during the NE monsoon.

Zooplankton biomasses in the northern Somali Basin during the IIOE 1959–1965 and the INDEX 1979 show very small seasonal differences (Fig. 6). After pooling the northern Somali Basin stations US1, US2, SI and SB2, the mean zooplankton biomasses from RMT1 catches (0–300 m, night) during the SW and NE monsoon were not significantly different (Table 3). Thus, results from previous expeditions and the present study paradoxically show that despite the lower mean primary production, the NE monsoon does not clearly provide a poor secondary trophic level measured by zooplankton biomass. In addition to high

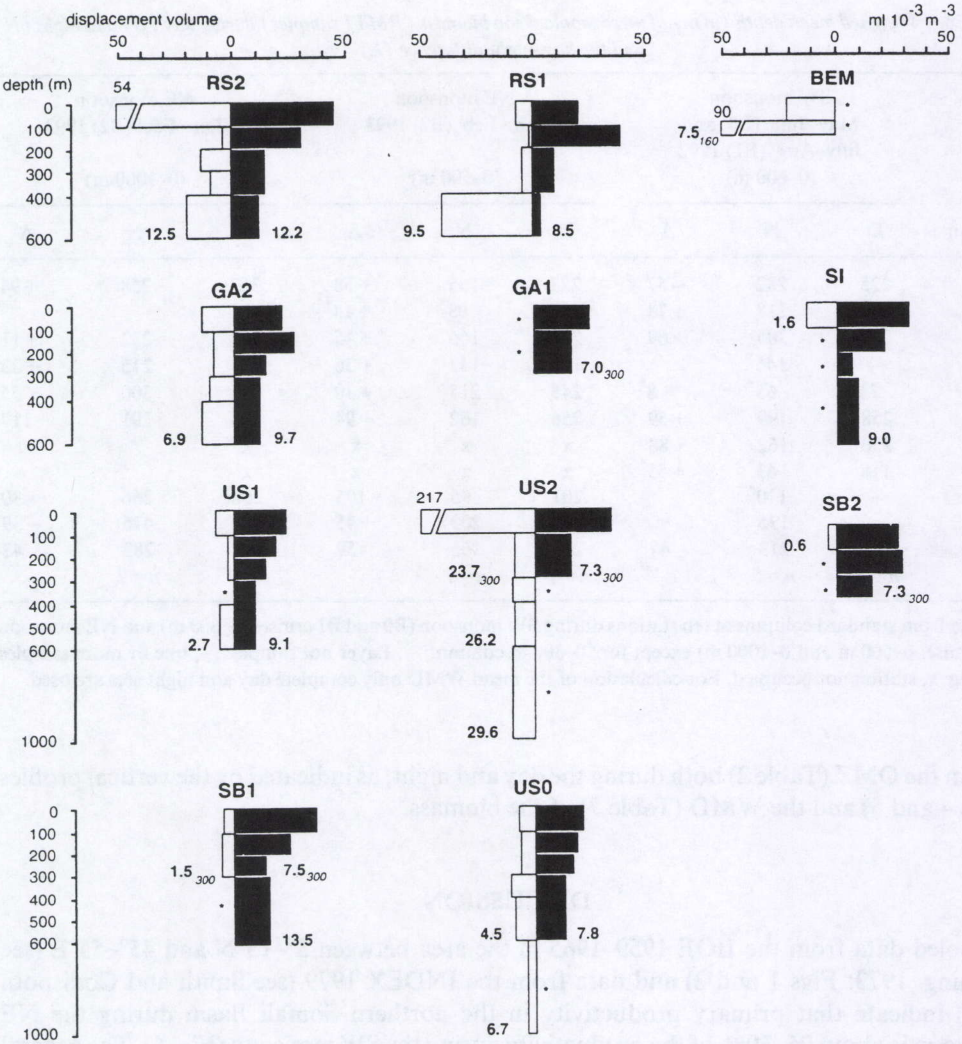

Fig. 4. Vertical distribution of macrozooplankton and micronekton biomass (displacement ml 10^{-3} m^{-3}) from RMT8 hauls (4.5 mm mesh) during SW monsoon (B0 and B1 cruise combined) for day (open bars) and night (solid bars). Vertical axes represents length of sampled water column. Numbers in bold indicate biomass (displacement ml m^{-2}) in 0–600 m and 0–1000 m water column, unless otherwise indicated with suffix; *, more than one sample missing, no calculations made.

primary production during the NE monsoon induced by winter cooling, horizontal advection of zooplankton from the Gulf of Aden and the NW Arabian Sea also could explain the high zooplankton biomasses in the Somali Basin. In contrast to the Somali Basin, for example, distinct seasonal variation in primary and secondary production is found in the eastern Banda Sea in Indonesia, where the pelagic system is ruled by alternating monsoons with coastal upwelling in summer (Zijlstra *et al.*, 1990). For this area a comparison with the present results from the Somali Basin was possible because the same

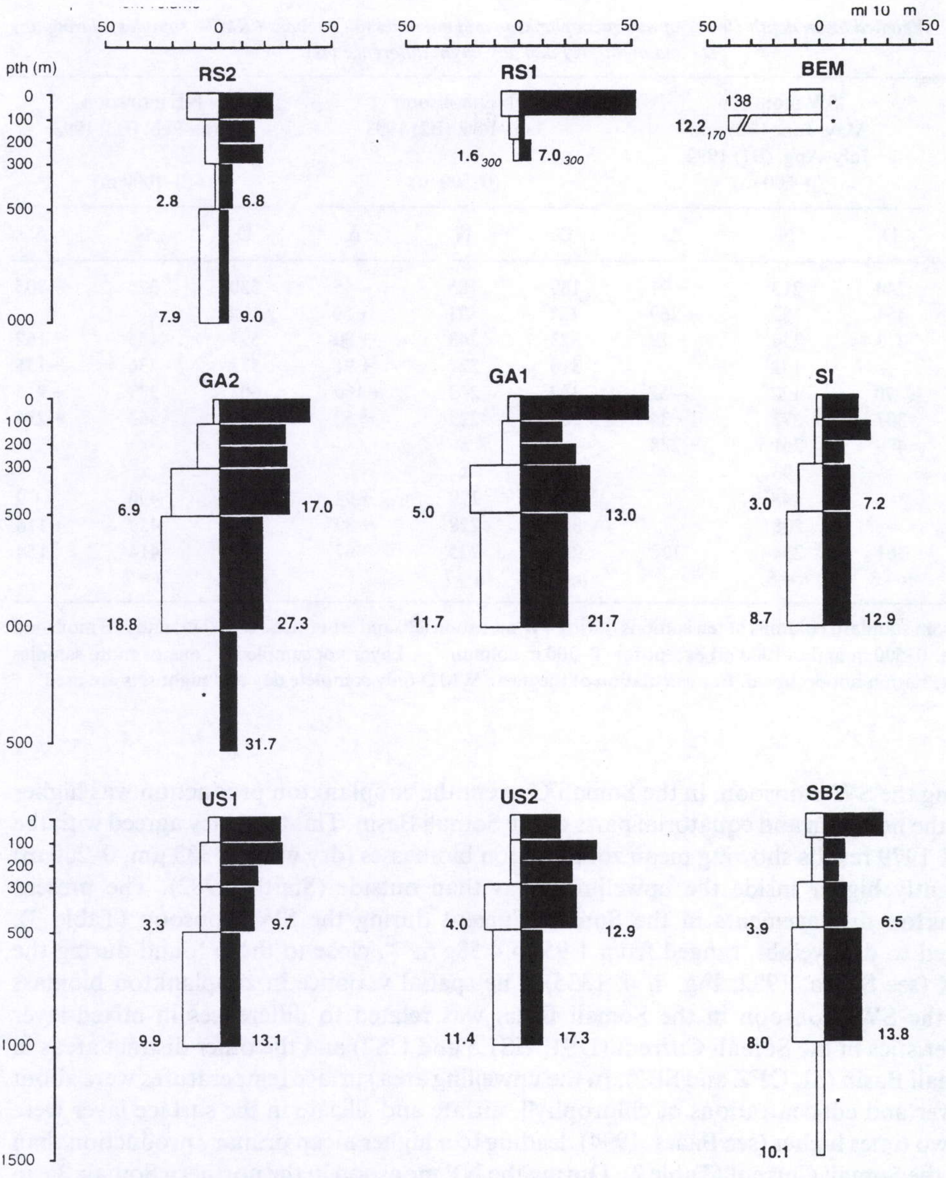

Fig. 5. Vertical distribution of macrozooplankton and micronekton biomass (displacement ml 10^{-3} m^{-3}) from RMT8 hauls (4.5 mm mesh) during NE monsoon (B2 cruise) for day (open bars) and night (solid bars). Vertical axes represents length of sampled water column. Numbers in bold indicate biomass (displacement ml m^{-2}) in 0–500 m, 0–1000 m and 0–1500 m water column, unless otherwise indicated with suffix; *, more than one sample missing, no calculations made.

equipment and methods were used [see Gieskes *et al.* (1990) for primary production and Schalk (1987) for zooplankton]. During the SE monsoon (the upwelling season) in the eastern Banda Sea, mean primary production (as well as mean zooplankton biomass from the RMT1) is about twice as high as during the NW monsoon (Fig. 6), thus displaying a clear seasonal response.

Table 7. Weighed mean depth (in m) of macrozooplankton and micronekton biomass (RMT8 samples) during day (D) and night (N) and day–night difference (Δ)

	SW monsoon May–June (B0) and July–Aug. (B1) 1992 (0–600 m)			NE monsoon Jan.–Feb. (B2) 1993 (0–500 m)			NE monsoon Jan.–Feb. (B2) 1993 (0–1000 m)		
Station	D	N	Δ	D	N	Δ	D	N	Δ
RS2	244	213	+21	139	185	−45	530	325	+205
RS1	451	182	+269	121*	71*	+50*			
GA2	313	234	+79	323	243	+80	597	435	+162
GA1	—	172*		318	227	+91	572	436	+136
US2	70*	122*	−52*	372	263	+109	603	388	+215
US1	307	273	+34	281	229	+52	597	363	+234
US0	489	261	+228	x	x		x	x	
SB1	–	193		x	x		x	x	
SB2	–	148*		293	199	+94	499	490	+9
SI	–	208		326	228	+89	575	459	+116
Mean	361	234	128	293	225	67	567	414	154
	n=5	*n*=5		*n*=7	*n*=7		*n*=7	*n*=7	

Data from standard columns at ten stations during SW monsoon (B0 and B1 cruises: 0–600 m) and NE monsoon (B2 cruise: 0–500 m and 0–1000 m) except for *0–300 m column. —, Layer not sampled; –, one or more samples missing; x, station not occupied. For calculation of the mean WMD only complete day and night sets are used.

During the SW monsoon, in the Somali Current the zooplankton production was higher than in the northern and equatorial parts of the Somali Basin. This tendency agreed with the INDEX 1979 results showing mean zooplankton biomasses (dry weight, 333 µm, 0–200 m) significantly higher inside the upwelling areas than outside (Smith, 1982). The present zooplankton displacements in the Somali Current during the SW monsoon (Table 3), converted to dry weight, ranged from 1.95 to 4.58g m^{-2}, close to those found during the INDEX (see Smith, 1982: Fig. 4, p. 1335). The spatial variance in zooplankton biomass during the SW monsoon in the Somali Basin was related to differences in mixed-layer characteristics in the Somali Current (US1, US1.5 and US2) and the other distinct areas in the Somali Basin (SI, OFZ and SB2). In the upwelling area surface temperatures were about 5°C lower and concentrations of chlorophyll, nitrate and silicate in the surface layer were about two times higher (see Baars, 1994), leading to a higher mean primary production than outside the Somali Current (Table 2). During the NE monsoon in the northern Somali Basin mixed-layer characteristics were less heterogeneous.

Although the zooplankton from the RMT1 catches in the northern Somali Basin showed smaller seasonal difference in biomass than expected from the lower primary production, mean zooplankton displacements from 200 µm vertical net hauls (0–150 m) in the northern Somali Basin were 47.1 ml m^{-2} during the SW monsoon and 23.8 ml m^{-2} during the NE monsoon (Baars *et al.*, 1995). Overestimation as a result of patchiness and contamination by phytoplankton during the productive SW monsoon could explain at least part of this strong seasonal difference. Standard numbers of copepods in the northern Somali Basin from the 200 µm vertical net catches were four times higher during the SW monsoon than during the NE monsoon, whereas in the RMT1 catches they remained about the same (M. A. Baars,

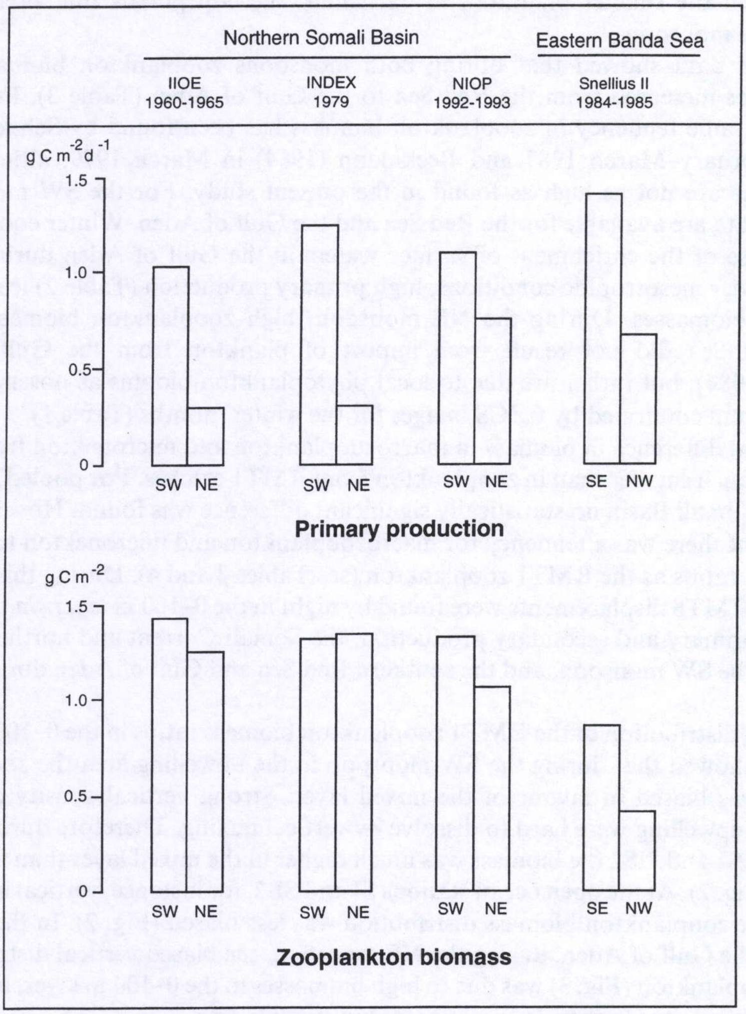

Fig. 6. Seasonal variation in primary production (g C m^{-2} day^{-1}) and zooplankton biomass (g C m^{-2}) in the northern Somali Current and the eastern Banda Sea [adapted and modified from Baars *et al.* (1995)]. IIOE data from Cushing (1973), interpolated for three squares between 5° and 15°N, and 45° and 55°E. Number of zooplankton night hauls was five for SW and five for the NE monsoon (0–200 m, 330 µm mesh). INDEX data from Smith and Codispoti (1980) with 23 vs 12 ^{14}C incubations, and from Smith and Lane (1981), with 16 vs 8 night hauls (0–200 m, 333 µm mesh). NIOP data for primary production from Veldhuis *et al.* (1997), with 12 vs 10 ^{14}C incubations, and the present results for zooplankton from pooled stations US1, US2, SI and SB2 (0–300 m night catches, 320 µm mesh). SNELLIUS II data from Gieskes *et al.* (1990), with 16 ^{14}C incubation for the SE and 16 for the NW monsoon (converted from 12 to 24 h by 0.75), and from Schalk (1987), with 16 vs 16 zooplankton night hauls (0–300 m, 320 µm mesh). Zooplankton displacements (NIOP) converted to carbon by 0.043 and from dry weight (INDEX) to carbon by 0.4 (Baars *et al.*, 1990).

personal communication, 1995; see also Baars and Brummer, 1995). A seasonal size difference of the copepods could be one explanation. Apparently, the RMT1 net was too coarse to catch the smaller plankton, in particular, the copepodids that predominated during the SW monsoon.

The present data showed that during both monsoons zooplankton biomasses from RMT1 samples increased from the Red Sea to the Gulf of Aden (Table 3). For the NE monsoon the same tendency in zooplankton biomass has been found by Schneider *et al.* (1994) in February–March 1987 and Beckmann (1984) in March 1979, although their biomass values are not as high as found in the present study. For the SW monsoon no comparable data are available for the Red Sea and the Gulf of Aden. Winter cooling seems to be the cause of the enrichment of surface waters in the Gulf of Aden during the NE monsoon. Under mesotrophic conditions, high primary production (Table 2) leads to high zooplankton biomasses. During the NE monsoon, high zooplankton biomasses in the southern Red Sea did not result from import of plankton from the Gulf of Aden (Beckmann, 1984), but rather are due to local phytoplankton blooms as observed during the B2 cruise and confirmed by CZCS images for the winter months (Table 1).

The seasonal difference in biomass in macrozooplankton and micronekton from RMT8 samples was much smaller than in zooplankton from RMT1 catches. For pooled stations in the northern Somali Basin no statistically significant difference was found. However, in the Somali Current there was a tendency for macrozooplankton and micronekton to show the same seasonal ratios as the RMT1 zooplankton (see Tables 3 and 4). During this study the highest mean RMT8 displacements were found by night in the 0–100 m layers in those areas with highest primary and secondary production: the Somali Current and northern Somali Basin during the SW monsoon, and the southern Red Sea and Gulf of Aden during the NE monsoon.

The vertical distribution of the RMT1 zooplankton biomass ratios in the 0–100 and 100–300 m layers showed that during the SW monsoon in the upwelling area the zooplankton distribution was biased in favour of the mixed layer. Strong vertical density differences caused by the upwelling were hard to dissolve by vertical mixing. Therefore during the SW monsoon at US1 and US2 the biomass was much higher in the mixed layer than in the 100–300 m layer (Fig. 2). At the open ocean stations SI and SB2, for instance, vertical mixing was deeper and the zooplankton biomass distribution was less biased (Fig. 2). In the southern Red Sea and the Gulf of Aden, during the NE monsoon, the biased vertical distribution of the RMT1 zooplankton (Fig. 3) was due to high biomasses in the 0–100 m layer, in response to the high primary production in local phytoplankton blooms.

The vertical distribution of macrozooplankton and micronekton biomass in RMT8 samples showed the normal day–night difference owing to the performance of diurnal vertical migration of pelagic organisms. Remarkably, during both monsoons, vertical migration for a part took place in the oxygen minimum zone. Apparently, oxygen concentrations in the Red Sea, the Gulf of Aden and the Somali Basin were not too low to prevent at least some of the macrozooplankton and micronekton occurring in the OMZ by day; this group consisted particularly of crustaceans and myctophids.

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CHAPTER 2

Vertical distribution and feeding pattern of Euphausiacea (Crustacea) in the eastern Banda Sea (Indonesia) during the SE and NW monsoons

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Vertical distribution and feeding pattern of Euphausiacea (Crustacea) in the eastern Banda Sea (Indonesia) during the SE and NW monsoons

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Abstract. The vertical distribution of Euphausiacea (Crustacea) in the eastern Banda Sea (Indonesia) during the SE and NW monsoon seasons was studied. In August 1984 and February/March 1985, stratified day and night sampling was carried out between 0 and 500 m at four stations. A total of 31 species was found, of which most were present in both monsoon seasons. Species with a high presence in samples and performing diurnal vertical migration in both monsoon seasons were *Euphausia diomedeae*, *Euphausia pseudogibba*, *Thysanopoda monacantha*, *Thysanopoda tricuspidata* and *Nematoscelis microps*. Species with a high presence in samples showing no diurnal vertical migration in both monsoon seasons were *Euphausia similis*, *Nematobrachion boopis*, *Nematoscelis tenella*, *Stylocheiron maximum* and *Thysanopoda orientalis*. The density of Euphausiacea at the sampled stations was higher, but more heterogeneous, in the nutrient-enriched SE monsoon period than in the relatively nutrient-poor NW monsoon season, when densities were lower and more similar. The vertical distributions and diurnal vertical migration of species did not show a unanimous and strong response to seasonal hydrographic differences. The day–night depth distribution pattern of the Euphausiacea population in the upper 500 m is largely the same in both seasons, with comparable migration ranges. Some species showed a somewhat upward shifted depth distribution in the nutrient-enriched period. For mesopelagic and bathypelagic species especially, food resources were then favourable in the upper layers, as indicated by rare records of *Thysanopoda cristata*. Analyses of stomach contents showed mainly a nocturnal feeding pattern for the diurnal vertical migrating species and a continuous feeding pattern for the non-migrating species.

Introduction

Theme 3 of the Indonesian–Dutch Snellius-II Expedition (1984–1985) studied the pelagic ecosystem in the eastern Banda Sea and the northern Arafura Sea (Indonesia) during the SE and NW monsoon seasons in August 1984 and February/March 1985, respectively (Zijlstra and Baars, 1987). The alternating monsoon winds caused important changes in the hydrography. Surface currents in the Banda and Arafura Seas are predominantly westward during the SE monsoon and eastward during the NW monsoon. Wyrtki (1961) postulated the occurrence of upwelling above the deep basins of the region during the SE monsoon. In his model, downwelling occurs where the east-going surface waters are obstructed in eastward and sideways outflow during the NW monsoon (Figure 1). Hydrographic study revealed that upwelling during the SE monsoon season was limited to the upper 150 m and occurs locally only (Zijlstra *et al.*, 1990). In August, the fastest upward displacement was found above the Aru Basin (average 345 cm day^{-1}). In the shallow part of the Arafura Sea SW of Irian Jaya (Figure 2), a strong coastal upwelling of ~300 cm day^{-1} was observed; this is probably the most important upwelling in the area (Wetsteyn *et al.*, 1990). In the same period, above the Weber Deep and the Banda Basin, upward displacement was moderate, 0–42 cm day^{-1}, not really confirming

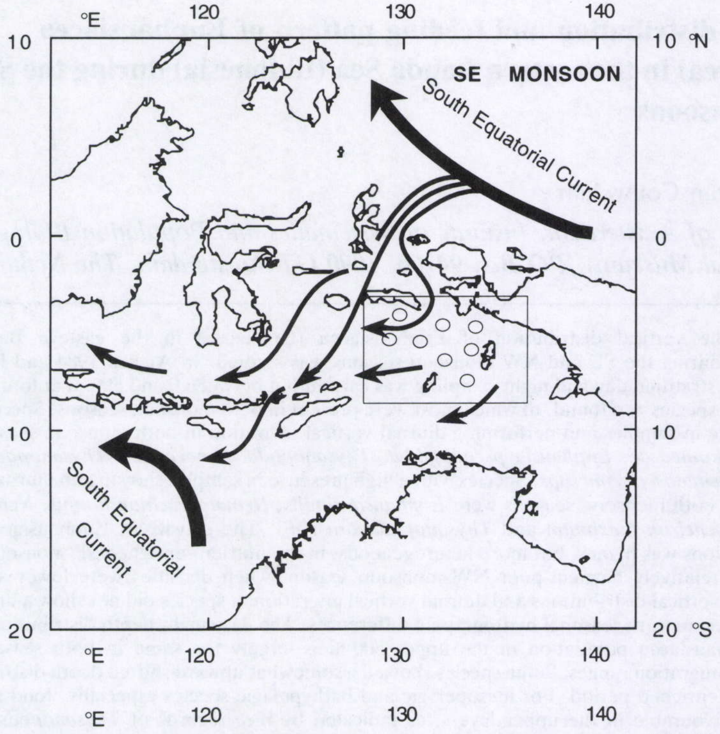

Fig. 1. Surface current patterns in the Indonesian waters during the SE monsoon (**above**) and NW monsoon (**below**). Open circles mark upwelling conditions, closed circles mark downwelling conditions (after Wyrtki, 1958). The rectangle encloses the investigated area.

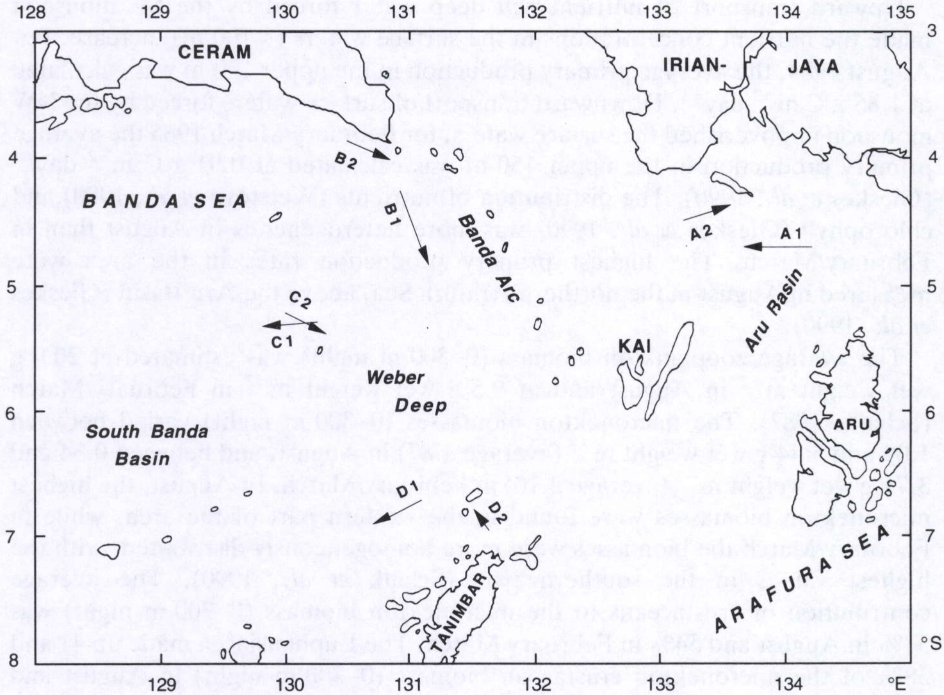

Fig. 2. The eastern Banda Sea with the locations of the four drogue stations (lines): A1, B1, C1 and D1 for the August 1984 cruise; A2, B2, C2 and D2 for the February/March 1985 cruise. Arrows indicate the direction of drift of the drogues.

Wyrtki's model. During the NW monsoon season, the situation in the upper 150 m was the reverse. In the sample period, February/March downwelling was 67–150 cm day $^{-1}$ in the eastern Banda Sea (Weber Deep and Banda Basin), being stronger than above the Aru Basin where downwelling was very weak or even absent (Zijlstra *et al.*, 1990).

During the so-called upwelling season, despite upward transport, stratification and a mixed layer were present. At the sample sites a depth of ~40 m was attained. 'Upward entrainment' is a better term in this area than 'upwelling' (Zijlstra *et al.*, 1990). In general, vertical displacement was replenished through advection by a west–east counterflow in the upper 100–150 m. No deep-sea water was involved in the process of upwelling and vertical mixing (Zijlstra *et al.*, 1990).

Temperature profiles during the SE monsoon showed a well-developed mixed layer rising from west to east (from Banda Basin to Arafura Shelf). During the NW monsoon, the mixed layer was shallower and less distinct than in the preceding season. Below 80–100 m, the temperature profiles were similar for both seasons (Witte and Wetsteyn, 1990). The thermocline ranged from 100 to 300 m. Surface temperatures were ~25°C in August 1984 and ~29°C in February/March 1985; mean surface salinity was similar during both cruises (Zijlstra *et al.*, 1990).

Upward transport of nutrient-rich deep water forced by the SE monsoon made the nutrient concentrations in the surface waters (<100 m) increase. For August 1984, the average primary production in the upper 150 m was calculated at 1.85 g C m^{-2} day^{-1}. Downward transport of surface waters forced by the NW monsoon impoverished the surface waters, for February/March 1985 the average primary production in the upper 150 m was calculated at 0.91 g C m^{-2} day^{-1} (Gieskes *et al.*, 1990). The distribution of nutrients (Wetsteyn *et al.*, 1990) and chlorophyll (Gieskes *et al.*, 1990) was more heterogeneous in August than in February/March. The highest primary production rates in the area were measured in August in the northern Arafura Sea, above the Aru Basin (Gieskes *et al.*, 1990).

The average zooplankton biomass (0–300 m night) was estimated at 20.0 g wet weight m^{-2} in August and at 9.5 g wet weight m^{-2} in February/March (Schalk, 1987). The micronekton biomasses (0–300 m night) varied between 1.09 and 5.44 g wet weight m^{-2} (average 2.87) in August, and between 0.34 and 3.71 g wet weight m^{-2} (average 2.10) in February/March. In August, the highest micronekton biomasses were found in the western part of the area, while in February/March the biomasses were more homogeneously distributed, with the highest values in the southern part (Schalk *et al.*, 1990). The average contribution of crustaceans to the micronekton biomass (0–300 m night) was 57% in August and 54% in February/March. The Euphausiacea made up 41 and 38% of the micronekton crustacean biomass (0–300 m night) in August and February/March, respectively (Schalk *et al.*, 1990).

Aberrant depth distributions for deep-sea zooplankton species have been noticed in the Banda Sea. Meso- and bathypelagic species were found in samples from shallow depth, concerning Coelenterata, Pteropoda and Pisces (Van der Spoel and Bleeker, 1988; Van der Spoel and Schalk, 1988; Van der Spoel, 1992). An upward shifted depth distribution of bathypelagic species, according to the hypothesis by Van der Spoel and Schalk (1988), is due to a higher energy requirement because of a higher metabolic rate, induced by increased ambient temperature in deep sea. The upward shifted depth distribution is the result of a new balance between higher food requirement at higher ambient temperature, and greater food availability higher in the water column.

The present study concerns the Euphausiacea of the eastern Banda Sea collected with R.V. 'Tyro' during the Snellius-II Expedition. Not much is known about Euphausiacea from this particular area. Earlier expeditions in this region, such as Siboga 1899–1900 (Hansen, 1910) and NAGA (see Brinton, 1975), visited the eastern Banda Sea scarcely or not at all.

A study was made of the vertical distributions for diurnally vertically migrating and non-migrating species in the upper 500 m of the water column. Comparisons were made during the two different monsoon seasons. Stomach content and feeding patterns related to vertical distribution were studied in order to find out whether bathy- and mesopelagic Euphausiacea show aberrant depth distributions in this area, as has been found in other groups mentioned above.

Method

Two cruises were made, one during the peak of the SE monsoon from 26 July to 2 September 1984, and one during the NW monsoon from 8 February to 11 March 1985 (Zijlstra and Baars, 1987). During both cruises macrozooplankton and micronekton were sampled at four stations in daytime and night series between 0 and 500 m depth (in one case 600 m), in discrete layers of ~100 m thickness (occasionally 200 m due to lack of time). Sampling was done near a radio drogue buoy in order to sample the same surface water mass. Figure 2 shows the study area and the position of the stations during both cruises. The stations were sampled from 17 to 30 August 1984, and from 23 February to 5 March 1985 (Schalk, 1990). Sampling was done in oblique downward hauls with a Rectangular Midwater Trawl 1 + 8 (Baker *et al.*, 1973), an opening and closing net system with two combined nets: one with mesh size 0.32 mm and an effective mouth area of 0.73 m^2 at a speed of 2 knots, and one with mesh size 4.5 mm and an effective mouth area of 9.24 m^2 at a speed of 2 knots (Roe *et al.*, 1980). The opening and closing of the nets is controlled and depth, temperature and netflow are monitoried with an acoustic system. During sampling the net speed was maintained between 1.8 and 2.4 knots (Schalk, 1990). Effective mouth area and filtered volume were calculated in relation to tow speed according to Roe *et al.* (1980). The filtered volume of water per haul was generally ~24 000 m^3 for the RMT 8 (Schalk, 1990). For technical reasons, some layers could not be sampled at some stations. In August failures were: station A day 100–200 m and 400–500 m; station C day 200–300 m. At station A, due to considerable drift, the night series were carried out in different intermediate water masses than the daytime series. In February/March failures were: station A day 300–400 m; at station D no daytime series could be carried out at all. Samples were collected between approximately 9 a.m. and 6 p.m., and 8 p.m. and 4 a.m. (Zijlstra and Baars, 1987).

For the present study only RMT 8 samples have been used. This implies that the body length of the studied specimens of Euphausiacea is greater than ~5 mm, and larvae and small juveniles are excluded. In general, all specimens were identified and counted. For two samples that contained many specimens, aliquots had to be made: B (August) day 0–100 m and night 0–100 m. Identification was carried out with the aid of Brinton (1975) and Lomakina (1978). Brinton (1975) was followed for nomenclature. Owing to damage to the animals in 12 out of 68 samples, a remaining group of unidentified euphausiid specimens remained at the generic or family level.

Samples and all species found were arranged by using the classification technique of Two Way Indicator Species Analysis (TWINSPAN). The TWINSPAN program by Hill (1979) constructs a two-way table from a sample by species matrix. First a dichotomy is made, ordinating the samples by correspondence analysis on the basis of species composition and abundance, and the division is then improved by iterative character weighting. After this, the species are classified by TWINSPAN on the basis of the fidelity in which they are confined to particular groups of samples. With both classifications the species are ordered in such a way that, if present, a positive diagonal (from upper left to lower right) can be formed (Jongman *et al.*, 1987). The input parameters were as follows: for pseudospecies the cut off levels 0.0, 2.0, 5.0, 10.0 and 20.0 were used, and the weights for levels of pseudospecies were set to 1. Specimens that could not be identified at the species level and samples without euphausiids were not included in the TWINSPAN analysis.

For study of vertical migration of populations or species, the depth of the centre of mass (X_L) of the plankton population is calculated from:

$$X_L = \frac{0.5\,H_1 \cdot a_1 + (H_1 + 0.5\,H_2) \cdot a_2 + \ldots + (H_1 + H_2 + \ldots + H_{n-1} + 0.5\,H_n) \cdot a_n}{a_1 + a_2 + \ldots + a_n}$$

[Zakhvatkina (1964) in Vinogradov (1970)], where L is the length of the sampled water column and a is the density of the plankton in the sampled layer with thickness H. In the present study, in general differences of >100 m between the day and night position of the centres of mass are arbitrarily understood as indications for diurnal vertical migration.

To study the feeding pattern in relation to seasonal changes in food supply, the vertical distribution and eventual diurnal vertical migration of species, the stomach contents of the animals were examined quantitatively. The degree of filling of the stomach was estimated visually, either after dissection of the stomach or with the stomach still in the body of the animal, full stomachs being easily visible through the carapace. Stomach filling is expressed in the following five categories as: 0, 0–25%, 25–50%, 50–75% and 75%–full.

Results

In total, 68 samples have been collected and 31 species of Euphausiacea could be identified. In Table I the species are listed with values for their abundance in the sampled column at night for both sample periods. Because of the heterogeneity in the pelagic system in August, the calculations are made for the stations separately. In February/March, differences are rather small, therefore stations A, B and C are taken together; station D is kept apart since sampling was done in water between islands with a mean depth of only 400–600 m. The average total number of Euphausiacea at the four stations is higher in August 1984 than in February/March 1985, calculated at 12.2 and 4.9 individuals m^{-2}, respectively, in night series over 0–500 m. In August, differences between total densities of Euphausiacea at the four stations are remarkably great (Table I and Figure 3a); in February/March these differences are only small (Table I and Figure 3b). In most cases, the total density of animals sampled between 0 and 500 m is not in balance between day and night. In August, the total density at night is on average four times greater than in the daytime (Figure 3a) and in February/March the night density is on average 2.5 times greater than the daytime density (Figure 3b). The difference between the day and night depths of the centres of mass of the population, called the migration amplitude, at stations A and C is higher in August than in February/March. In the food-enriched SE

Table I. Abundance (N m^{-2}) of Euphausiacea species in the upper 500 m during the night. For February/March 1985, the average over stations A, B and C is given

	August 1984				February/March 1985	
	A upwelling	B downstream upwelling	C	D	A/B/C generally oligotrophic	D shallow waters
Total of Euphausiacea	1.65	37.77	3.52	6.56	5.68	4.09
Frequent species						
(Migrating species)						
Euphausia diomedeae	0.21	17.05	0.18	0.85	1.17	1.85
Euphausia pseudogibba	–	0.25	0.07	0.41	0.07	1.21
Nematoscelis microps	0.36	0.02	0.16	1.75	1.15	–
Thysanopoda monacantha	0.04	0.61	0.26	0.44	0.46	0.06
Thysanopoda tricuspidata	0.01	12.16	0.53	0.04	1.19	0.15
(Non-migrating species)						
Euphausia similis	0.20	0.36	0.01	0.25	0.58	0.03
Nematobrachion boopis	0.07	0.36	0.02	0.21	0.13	0.07
Nematoscelis tenella	0.21	2.33	–	1.06	0.22	0.04
Stylocheiron maximum	0.01	0.10	0.07	0.14	0.06	0.15
Thysanopoda orientalis	*	0.17	0.36	0.05	0.88	0.38
Less frequent species						
Stylocheiron abbreviatum	0.39	–	0.09	0.58	0.37	–
Stylocheiron longicorne	–	0.09	–	0.60	0.03	–
Stylocheiron affine	0.02	0.29	–	0.17	0.11	–
Unidentified (damaged)	0.07	0.36	0.34	–	0.10	0.06
Thysanopoda astylata	–	–	0.02	–	0.15	0.01
Euphausia sanzoi	0.03	0.01	–	–	0.20	0.04
Stylocheiron sp. (damaged)	–	–	0.03	–	0.01	–
Nematoscelis gracilis	–	–	0.03	–	0.08	–
Nematoscelis sp. (damaged)	–	–	1.28	–	0.03	–
Stylocheiron carinatum	0.01	0.03	–	–	–	–
Thysanopoda cristata	–	–	0.005	–	0.01	–
Thysanopoda sp. (damaged)	–	–	0.002	–	–	–
Euphausia sibogae	–	–	–	–	0.02	–
Euphausia tenera	–	–	–	–	0.03	–
Stylocheiron insulare	0.01	–	–	–	0.03	0.05
Stylocheiron robustum	–	–	–	0.01	0.01	0.004
Euphausia gibba	–	–	0.003	–	–	–
Euphausia hemigibba	–	–	–	–	0.01	–
Euphausia paragibba	–	–	0.01	–	*	–
Nematobrachion sexpinosus	–	–	–	0.01	0.01	–
Nematoscelis atlantica	–	3.59	–	–	–	–
Pseudeuphausia latifrons	–	–	–	–	0.17	–
Thysanopoda aequalis	–	–	–	*	–	–
Thysanopoda obtusifrons	–	–	–	*	–	–
Thysanopoda pectinata	–	–	0.03	–	–	–

*Species only present in daytime samples.

monsoon period station A, located above the Aru Basin, was under the influence of a strong coastal upwelling in the shallow Arafura Sea, leading to the highest primary production rates measured in the area. However, at station A the total density in euphausiid species was the lowest established in August (Figure 3a), although sampling series were not complete.

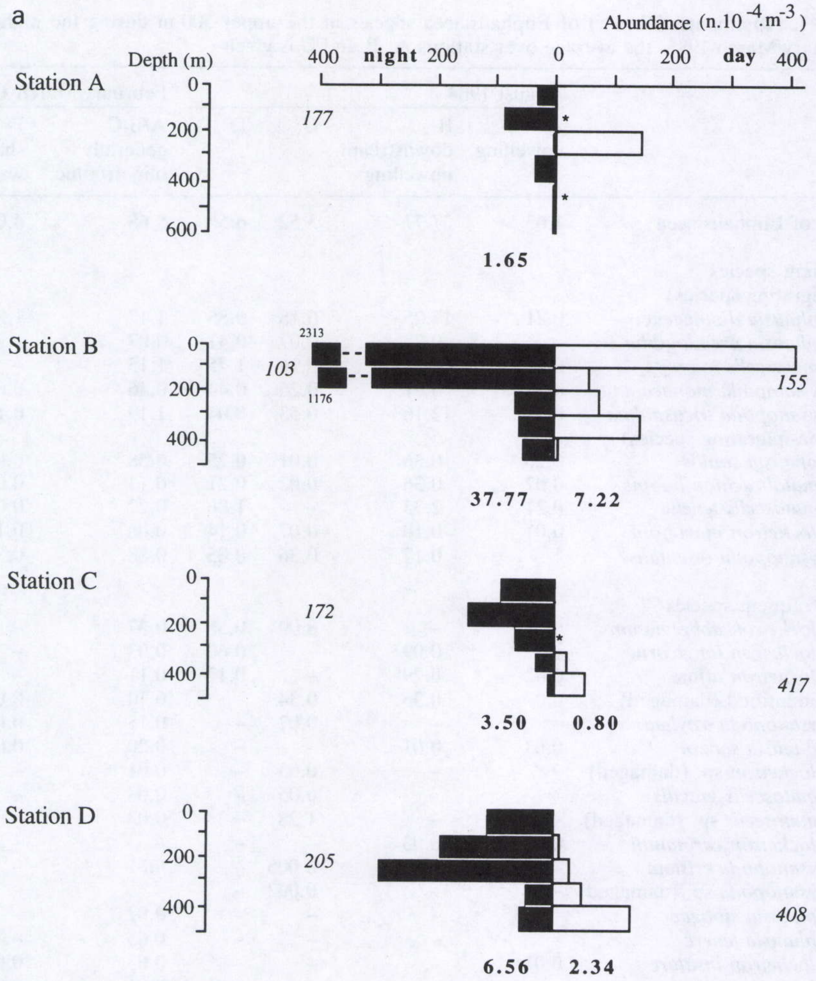

Fig. 3. Day and night depth distribution of the density ($N \times 10^{-4}$ m^{-3}) of the Euphausiacea (all species together) over the sampled water column at the four drogue stations A–D. (**a**) August 1984 sampling period. Depth (m) of the centre of mass of the population is in italics. Total number of Euphausiacea in the sampled column (N m^{-2}) is in bold. No calculations were made if more than one haul was missing (see*).

In the sample–species matrix from the August sample period made with TWINSPAN (Appendix 1), six sample groups are considered. In Table II, the average density is presented for each species in these groups, a seventh group is added for the empty samples.

Sample group 1 consists of samples from middle depth, made at night and daytime. This group is characterized by *Nematobrachion boopis*, *Stylocheiron abbreviatum*, *Stylocheiron maximum*, and *Thysanopoda orientalis*.

Sample group 2 consists of samples from middle–deep to deep depths, both

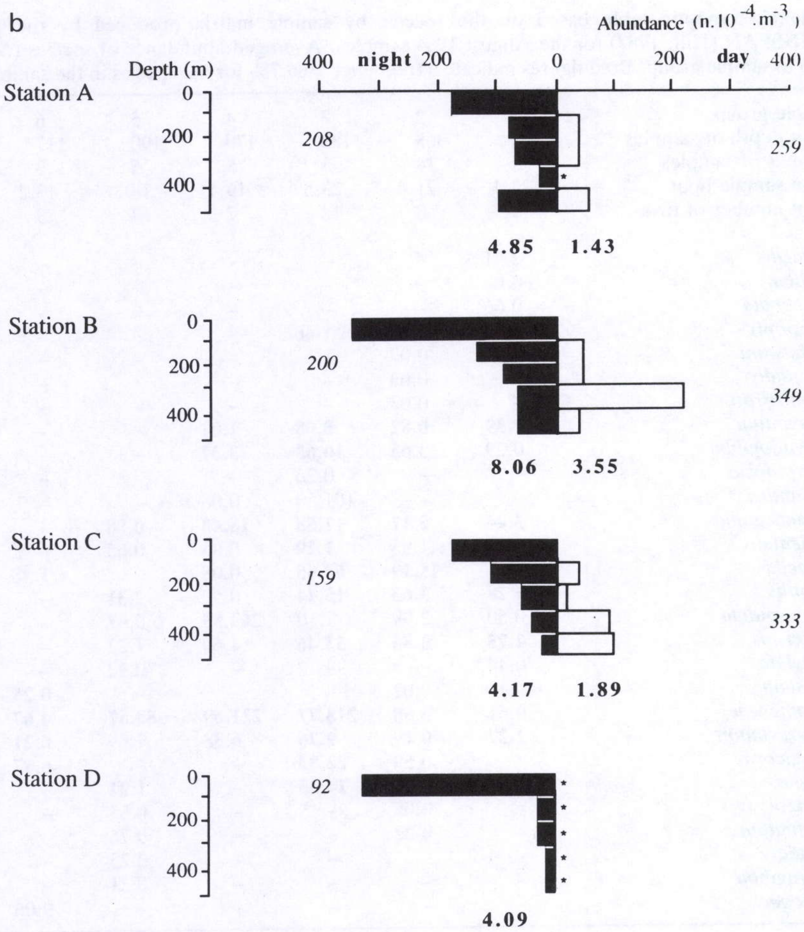

Fig. 3. Day and night depth distribution of the density ($N \times 10^{-4}$ m^{-3}) of the Euphausiacea (all species together) over the sampled water column at the four drogue stations A–D. (**b**) February/March 1985 sampling period. Depth (m) of the centre of mass of the population is in italics. Total number of Euphausiacea in the sampled column (N m^{-2}) is in bold. No calculations were made if more than one haul was missing (see*).

day and night. The characteristic species for this group are *Nb.boopis* and *Nematoscelis tenella*.

Sample group 3 and sample group 4 contain samples from shallow (night) and middle (day and night) depths. Group 3 is characterized by *Stylocheiron longicorne*, whereas group 4 is characterized by *Euphausia diomedeae*, *Thysanopoda monacantha* and *Thysanopoda tricuspidata*.

Sample group 5 contains shallow daytime and night samples and is characterized by *E.diomedeae*, together with *Euphausia sanzoi*, *Euphausia paragibba*, *Stylocheiron carinatum* and *Stylocheiron insulare*.

Table II. Synoptic table based on the species by sample matrix produced by the program TWINSPAN (Hill, 1987) for the August 1984 samples. Averaged abundance of species ($N \times 10^{-4}$ m^{-3}) in sample group. Bold figures indicate a frequency ⩾66.7% for the species in the sample group

Sample group	1	2	3	4	5	6	7
Mean depth of samples	275	368	183	170	190	117	75
Number of samples	4	14	3	5	5	3	4
Mean sample hour	22.4	21.0	23.5	19.4	18.3	13.2	10.1
Mean number of taxa	11	8	12	7	7	3	0
N.gracilis	2.51	–	–	–	–	–	–
E.gibba	0.08	–	–	–	–	–	–
T.pectinata	0.66	–	–	–	–	–	–
Nb.boopis	**5.46**	**7.93**	1.46	–	–	–	–
S.robustum	–	0.07	–	–	–	–	–
T.aequalis	–	0.03	–	–	–	–	–
T.obtusifrons	–	0.07	–	–	–	–	–
S.maximum	**2.59**	**0.82**	**5.08**	1.01	–	–	–
E.pseudogibba	0.29	3.65	**10.63**	**3.37**	–	–	–
N.sexpinosus	–	–	0.26	–	–	–	–
N.atlantica	–	–	101.50	0.08	–	–	–
T.monacantha	**3.44**	**5.17**	**17.58**	**18.48**	**0.58**	–	–
T.orientalis	**16.48**	1.93	**1.29**	0.95	0.65	–	–
N.tenella	–	**15.19**	**64.95**	0.08	–	1.48	–
E.similis	**15.28**	**3.63**	**15.44**	0.50	2.31	–	–
T.tricuspidata	0.50	2.99	7.10	**269.95**	0.67	–	–
N.microps	**2.75**	3.86	**53.46**	4.60	7.22	–	–
T.astylata	0.44	–	–	–	0.22	–	–
T.cristata	0.11	0.02	–	–	–	0.25	–
E.diomedeae	0.61	**3.58**	**218.77**	**221.69**	**88.87**	**4.67**	–
S.abbreviatum	**2.27**	0.19	**9.76**	6.38	7.69	**6.21**	–
S.longicorne		0.59	**22.85**	–	–	6.97	–
S.affine	–	0.04	**14.35**	–	1.21	–	–
E.sanzoi	–	0.05	–	–	0.53	–	–
S.carinatum	–	0.22	–	–	0.76	–	–
S.insulare	–	–	–	–	0.23	–	–
E.paragibba	–	–	–	–	0.21	–	–
E.sibogae	–	–	–	–	–	9.06	–

Sample group 6 contains shallow daytime samples. Characteristic for this group are *E.diomedeae*, *S.abbreviatum* and *S.longicorne*.

Sample group 7 contains only empty daytime samples from shallow depth.

In respect to the (co-)occurrence of the abundant species, *Euphausia similis*, *Nb.boopis*, *N.tenella*, *S.maximum* and *T.orientalis* form a group of species that are present in mainly deep samples belonging to groups 1, 2 and 3. All these species do not perform diurnal vertical migration. These species occur in high densities at stations B and D.

Another group of abundant species consists of *E.diomedeae*, *E.pseudogibba*, *Nematoscelis microps*, *T.monacantha* and *T.tricuspidata*. These species occur together in the deep daytime and shallow night samples, belonging to sample groups 3, 4 and 5. *Euphausia diomedeae* and *T.monacantha* are the main species of group 5. Vertical diurnal migration is performed by these species. *Stylocheiron abbreviatum* occurs in nearly all the shallow daytime samples (group 6).

Table III. Synoptic table based on the species by sample matrix produced by the program TWINSPAN (Hill, 1987) for the August 1984 samples. Averaged abundance of species ($N \times 10^{-4}$ m^{-3}) in sample group. Bold figures indicate a frequency ≥66.7% for the species in the sample group

Sample group	1	2	3	4	5
Mean depth of samples	325	307	200	70	50
Number of samples	12	7	3	5	3
Mean sample hour	21.2	16.5	15.0	22.1	12.3
Mean number of taxa	7	10	7	8	0
S.carinatum	0.29	–	–	–	–
T.cristata	0.07	–	–	–	–
E.gibba	0.06	–	–	–	–
N.sexpinosus	0.03	–	–	–	–
S.maximum	**2.52**	1.32	0.20	–	–
N.gracilis	1.82	2.85	–	–	–
T.orientalis	**21.98**	**11.22**	0.60	–	–
E.similis	**12.47**	**7.43**	–	–	–
Nb.boopis	**3.88**	**5.99**	0.30	–	–
N.tenella	1.32	**13.40**	1.50	–	–
S.robustum	–	0.13	–	–	–
T.monacantha	1.74	**5.66**	0.20	6.32	–
E.pseudogibba	0.10	**5.31**	–	26.38	–
N.microps	–	**21.58**	**7.70**	16.64	–
T.astylare	0.04	2.14	–	4.54	–
S.insulare	–	–	–	1.58	–
P.latifrons	–	–	–	6.64	–
S.affine	–	0.72	**2.90**	2.70	–
E.sibogae	–	–	0.20	0.34	–
E.paragibba	–	–	0.10	–	–
S.longicorne	0.12	0.31	**2.00**	–	–
E.tenera	–	1.05	1.10	0.60	–
T.tricuspidata	0.52	**7.50**	**3.20**	**47.26**	–
E.diomedeae	1.11	**3.46**	**13.80**	**103.86**	–
S.abbreviatum	3.86	0.21	0.90	5.68	–
E.sanzoi	0.92	0.12	–	2.46	–
E.hemigibba	0.06	–	–	–	–

In the sample–species matrix from the February/March sample period made with TWINSPAN (Appendix 2), four sample groups are considered. In Table III, the average density is presented of each species in these groups, a fifth group is added for the empty samples.

Sample group 1 consists of almost exclusively middle–deep and deep night samples and is characterized by *S.maximum.*

Sample group 2 consists of deep day samples and shallow night samples, and is characterized by *E.similis*, *Nb.boopis*, *N.microps*, *N.tenella* and *T.orientalis* on the one hand, and *T.monacantha* and *E.pseudogibba* on the other hand.

Sample group 3 contains middle–deep daytime samples, whereas group 4 contains only shallow night samples. Characteristic for these groups are *E.diomedeae*, *E.sanzoi*, *T.astylata* and *T.tricuspidata*.

Sample group 5 consists of samples without any Euphausiacea at all.

The abundant species *E.similis*, *Nb.boopis*, *N.tenella*, *S.maximum* and *T.orientalis* show co-occurrence in samples belonging to groups 1 and 2, and are present in only the deep samples, irrespective of sampling hour. They do not perform diurnal vertical migration.

The assemblage of the species *E.pseudogibba*, *N.microps* and *T.monacantha* show co-occurrence in deep daytime samples and shallow night samples (sample group 2). *Thysanopoda tricuspidata* and *E.diomedeae*, not in one species group, occur both in middle–deep day samples and shallow night samples (sample groups 2, 3 and 4). These species perform diurnal vertical migration.

Table IV shows for the centre of mass of the populations of the common migrating and non-migrating species, as well as the rare species, the average depth and SD over all stations for both sampling periods. Seasonal differences in depth distribution and vertical migration range can be found, but except in the epipelagic and mesopelagic diurnal vertically migrating *E.diomedeae* and *T.tricuspidata* these differences are rather small (Table IV, last two columns). When the total of Euphausiacea in the sampled column is considered, no important difference could be found between the average population depth in both sampling periods and the average length of the vertical migration range (Table IV last row).

In August 1984, four species have been found that were not collected in February/March 1985. These are *N.atlantica*, *T.aequalis*, *T.obtusifrons* and *T.pectinata*. In February/March three species, *E.hemigibba*, *E.tenera* and *P.latifrons*, have been found that were not collected in August. These species occurred only in small densities, except for the epipelagic *P.latifrons* and *N.atlantica*. At station C, at night between 0–100 m, it is more abundant in February/March 1985. The following species occurred at every station in both seasons: *E.diomedeae*, *E.pseudogibba*, *E.similis*, *N.microps*, *Nb.boopis*, *S.maximum*, *T.monacantha*, *T.orientalis* and *T.tricuspidata*.

Stomach filling and vertical distribution

The vertical migrating species *E.diomedeae*, *E.pseudogibba*, *N.microps*, *T.monacantha* and *T.tricuspidata* are found at night with filled stomachs in surface layers (Figure 4). Filled stomachs have been found in daytime samples as well. *Euphasia diomedeae* is remarkable, with a filled stomach in the 0–100 m daytime stratum at station B in August. These migrating species are found with a filled stomach at night in a wide vertical range. This range is greater in August than in February/March, when these species have filled stomachs only at night in the uppermost layers, except for *T.monacantha* which was found with a filled stomach over a large vertical range in the latter period.

The non-migrating species *E.similis*, *Nb.boopis*, *N.tenella*, *S.maximum* and *T.orientalis* completed with *S.abbreviatum* in general show a pattern of continuous feeding (Figure 4). Especially *E.similis* (with one exception) and *T.orientalis* are always found with filled stomachs. The non-migrating *T.cristata* (not depicted) has been found with a filled stomach in samples from 200 to 300 m or deeper (stations B and C in August).

Table IV. Mean depth (*d*) and standard deviation of the mean (SD) of the centre of mass of species populations. *n* = number of stations where the species was found. ○, migratory species; –, non-migratory species

	August 1984						February/March 1985						Day–night difference	
	Day			Night			Day			Night			August (m)	Feb./March (m)
	d (m)	SD	*n*	*d* (m)	SD	*n*	*d* (m)	SD	*n*	*d* (m)	SD	*n*		
○*E.diomedeae*	242	155	3	111	37	4	227	31	3	54	3	4	131	174
○*E.pseudogibba*	416	94	2	196	97	3	407	6	2	115	63	3	220	292
○*N.microps*	416	83	2	225	106	4	356	60	2	175	32	2	192	181
○*T.monacantha*	384	76	4	147	37	4	410	64	3	157	79	3	237	253
○*T.tricuspidata*	350	59	3	59	10	4	247	68	3	92	35	3	292	155
–*E.similis*	353	94	3	201	17	4	341	130	3	340	69	4	152	0
–*Nb.boopis*	360	98	3	370	22	4	373	62	3	403	35	4	–9	–30
–*N.tenella*	367	44	2	286	64	3	353	13	2	328	124	4	81	25
–*S.abbreviatum*	134	31	3	167	58	3	188	5	2	146	43	2	–33	41
–*S.maximum*	269	12	3	244	38	3	296	91	3	335	57	4	26	–39
–*T.orientalis*	376	90	4	289	65	3	369	36	3	318	84	4	87	52
S.longicorne	153	5	2	224	41	2	253	36	2	255	–	1	–70	–3
S.affine	50	–	1	148	96	3	192	51	2	122	19	2	–98	70
T.astylata	354	–	1	153	–	1	398	–	1	65	25	3	201	333
E.sanzoi				221	223	2				154	118	2	–	–
N.gracilis	259	–	1	455	–	1	402	–	1	303	49	2	–196	99
S.carinatum	50	–	1	241	270	2							–191	–
T.cristata	208	–	1	153	–	1				439	–	1	55	–
E.sibogae	146	–	1				228	–	1	49	–	1	–	179
E.tenera							304	–	1	49	–	1	–	255
S.insulare				50	–	1				50	1	2	–	–
S.robustum				438	–	1				173	33	2	–	–
E.gibba				455	–	1	200	–	1				–	–
E.hemigibba										54	–	1	–	–
E.paragibba				355	–	1	156	–	1				–	–
Nb.sexpinosus				150	–	1				491	–	1	–	–
N.atlantica	245	–	1	154	–	1							91	–
P.latifrons										50	1	2	–	–
T.aequalis	372	–	1										–	–
T.obtusifrons	483	–	1										–	–
T.pectinata				153	–	1							–	–
Total Euphausiacea	308	127	4	164	43	4	314	48	3	165	53	4	143	158

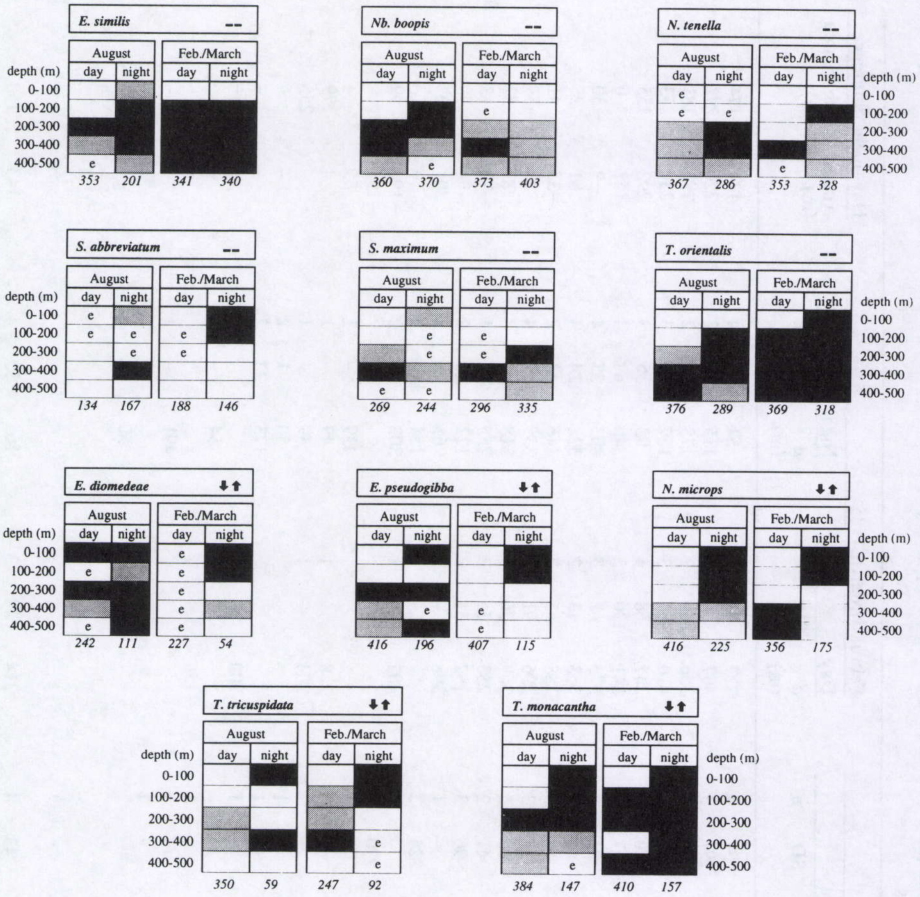

Fig. 4. Vertical distribution of stomach filling over sampled strata (0–500 m) in six euphausiid species not performing diurnal vertical migration (– –) and five species performing diurnal vertical migration (▲▼). Shading: dark: stomach filling 25–100%; grey: stomach filling 0–25%; e: stomach empty. Average depth (m) of the centre of mass of the species population is in italics.

Ovigerous females

Ovigerous females and spermatophore-bearing females were generally rare. In only four species and in 15 of the 68 collected samples were one or more ovigerous females found. In February/March 1985, only two such specimens were observed: one *N.microps* and one *S.maximum*. In August 1984, a total of only 77 ovigerous females or spermatophore-bearing females was found. The most important species in this matter were *E.similis* (50 spermatophore-bearing females at station B only) and *N.microps* (17 ovigerous females).

Discussion

Schalk *et al.* (1990) observed at the 12 survey stations (0–100 and 100–300 m night) for the total of Euphausiacea in the Banda Sea a higher density and a higher biomass in the nutrient-rich SE monsoon season than in the relatively nutrient-poor NW monsoon season. The present study, dealing with the four drogue stations (0–500 m day and night), confirms the seasonal difference in densities of Euphausiacea. The heterogeneous distribution of Euphausiacea densities during the SE monsoon sample period, and the more homogeneous distribution during the NW sample period, corresponds with the outcome of earlier zooplankton studies in the area (Schalk, 1987; Baars *et al.*, 1990; Schalk *et al.*, 1990).

The very high density of Euphausiacea at station B in August in the upper 200 m at night and in the 0–100 m layer during the day as well is remarkable. This station is located downstream of the upwelling area in the northern Arafura Sea. At station A, located close to the upwelling area in the northern Arafura Sea, the zooplankton biomass (Schalk, 1987; Schalk *et al.*, 1990) and density of Euphausiacea were very low in the comparable layers. The highest mesozooplankton biomasses (0–300 m at night) were found in August, generally in the western part of the area, including station B (Schalk, 1987). Firstly, this confirms the sequence of peaks of trophic levels in upwelling areas. In freshly upwelled waters phytoplankton blooms develop, leading to maxima in zooplankton and higher trophic levels more downstream as it takes more time to build up animal populations compared with algae. In the second place, an explanation can be found in the patchy distribution that is common in pelagic systems.

The species of the two ecologically different groups showed in some cases deviations from the patterns described as normal. For this reason, the common species are first considered separately and depth distribution in the Banda Sea is compared with literature data referred to in Table V. All species found are known from at least the tropical Pacific and tropical Indian Oceans.

In the Banda Sea, *E.diomedeae*, *E.pseudogibba*, *N.microps*, *T.tricuspidata* and *T.monacantha* form a distinct group of vertical migrators. *Euphausia diomedeae* is well represented in the eastern Banda Sea, where the performance of a diurnal vertical migration is obvious. In both seasons and at all stations, the concentration is highest in the upper layer at night, but in the daytime the centres of mass vary in depth. Compared to the vertical distribution in August, in February/March the range of vertical migration is shifted upwards and the amplitude is somewhat greater. In August, specimens of *E.diomedeae* are found with full stomachs at night over a wide depth range, while in February/March at night animals with full stomachs are found only in the upper 100 m. The vertical distribution and the diurnal vertical migration found for *E.diomedeae* correspond to literature data. The high density of animals with filled stomachs in the daytime in the surface layer at station B in August is remarkable.

Euphausia pseudogibba is known to perform a diurnal vertical migration. In the Banda Sea, its depth distribution is according to literature data. In August, the vertical range for day and night distribution is greater than in February/March, but the average amplitude of the vertical migration is greater in the latter period. At night, animals in the upper layers have full stomachs, in the daytime

Table V. Day and night depth ranges (in m) of Euphausiacea compared for Banda Sea and tropical waters

	Depth distribution in Banda Sea in upper 500 m (1)				Depth distributions according to the literature					
	August		February/March		Day	Night	Total range	Depth classification	Performance vertical migration	Reference
	Day	Night	Day	Night						
E.diomedeae	100–500	0–500	100–300	0–500	0–700	surface	0–700	e	+	4
E.pseudogibba	200–500	0–500	200–500	0–500	250–1000	surface		e–m	+	4,5
N.microps	300–500	0–400	100–500	0–300	500–800	200–400	100–900	m	+	5,7
T.monacantha	200–500	0–500	100–500	0–500	400–800,>700	0–500		m	+	2,3,4,7
T.tricuspidata	200–500	0–400	100–500	0–500	500–1000	surface		m	+	2,4,5,7
E.similis	200–500	0–600	100–500	100–500	>500	–	0 to>1000	m	–	4,5
Nb.boopis	200–500	200–600	200–500	200–500	–	–	>400	m	–	2–5,7
N.tenella	100–500	100–600	100–500	100–500	100–300	100–400	100–100(2000)	m	–	2,4,5,7
S.maximum	200–500	100–600	100–400	200–500	–	–	500 to >2000	m–b	–	2,4,5
T.orientalis	200–500	100–500	100–500	100–500	–	–	300 to >1000	m	–	2,4,5
S.abbreviatum	0–300	0–500	100–300	0–300	75–400	50–300			–	2,4,7
S.longicorne	100–400	100–500	100–400	200–400	400–600	200–500	100–140–700	e–m	–	2,4
S.affine	0–100	0–500	110–300	0–300			0–400	e–m	–	4,5,7
T.astylata	200–300	100–200	300–500	0–300	–	–	–		?	
E.sanzoi	–	0–400	–	0–400	–	–	–		?	
N.gracilis	200–300	400–500	100–400	200–300	0–700	100–300	0–700		+	2,4,5
S.carinatum	0–100	300–500	100–300	–	0–700	0–100		e	(+?)	3,4,5,7
T.cristata	100–400	100–200	–	200–500	–	–	200–2000	m(b)	–	4,5,7
E.sibogae	100–200	–	100–300	0–100			0–300	e	?	2,4
E.tenera	–	–	100–400	0–100	300–500	<140			+	2,7
S.insulare	–	0–100	–	0–100	–	–	0–150(2000)		?	4
S.robustum	–	400–500	–	100–200	200–1000	surface		m–b	–	2,4,5
E.gibba	–	400–500	100–300	–	300–600	surface			+	2,3,5,7
E.hemigibba	–	–	100–300	0–100	300–700	0–300	–	e	+	2,4,5
E.paragibba	–	300–400	100–200	–	300–700	<140	0–700	e	+	2,4,5
Nb.sexpinosus	–	100–200	–	300–500		–	200–1000	m	–	4
N.atlantica	200–300	100–200	–	–	>100	<150	>100	e–m		2,4,5
P.latifrons	–	–	–	0–100			0–100	e	–	2,4,5
T.aequalis	300–400	–	–	–	140–700	0–500	0 to <900		(+?)	2,4,5,7
T.obtusifrons	400–500	–	–	–	>280	100–500		m	(+?)	2,4,5
T.pectinata	–	100–200	–	–	400–800	100–500	150 to >1000	m	(+?)	2,3,5,6,7

Refs: 1, current research; 2, Brinton, 1962; 3, Hu, 1978; 4, Lomakina, 1978, 5, Mauchline and Fisher, 1969; 6, Vinogradov, 1970; 7, Youngbluth, 1975.
Depth classification: e = epipelagic (0–150(200) m); m = mesopelagic (150(200)–1000 m); b = bathypelagic (>100 m).

animals with full, or partially filled stomachs (in state of digestion), are found in deeper layers. The patterns for diurnal distribution and stomach content are matching, as expected for a species that occurs and feeds in surface layers at night and migrates downwards at daytime; digestion occurs at greater depths.

Nematoscelis microps is a mesopelagic species. It is found at shallow depths at night, indicating the performance of diurnal vertical migration (Mauchline and Fisher, 1969). In the Banda Sea, the species is found below 300 m at daytime and mainly from 0 to 300 m at night. In August, diurnal vertical migration is only evident at station D. At this station, animals with filled stomachs are found at night over a large depth range, but during the day filled stomachs are only found below 400 m. At the other stations in August either *N.microps* is absent in the day series (stations A and C) or the centres of mass are close to each other (station B). In February/March, diurnal vertical migration is evident at stations B and C (in this period the species is not found at stations A and D). At station B, this species is found at night in the upper 200 m with filled stomachs, which seems rather high for a mesopelagic species. In the daytime, *N.microps* is found below 300 m also with filled stomachs, so possibly this species is feeding day and night well over a large depth range.

For the mesopelagial *T.tricuspidata*, the described daytime depth distribution lies below 500 m. In the Banda Sea, it is found during the SE monsoon season up to 200 m during the day and in the uppermost stratum at night. During the NW monsoon season, it is found up to 100 m, its daytime distribution thus reaches higher than is recorded in the literature. In February/March, the migration range is shorter and lower than in August.

Thysanopoda monacantha is a mesopelagic species recorded incidentally in the Banda Sea (see Brinton, 1975). However, the species was found in the 0–100 and 100–300 m layers at night, at more than two-thirds of the 12 survey stations (Zijlstra and Baars, 1987) in the research area (authors' unpublished data). In both seasons, *T.monacantha* was found in the daytime and at night from 0 to 500 m, but the highest concentration was found below 300 m (August) and below 400 m (February/March) in the daytime, and above 400 and 300 m at night, respectively. Its daytime distribution reaches higher than the minimum of 700 m mentioned in the literature (Brinton, 1962; Lomakina, 1978). In both sample periods *T.monacantha*, if present, shows an obvious diurnal vertical migration. At night, disregarding the season, the species shows a wide depth range and most specimens have their stomachs filled. This indicates feeding at all depths.

The species in the Banda Sea that do not perform diurnal vertical migration in both sampling periods are *E.similis*, *Nb.boopis*, *N.tenella*, *S.maximum* and *T.orientalis*.

Euphausia similis is a mesopelagic, oceanic species and is found at different depths in different parts of its geographical range during the daytime (Brinton, 1962). In the Pacific *E.similis* is found from 0 to 300 m during the daytime only in the northern and southern colder parts of its range; in the equatorial waters of the Indo-Australian Archipelago it is found below 500 m (Brinton, 1962; Mauchline and Fisher, 1969). This indicates tropical submergence. However, in the Banda Sea the species is frequently shallow: up to 200 m in August and up to 300 m in February/March. In both seasons it was found at night up to 100 m; in August even above 100 m at stations A and D. These results do not confirm the known depth distributions. At night, animals with filled stomachs are found all over the sampled water column. This indicates active feeding and the capacity for surviving even in epipelagic circumstances. A diurnal vertical migration is not known for *E.similis*, but in August a remarkable day–night difference was found.

Nematobrachion boopis is a cosmopolitan, mesopelagic, non-migrating species, and shows tropical submergence. In the Pacific it does not occur above 700 m during the daytime and can be found at night between 500 and 700 m (Brinton, 1962). In the Banda Sea, *Nb.boopis* is found with filled stomachs in night and day samples up to 200 m, on average the centre of mass lies at 378 m (range 264–459 m) for all stations day and night. The upper limit of its vertical distribution in the Banda Sea was shallower than indicated by data from the literature. The species is known as carnivorous, but phytoplanktonic fragments have been found in stomachs of Banda Sea specimens.

Nematoscelis tenella is a panoceanic, mesopelagic species from the tropical and subtropical zones. In the eastern Banda Sea, in both seasons, the species is found in all strata except 0–100 m for day and night, corresponding with literature data. Feeding occurs in August over a wider and deeper depth range. In February/March, the species feeds higher at night.

The panoceanic *S.maximum* is considered mesopelagic, mainly depths beneath 500 m are reported. No evidence for a diurnal vertical migration is recorded. In the Banda Sea, the species is found in samples from 100 m and deeper. For all stations in both seasons the vertical distribution of the species in the Banda Sea extends shallower compared to data in the literature. Frequently, specimens of *S.maximum* with empty stomachs were found, but at station B in both seasons animals with filled stomachs were found at depths between 200 and 400 m. The stomachs contain, as far as is recognizable, mainly fragments of crustaceans, confirming the carnivorous behaviour of the species. However, phytoplanktonic fragments were also found, indicating an opportunistic feeding behaviour. This could be related to the wide depth distribution, reaching in to even the epipelagic.

The mesopelagic *T.orientalis* was not found above 200 m in the daytime and not above 100 m at night in the area, confirming literature data. *Thysanopoda orientalis* is known as a species that performs a diurnal vertical migration (Mauchline and Fisher, 1969), but in the Banda Sea the amplitude of migration is small, if not absent. The average depths of the centres of mass do not differ essentially between the two seasons. Specimens with filled stomachs were found over all depth ranges, irrespective of day or night. Stomachs contain fragments of crustaceans, diatoms, radiolarians and hooks of chaetognaths. The absence of a clear pattern of diurnal vertical migration, and frequently filled stomachs over wide depth ranges, indicates for this species an opportunistic feeding behaviour and an optimal food supply in both seasons.

The less abundant species could not be arranged within the groups of migrating or non-migrating species because of their irregular presence in the samples. Some of them are briefly discussed below.

According to Lomakina (1978), *S.abbreviatum* is seldom found at the surface and predominantly found between 100 and 400 m. Brinton (1962) and Mauchline and Fisher (1969) mention a range from 75 to 300 m. In the Mediterranean Sea, the species is found at maximum depths of 100 m (Souliere, 1963). *Stylocheiron abbreviatum* performs no diurnal vertical migration (Brinton, 1962). In the eastern Banda Sea, in August, its depth range lies between 0 and 300 m (occasionally 0–500 m at night), confirming the literature data. In February/March, the daytime range is shifted somewhat downwards and the range at night is narrower. Specimens with filled stomachs have been found at night above 100 m, and between 300 and 400 m during the day. The species can be considered as feeding at all depths of the sampled range.

Thysanopoda cristata is a (sub)tropical mesopelagic species found in the Pacific, Indian and Atlantic Oceans. Its depth range is wide, from 500 to 2000 m (Brinton, 1962; Lomakina, 1978). In the Pacific, *T.cristata* has been recorded above 500 m (Brinton, 1962). Youngbluth (1975) recorded for the eastern South Pacific juveniles and one adult of this species in the thermocline (200–400 m) during day and night. Brinton (1975) gives no records for the Banda Sea, but mentions records for the South China, the Timor and Celebes Seas. In the present material, adults were found at station B in both sample periods at depths up to 200 m at night, and between 100 and 400 m during the day. It was found at station C between 100 and 200 m at night in August only. All the above-mentioned stations are located in the pathways between the Pacific and Indian Oceans. Its vertical distribution, as found in the area, is in agreement with the wide depth range as recorded in the literature, although its minimum depth in the Banda Sea is the shallowest record so far. Regarding the general flow of deep and intermediate waters in the eastern Indonesian basins (Van Bennekom *et al.*, 1988), it is likely that *T.cristata* is imported through these waters from both the Timor and Celebes Seas into the Banda Basin.

In the present material, females of *E.similis* with spermatophore have been found. Brinton (1962) mentions that there is no evidence that the species reproduces in the Indo-Australian Archipelago and the tropical Indian Ocean. The East China Sea is considered as the primary reproductive area (Brinton, 1975). The Banda Basin is deep enough to find low temperatures corresponding to the 200 m depth temperatures in the biantitropical zones of distribution wherein the species occurs from 0 to 300 m (Brinton, 1962). By submergence into the deep waters of the Banda Sea, *E.similis* could survive as a standing population.

Pseudophausia latifrons is an epipelagic neritic species, found in the tropical western part of the Pacific Ocean and in the northwestern Indian Ocean including the Red Sea (Brinton, 1962; Mauchline and Fisher, 1969). The species occurs in high densities in the Indo-Australian Archipelago (Brinton, 1975). Nevertheless, during the present study *P.latifrons* has only been found at stations B and C in February/March, from 0 to 100 m at night. Eastward surface current driven by the NW monsoon bringing neritic waters into the open Banda Sea may explain the presence of *P.latifrons*.

As an outcome of the analysis, the pattern of depth distribution is less clear in August than in February/March. The non-migrating species are classified well in the middle–deep and deep samples, day and night for both periods. The migrating species, however, show less distinct day/night patterns in the August sample period than in the February/March period. It is possible here to presume a different migration pattern in response to the greater food resources in this period. One assumed advantage of diurnal vertical migration is energy conservation in deeper and colder layers. In a food-rich period, this mechanism probably becomes less optional.

It is possible that mesopelagic euphausiid species in the Banda Sea area live at shallower depths than recorded in the literature. Favourable food resources must be assumed to make this upward shift possible. Stomach contents and the vertical distribution of stomach filling in this study confirm the omnivorous behaviour and opportunistic capacities of euphausiids to live in favourable layers, disregarding the assumed boundaries related with the bathy-, meso- and epipelagic. In the nutrient-rich SE monsoon season more food is available at any depth within the epipelagic and upper mesopelagic range, so that specimens of vertical migrating species can live at shallower maximum depths, especially at night. In the same season, the migration range tends to narrow.

Non-migrating species show an upward shifted depth distribution in the nutrient-rich SE monsoon season. The feeding pattern of these species is parallel with the feeding cycle of the vertical migrating species, as demonstrated by carnivorous feeders such as *Nb.boopis* and *S.maximum*. The stomachs of non-migrating species are full at greater depths during the day and at shallower depths at night. Within their depth range, they always find prey to feed on. Also, the more herbivorous *E.similis* and *T.orientalis* are feeding constantly at almost any depths within their depth ranges.

The intermediate waters of the Indo–Australian Archipelago form a connection for mesopelagic species such as *E.similis*, *T.obtusifrons* and *T.monacantha*, that occur in the Pacific and Indian Oceans. Shallow sills and only a few deep troughs are decreasing the effectiveness of the connections between these oceans.

The diurnal vertically migrating species in the Banda Sea feed in the upper layers at night. Examples are *E.diomedeae*, *E.pseudogibba*, *N.microps*, *T.monacantha* and *T.tricuspidata*. This behaviour corresponds with data from the literature (Ponomareva, 1971; Hu, 1978; Hirota and Nemoto, 1990). In addition to this, the Banda Sea species show a downwards extended feeding range during the nutrient-rich SE monsoon season. For some of these species there is no great difference in the amplitude of migration for both seasons (*E.diomedeae*, *N.microps* and *T.monacantha*), the remaining migrating species have a smaller nocturnal feeding range in the nutrient-poor NW monsoon season (*E.pseudogibba*, *T.tricuspidata*).

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Appendix 1. Two-way sample by species table produced by the program TWINSPAN (Hill, 1978) for the August 1984 samples. Values denote the categories of abundance in numbers (N in $n \times 10^{-1}$ m^{-3}): (1) $N < 1$; (2) $1 \leqslant N < 5$; (3) $5 \leqslant N < 10$; (4) $10 \leqslant N < 20$; (5) $N \geqslant 20$. Vertical lines separate sample groups; sample numbers along top margin. Hierarchy is in binary notation along bottom and right margin for samples and species, respectively.

Order of samples (empty samples excluded). Denoted with sample number; station (A–D); depth of stratum (1 = 100; 2 = 200; 3 = 300; 4 = 400; 5 = 500; 6 = 600 m) and sampling period (○ = day; ● = night).

4 A 2-3 o
26 C 1-2 •
27 C 2-3 •
29 C 4-5 •
5 A 3-4 o
8 A 2-3 •
10 A 4-6 •
15 B 4-5 o
9 A 3-4 •
23 D 2-3 o
38 D 3-4 •
18 B 2-3 •
19 B 3-4 •
20 B 4-5 •
39 D 4-5 •
14 B 3-4 o
33 D 3-4 o
34 D 4-5 o
17 B 1-2 •
36 D 1-2 •
37 D 2-3 •
24 C 4-5 o
25 C 0-1 •
35 D 0-1 •
13 B 2-3 o
16 B 0-1 •
6 A 0-1 •
11 B 0-1 o
32 C 3-4 o
7 A 1-2 •
28 C 3-4 •
2 A 0-1 o
12 B 1-2 o
31 D 1-2 o

```
                             1        2         3   4       5   6

                            222|  11 331123133|133|22311| 12 2| 13
                           4679|58059288909434|767|45536|61378|221

Nematoscelis gracilis      5--2|--------------|---|-----|-----|---   00000
Euphausia gibba            ---1|--------------|---|-----|-----|---   00000
Thysanopoda pectinatus     -2--|--------------|---|-----|-----|---   00000
Nematobrachion boopis      4-11|11113131534435|--2|-----|-----|---   00001
Stylocheiron robustum      ----|----------1---|---|-----|-----|---   00001
Thysanopoda aequalis       ----|------------1-|---|-----|-----|---   00001
Thysanopoda obtusifrons    ----|-------------1|---|-----|-----|---   00001
Stylocheiron maximum       2221|--11-22-11111-|313|---3-|-----|---   0001
Euphausia pseudogibba      --1-|------232234-4|325|-3312|-----|---   0001
Nematobrachion sexpinosus  ----|--------------|-1-|-----|-----|---   0001
Nematoscelis atlantica     ----|--------------|5--|---1-|-----|---   0001
Thysanopoda monacantha     2231|11121-1211-544|445|54415|1111-|---   001
Thysanopoda orientalis     5441|---1---2322312|11-|2--1-|--1-1|---   001
Nematoscelis tenella       ----|-1114355455544|545|---1-|-----|-21   001
Euphausia similis          511-|-11-311311-135|525|--2--|1--3-|---   01
Thysanopoda tricuspidata   -11-|--------13-531|5--|15255|1-111|---   01
Nematoscelis microps       -552|---1--1-1--425|-55|334--|--155|---   10
Thysanopoda astylata       -1--|--------------|---|-----|--1--|---   10
Thysanopoda cristata       -1--|-----------1--|---|-----|-----|-1-   10
Euphausia diomedeae        -11-|----1511233213|525|14555|45421|-33   110
Stylocheiron abbreviatum   2221|----2---------|-44|-15--|3--51|323   110
Stylocheiron longicorne    ----|------3-1-11--|315|-----|-----|-42   110
Stylocheiron affine        ----|----------1---|514|-----|22---|---   110
Euphausia sanzoi           ----|--------1-----|---|-----|2--1-|---   1110
Stylocheiron carinatum     ----|--------11----|---|-----|12---|---   1110
Stylocheiron insulare      ----|--------------|---|-----|1----|---   1110
Euphausia paragibba        ----|--------------|---|-----|----1|---   1110
Euphausia sibogae          ----|--------------|---|-----|-----|-5-   1111

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                               00000001111111    00011
                               00001110000111
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Appendix 2. Two-way sample by species table produced by the program TWINSPAN (Hill, 1978) for the February/March 1985 samples. Values denote the categories of abundance in numbers (N in $n \times 10^{-1}$ m^{-3}): (1) $N < 1$; (2) $1 \leqslant N < 5$; (3) $5 \leqslant N < 10$; (4) $10 \leqslant N < 20$; (5) $N \geqslant 20$. Vertical lines separate sample groups; sample numbers along top margin. Hierarchy is in binary notation along the bottom and right margin for samples and species, respectively.

Order of samples (empty samples excluded). Denoted with sample number; station (A–D); depth of stratum (1 = 100; 2 = 200; 3 = 300; 4 = 400; 5 = 500; 6 = 600 m) and sampling period (○ = day; ● = night).

```
 3 A 1-3 ○    27 C 4-5 ●    15 B 1-2 ●    20 C 2-3 ○
 6 A 1-2 ●    30 D 2-3 ●    22 C 4-5 ○    14 B0-1 ●
 7 A 2-3 ●    31 D 3-5 ●    25 C 2-3 ●    23 C 0-1 ●
16 B 2-3 ●     4 A 4-5 ○    21 C 3-4 ●    24 C 1-2 ●
 8 A 3-4 ●    26 C 3-4 ●    29 D 1-2 ●    28 D 0-1 ●
 9 A 4-5 ●    12 B 3-4 ○    11 B 1-3 ○     5 A 0-1 ●
17 B 3-5 ●    13 B 4-5 ○    19 C 1-2 ○
```

```
                                    1      |   2   | 3 |  4

                               1  1233 2|1112222|112|1222
                            367689770146|2352519|190|43485

Stylocheiron carinatum      2-----------|-------|---|-----  000
Thysanopoda cristata        ---1--1-----|-------|---|-----  000
Euphausia gibba             1-----------|-------|---|-----  000
Nematobrachion sexpinosus   ------1-----|-------|---|-----  000
Stylocheiron maximum        1-23112-33-1|2---21-|1--|-----  0010
Nematoscelis gracilis       2-14--------|4------|---|-----  0010
Thysanopoda orientalis      255534544255|3344344|1--|-----  0011
Euphausia similis           2354454121--|512431-|---|-----  0011
Nematobrachion boopis       1--324131222|42-413-|--1|-----  0011
Nematoscelis tenella        ---1222211--|525--52|2--|-----  01
Stylocheiron robustum       ------------|--1---1|---|-----  01
Thysanopoda monacantha      ---4--111-1-|-4511--|1--|5-23-  10
Euphausia pseudogibba       ------1----1|51-2-11|---|3-25-  10
Nematoscelis microps        ------------|435553-|143|5-5--  10
Thysanopoda astylata        ---1--------|--23-2-|---|51-1-  10
Stylocheiron insulare       ------------|-------|---|2--2-  11000
Pseudeuphausia latifrons    ------------|-------|---|15---  11000
Stylocheiron affine         ------------|--2-1--|22-|321--  11001
Euphausia sibogae           ------------|-------|1--|1----  11001
Euphausia paragibba         ------------|-------|-1-|-----  11001
Stylocheiron longicorne     ---1--------|--1--1-|2-2|-----  1101
Euphausia tenera            ------------|3------|2--|2----  1101
Thysanopoda tricuspidata    2------2-1-1|5-11133|3-2|5553-  1101
Euphausia diomedeae         4---1-1-----|211214-|442|55-55  111
Stylocheiron abbreviatum    25----------|----1--|-11|-11-5  111
Euphausia sanzoi            -----------4|------1|---|-232-  111
Euphausia hemigibba         1-----------|-------|---|----1  111

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                            000000000000111111100000001
                            011111111111011111110001111
                            01111111111 000011
                            0000000011
                            00111111
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CHAPTER 3

Euphausiid distributions in the monsoon-influenced northwestern Indian Ocean, southern Red Sea and Banda Sea (Indonesia)

submitted to Journal of Plankton Research

EUPHAUSIID DISTRIBUTIONS IN THE MONSOON-INFLUENCED NORTHWESTERN INDIAN OCEAN, SOUTHERN RED SEA, AND BANDA SEA (INDONESIA)

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Keywords: Euphausiacea, NW Indian Ocean, Red Sea, Banda Sea, monsoon, upwelling, zoogeography

Abstract

Temporal and spatial distributions of Euphausiacea were studied off Somalia, in the Gulf of Aden and southern Red Sea in May and July-August 1992 during the SW monsoon and in January-February 1993 during the NE monsoon. Euphausiids were collected using an RMT1+8 in systematically stratified depth sampling in day and night series, to 500 m depth. In total 29 species were found, *Euphausia diomedeae*, *E.sibogae*, *Stylocheiron abbreviatum*, and *S.affine* were the most abundant during both sampling periods. During SW monsoon, maximum stocks (0-500 m, night catches) were 16 euphausiids m^{-2} in the Somali Current after upwelling, and downstream upwelling in the Great Whirl where *E.diomedeae* accounted for >75% for these stocks. Elsewhere *S.affine*, or *E.sibogae* were more abundant. During the NE monsoon, when upwelling was absent, again highest stocks (15 euphausiids m^{-2}) were found in the Somali Basin, *E.diomedeae* and *E.sibogae* were the most abundant species. In the Red Sea, during the onset of the SW monsoon, *S.affine* and *E.diomedeae* were the most abundant species, against *E.sibogae* during the NE monsoon. In contrast to these epipelagic species, seasonal variation was small in abundances of mesopelagic species. Vertical segregation was found in diurnally vertically migrating (DVM) species especially during night when species occurred at shallow depth. Under upwelling conditions during the SW monsoon, in the Somali Current certain DVM species were found shallower during the day compared to the NE monsoon when upwelling was absent. In the Red Sea, the similar deviating depth distributions were found during the NE monsoon when surface layers were mesotrophic, compared to the oligotrophic conditions during the onset of the SW monsoon. The present sample set was merged with similarly made stratified euphausiid samples from the Banda Sea (Indonesia), which is under the influence of the SE and NW monsoon. With cluster analysis, four main euphausiid assemblages were found. Two of them were confined to the southern Red Sea, and the 0-100 m stratum in both the Banda Sea and the NW Indian Ocean during night. The other two were predominant for midwater depths in both the NW Indian Ocean and the Banda Sea. None of the assemblages was typical for any of the monsoons. Seasonal variations were greatest in the 0-100 m stratum during night. Under the epipelagic, the euphausiid faunas in the respective basins, apparently remained relatively stable in space and time.

Introduction

Among the world's oceans, the Indian Ocean is unique because in the northern part (roughly above 10°S) the surface circulation reverses biannually with the alternation of the SW monsoon from May-September, and the NE monsoon from December-April. The South Equatorial Current between about 10° and 20°S (Figure 1), flows westward throughout the year and forms the southern boundary of the monsoon gyre system where current directions change seasonally (Wyrtki, 1973; Molinari *et al*., 1990).

During the SW monsoon, the strong tropospheric Findlater jet blows from NE Africa towards India, forming the core of the SW monsoon wind (Findlater, 1969) and driving the large clockwise gyre north of 10°S that is characterized by the conspicuous Somali Current and the Indian Monsoon Current (Figure 1). During the SW monsoon, along East Africa from about 4 to 10°N, and along the Arabian Peninsula, a series of small-scale clockwise gyres develops, of which the Great Whirl off Somalia between 5° and 10°N is the largest and most persistent. Associated with the SW monsoon, strong coastal upwelling off Somalia starts in May with an upwelling center at 4°N, and about one month later followed by a second center at 10°N. Together these centers display a two-wedge pattern, with the Great Whirl situated between them (Schott *et al*., 1990). In the upwelling area surface temperatures drop to about 18°C (Smith, 1982; Schott, 1983; Baars *et al*., 1994).

During the NE monsoon winds are less strong, and surface currents in the Arabian Sea reverse direction and are predominantly to the (north)west, fed by the North Equatorial Current between 0 and 10°N. The Somali Current also reverses direction and now flows to the southwest, merging with the East African Coastal Current, forming the eastward flowing Equatorial Counter Current between 0 and 10°S (Figure 1). The NE monsoon circulation north of the equator is not simply an anti-clockwise gyre, since northerly and north-east currents were observed off Somalia and the Arabian peninsula already in March, when winds are still northeast (Schott, 1983; Swallow, 1991).

Obviously, there is a strong influence of the monsoon regime on the biology of the NW Indian Ocean. With upwelling during SW monsoon, large amounts of nutrients are brought into the surface waters (Schott, 1983) leading to subsequent high chlorophyll *a* concentrations >0.50 mg m^{-3} (Krey, 1973; Yentsch and Phinney, 1992). The enriched water is transported with the Somali Current into the Great Whirl and, along Socotra, into the Arabian Sea, diluting out in a vast area of the ocean (c.f. Keen *et al*., 1997). High primary production in the surface layers, leads to high secondary and tertiary production with a consequently high oxygen consumption in upper and subthermocline layers. Bacterial decay of organic matter in the subthermocline further demands oxygen, and together with the old age of the water results in a strong depletion of oxygen at depths generally below 100 m with minimum values decreasing from 1 to >0.2 ml l^{-1} [or 43 to >8.6 μM] going from the equator to higher latitudes (Wyrtki, 1973).

In the NE monsoon winds are reversed and the flow in the Somali Current is in SW direction. Nutrient concentrations are then lower than during SW monsoon and chlorophyll *a* concentrations are fairly equal in the area, but less than 0.20 mg m^{-3} (Krey, 1973). Lower primary production rates during the NE monsoon suggest a relative poor state of the pelagic system in

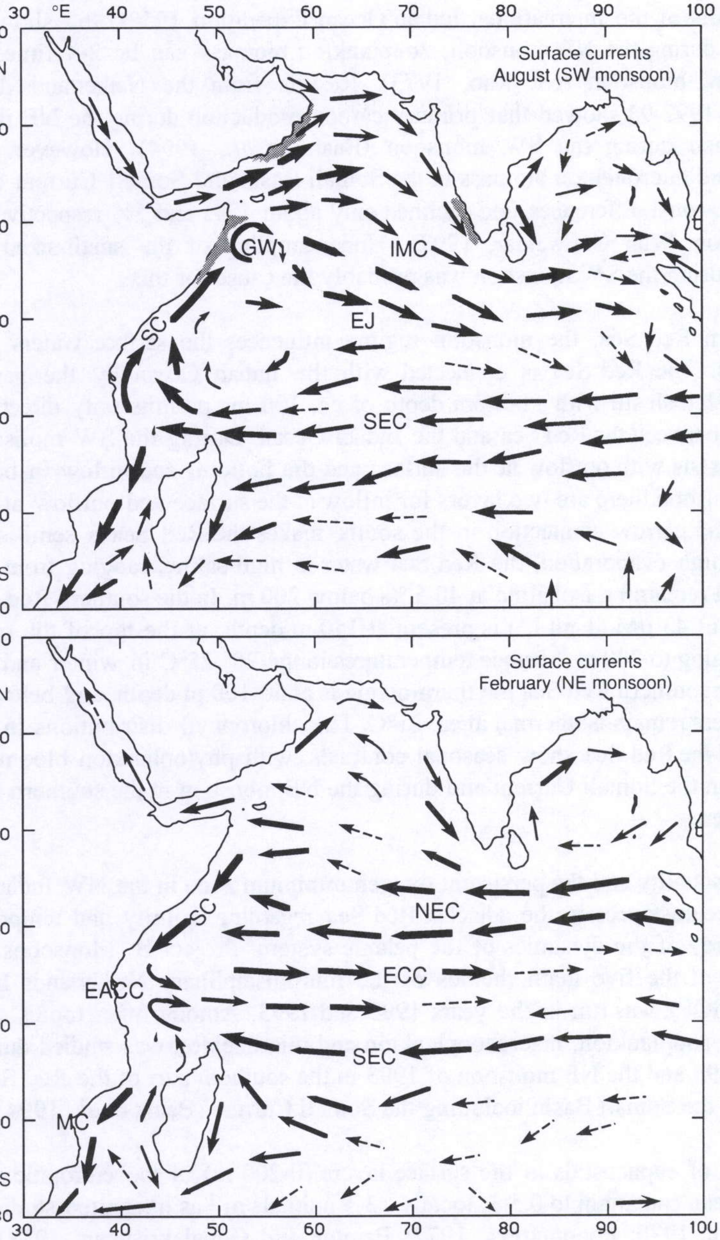

Fig. 1 The surface circulation pattern in the Indian Ocean during the NE monsoon in February (upper panel) and during the SW monsoon in August (lower panel). SEC - South Equatorial Current; ECC - Equatorial Counter Current; NEC - Northern Equatorial Current; SC - Somali Current; EACC - East Africa Coastal Current; GW - Great Whirl; IMC - Indian Monsoon Current. The Mozambique Current - MC - merges with southern branches of the SEC into the southward Agulhas Current (not depicted) along South Africa. Redrawn after Wyrtki (1973) and slightly adapted to Molinari *et al.* (1990). Stippled areas off Somalia and Oman with coastal upwelling during the SW monsoon.

the Somali Basin. This periodicity should also be found in the secondary production. Integrated results of the International Indian Ocean Expedition 1959-1965 show that in the Somali Basin during the NE monsoon, zooplankton biomass can be 2-4 times lower than during the SW monsoon (c.f. Rao, 1973). Results from the Netherlands Indian Ocean Programme in 1992-93 showed that primary carbon production during the NE monsoon was 33% lower than during the SW monsoon (Baars *et al.*, 1994). However, the average zooplankton and micronekton biomass in the Somali Basin and Somali Current did not show the expected seasonal differences, and declined only about 17% and 5% respectively from SW to NE monsoon (Van Couwelaar, 1997). Undersampling of the small-sized herbivorous zooplankton during the SW monsoon was probably the cause for this.

In the southern Red Sea, the monsoon regime influences the surface waters up to 20°N (Halim, 1984). The Red Sea is connected with the Indian Ocean by the narrow Bab-el-Mandab. The Hanish sill with a bottom depth of ca. 100 m, permits only direct exchange of surface waters between the Red Sea and the Indian Ocean. During the SW monsoon, a three-layer system exists with outflow at the surface and the bottom, and inflow in between. During the NE monsoon there are two layers for inflow at the surface and outflow at the bottom. The shallow and narrow connection in the south, makes the Red Sea a semi-isolated water mass. Due to high evaporation, the Red Sea water is high-saline, ranging from 37-40 ‰ at the surface and remaining isohaline at 40.5 ‰ below 200 m. In the southern Red Sea an oxygen minimum of 43 μM (1 ml l^{-1}) is present at 150 m depth, at the top of the oxygen minimum zone ranging to 700 m. Surface temperatures range 20°-25°C in winter and 25°-31°C in summer. In the southern Red Sea the thermocline is at 50-100 m depth, and below ca. 100 m the deeper waters remain isothermal at ca. 21°C. The chlorophyll distributions in the NW Indian Ocean and the Red Sea show seasonal contrasts, with phytoplankton blooms during the SW monsoon in the Somali Current and during the NE monsoon in the southern Red Sea and the Gulf of Aden.

The strong seasonality and the persistent oxygen minimum zone in the NW Indian Ocean and the extreme circumstances in the adjacent Red Sea regarding salinity and temperature, gave reason for a study of the dynamics of the pelagic system. Project B "Monsoons and Pelagic Systems", one of the five main themes of the multidisciplinary Netherlands Indian Ocean Programme (NIOP), was run in the years 1992 and 1993. Among other topics, the seasonal response of the zooplankton, macrozooplankton and micronekton was studied during the SW monsoon of 1992 and the NE monsoon of 1993 in the southern part of the Red Sea, the Gulf of Aden and in the Somali Basin including the Somali Current (Baars *et al.*, 1994).

Concentrations of euphausiids in the surface layers (0-200 m) of the eutrophic areas of the NW Indian Ocean can attain to 0.5-3, locally >3-5 animals m^{-3} as integrated studies point out (e.g. Weigmann, 1970; Ponomareva, 1972; Brinton and Gopalakrishnan, 1973). Regarding these high concentrations, in the NW Indian Ocean the euphausiids are considered as one of the important players in the ocean's biological system as consumers of phytoplankton, and as pelletizers contributing to the vertical organic flux (Peterson, 1991).

As in the NW Indian Ocean, the upper water layers of the Indo-Malayan region undergo strong hydrographic changes related to the half yearly alternating local SE and NW monsoons (Wyrtki, 1958, 1961). In the eastern Banda Sea (Indonesia), the upper layers are nutrient entrained by low rated upwelling during the SE monsoon (Zijlstra *et al.*, 1990). This accounts for a rich state of the pelagic system during this season compared to the NE monsoon, when upwelling is absent. For several non-vertically migrating mesopelagic euphausiid species in the Banda Sea, indications for an upward shift in the vertical distribution were found under the nutrient enriched circumstances during the SE monsoon (Van Couwelaar, 1994).

These findings were reason to search for a similar signal in euphausiid species under upwelling conditions in the NW Indian Ocean. The vertical and horizontal distribution of the euphausiids in the NW Indian Ocean and the southern Red Sea was studied during the SW monsoon of 1992 and the NE monsoon of 1993 based on stratified day and night sampling down to depths of 500-600 m. The results from a comparable study on euphausiids from the Banda Sea under monsoon related upwelling conditions (Van Couwelaar, 1994) will be incorporated in the discussion of horizontal and vertical distribution patterns. A study in monsoon ruled areas as the NW Indian Ocean and the Banda Sea in Indonesia could give an answer as to whether eusphausiid species react similar under similar circumstances in different geographical areas.

MATERIAL AND METHODS

For the NIOP Theme B, with the RV *Tyro* three cruises were made (Table I): B0 from 21 May to 12 June 1992 (pre-monsoon), B1 from 11 July to 8 August 1992 (SW monsoon) and B2 from 11 January to 6 February 1993 (NE monsoon). In total 16 stations were sampled (Figure 2), all were oceanic with bottom depths ranging from about 1100 to 4000 m, except for the stations in the Gulf of Aden (700-1500 m), the southern Red Sea (500-1000 m) and north of the strait Bab-el-Mandab (170 m).

Sampling for zooplankton and micronekton was carried out using a Rectangular Midwater Trawl 1+8 (Baker *et al.*, 1973). This is an opening and closing net system with two nets working synchronously: one an RMT1 with mesh size 0.32 mm and a nominal mouth opening of 1 m^2, the other an RMT8 with mesh size 4.5 mm and a nominal mouth opening of 8 m^2. Both day and night series were collected systematically in oblique downward hauls, generally in layers from 0-100 m, 100-200 m, 100-300 m (only in the day series), 200-300 m, 300-400 m, 400-600 m, or 300-600 m (B0/B1 cruise) or 300-500 m (B2 cruise) to maximum depths of 600 m (cruises B0 and B1) or 1000 m (cruise B2) (Table I). Sampling was completed between 8 a.m. and 5 p.m. for the day series and between 9 p.m. and 4 a.m. for the night series (local time). The speed of the net was monitored in real time and was maintained between 1.1 and 3.7 knots (mean 1.9 knots). Filtered volume was calculated from net speed and sampling time according to Roe *et al.* (1980). Tow duration's were about 60 minutes and the volumes of water filtered by the RMT8 ranged from 20000 to 40000 m^3. With the B0 and B1 cruises fifteen stations were made (Figure 2) of which five with complete day and night series (stations RS2, RS1, GA2, US1 and US0). Due to heavy weather and rough seas during the B1 cruise (SW monsoon), the day and night series at stations SB1, US2, SB2 and SI could not be completed. At stations SB0 and OFZ by day, and at stations US1.5 and GA1 by night, it was only possible to accomplish either a 0-100 m or a 0-300 m haul. During the B2 cruise (NE monsoon) 10 stations were made (Figure 3) of which eight with complete day and night series (stations RS2, RS1, GA2, GA1, SI, SB2, US2 and US1). Complete station and haul data can be found in Schalk and van Couwelaar (1994). Temperature, salinity and oxygen data were obtained from CTD upcasts (Hiehle and Baars, 1995).

Table I. Station data (date and position at the beginning of sampling are given), mixed layer characteristics, depth of the pycnocline/ nitracline, primary production, and the oxygen minimum zone for all RMT stations during the legs B0 (start SW monsoon), B1 (SW monsoon) and B2 (NE monsoon). Hydrographic data averaged from CTD rosette casts (Hiehle and Baars, 1994), between 1-6 per station. Primary production according to ^{14}C incubations (adapted from Veldhuis *et al.*, 1997); nd = not determined. Oxygen minimum zone defined as the zone with oxygen concentrations <43 µM (1 ml l^{-1}) as determined by the Sensormedics oxygen sensor on the CTD. Note that casts sometimes were not deep enough to determine the lower limit. Values were averaged for down- and upcasts to compensate for the lagging behind the sensor; if values were always >43 µM, the zone <86 µM is given in parenthesis. Lowest oxygen value originates from photometric Winkler titration on descrete samples during upcast.

Station	date	position		Mixed layer					Pycno-cline	Prim. prod.	Oxygen minimum zone	
		Lat. N	Long. E	Type of water	Temp (°C)	Nitrate (µM)	Chl (mg m^{-3})	Depth (m)	(m)	(g Cm^{-2}. $24h^{-1}$)	depth range (m)	lowest conc. (µM)
Start SW monsoon (1992)												
RS4	24-05	21° 05'	38° 08'	oligotrophic	26.7	0.0	0.1	42	42	nd	250-300	25 at 280 m
RS2	26-05	15° 58'	41° 36'	oligotrophic	30.0	0.0	0.2	10	43	nd	90->400	12 at 248 m
RS1	27-05	14° 45'	42° 16'	oligotrophic	30.1	0.1	0.2	13	59	0.6	90-500	16 at 197 m
BEM	29-05	12° 45'	43° 14'	oligotrophic	30.2	0.0	0.2	18	32	0.5	(125->145)	(56 at 143 m)
US2	02-06	10° 00'	50° 05'	recent upwelling	25.8	3.2	0.8	35	35	1.7	350-1160	23 at 496 m
SW monsoon (1992)												
SB0	14-07	2° 15' S	44° 56'	mesotrophic	26.6	0.5	0.4	93	93	nd	(510->750)	(52 at 750 m)
SB1	15-07	0° 04' S	45° 39'	mesotrophic	26.6	0.4	0.4	84	101	0.7	(560-1390)	(46 at 1000 m)
US0	17-07	3° 08'	48° 17'	mesotrophic	26.4	0.7	0.4	58	96	1.2	1020-1095	41 at 1082 m
US1	19-07	7° 02'	49° 45'	upwelling	20.8	12.1	0.6	20	0	0.8	220-1160	24 at 598 m
US2	21-07	10° 45'	51° 53'	recent upwelling	18.8	17.6	0.3	64	0	0.9	200-1300	18 at 749 m
US1.5	29-07	9° 27'	51° 19'	upwelling	18.1	18.8	0.7	18	0	nd	200-220 + 560->705	30 at 701 m
OFZ	26-07	7° 33'	55° 59'	downstream upw.	25.5	3.7	0.4	66	0/169	1.0	200-220 + 590-1160	23 at 802 m
SB2	27-07	6° 45'	54° 30'	downstream upw.	25.2	2.9	0.4	37	0/161	1.0	175-210 + 480->860	30 at 801

Table I. (continued)

Station	date	position		Mixed layer					Pycno-cline	Prim. prod.	Oxygen minimum zone	
		Lat. N	Long. E	Type of water	Temp (°C)	Nitrate (µM)	Chl (mg m^{-3})	Depth (m)	(m)	(g Cm^{-2}. 24h^{-1})	depth range (m)	lowest conc. (µM)
SI	31-07	12° 01'	56° 13'	downstream upw.	23.2	8.9	0.7	36	0/142	0.8	170-1305	5 at 196 m
GA1	04-08	12° 26'	49° 48'	oligotrophic	28.9	0.0	0.2	21	48	nd	110-1440	10 at 301 m
GA2	05-08	12° 12'	47° 01'	oligotrophic	29.7	0.0	0.2	54	54	0.5	80-1415	14 at 125 m
NE monsoon (1993)												
SB3	13-01	1° 55'	53° 34'	mesotrophic	26.3	0.6	0.3	53	53	1.0	(160-225 + (450->750 m)	(49 at 750 m)
SB2	15-01	6° 13'	52° 27'	mesotrophic	26.8	0.3	0.3	38	38	1.0	600-1230	28 at 699 m
US1	18-01	7° 34'	50° 30'	mesotrophic	26.6	0.3	0.3	67	67	0.6	180-1075	24 at 499 m
US2	20-01	10° 51'	51° 59'	mesotrophic	26.0	1.0	0.3	74	74	0.8	165-1400	20 at 749 m
SI	24-01	12° 03'	54° 58'	mesotrophic	26.0	0.9	0.3	77	77	0.9	150-1285	9 at 225
GA1	27-01	12° 50'	50° 05'	mesotrophic	25.8	0.5	0.5	92	92	1.3	130-1395	15 at 299
GA2	29-01	12° 24'	46° 58'	mesotrophic	25.2	2.2	0.6	62	62	1.0	120-1500	12 at 200 m
BEM	01-02	12° 44'	43° 14'	mesotrophic	26.1	0.3	0.4	58	58	nd	(130->150)	(78 at 151 m)
RS1	02-02	14° 36'	42° 20'	mesotrophic	25.6	0.2	1.0	76	76	1.4	95->300	13 at 149 m
RS2	03-02	15° 55'	41° 37'	mesotrophic	25.7	0.9	1.1	56	56	0.6	100-455	17 at 199 m

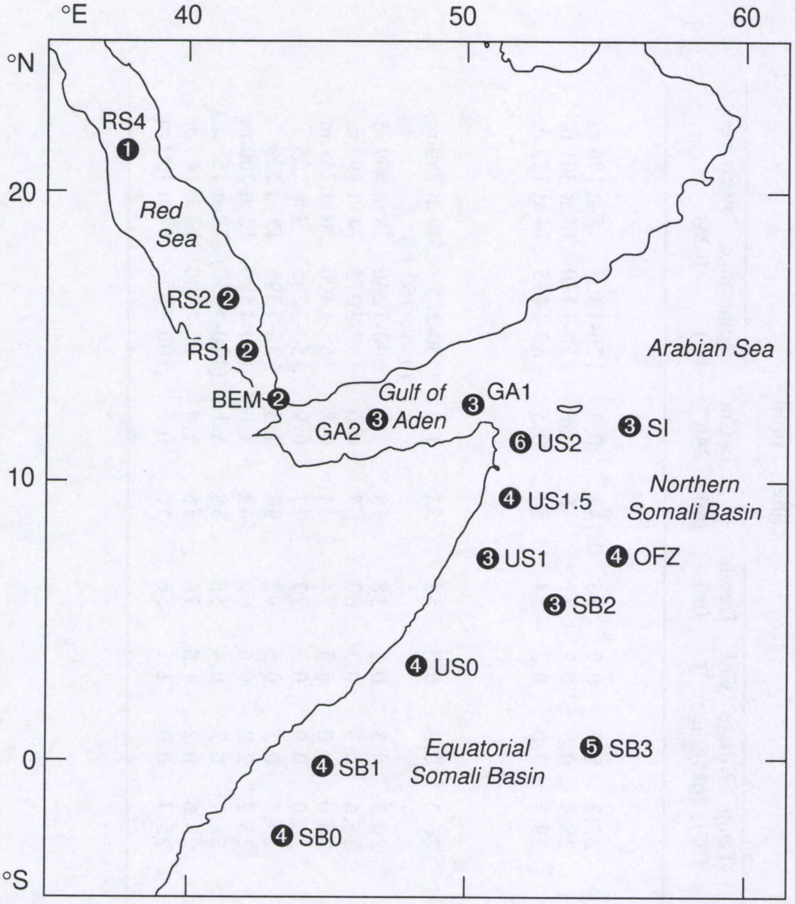

Fig. 2 Position of the 16 *Tyro* RMT stations during cruises B0 (21 May to 12 June 1992 - station code 1, 2, 6), B1(11 July to 8 August 1992 - code 3, 4, 6), and B2 (11 January to 6 february 1993 - code 4, 5, 6). RS, Red Sea; BEM, Bab el Mandab; GA, Gulf of Aden; US, Somali Current; SI, Socotra Island; OFZ, Owen Fraction Zone; SB, Somali Basin.

On board, the RMT8 samples were sorted into major systematic groups which were preserved in a borax-buffered 4% formalin solution in sea water. For the present study only the euphausiids from RMT8 samples were used. Thus eventual small euphausiid stages (larvae and juveniles) were excluded. Stomach filling of relevant species was quantitatively studied in relation to depth distribution and time of day. From each subsample, if possible a minimum of 20 specimens was studied and the results were averaged. The filling was rated in five classes: 0, 0-25, 25-50, 50-75, 75-100 %.

The vertical distribution of the euphausiids was studied at 10 stations, all with adequate sampling series, thus OFZ, US1.5, SB0, and SB3 were omitted. Eight stations were sampled in both seasons: RS1, RS2, GA1, GA2, US2, US1, SI and SB2. Stations US0 and SB1 were occupied during the SW monsoon only. The weighted mean depth (WMD) of the euphausiids in the sampled water column was calculated with

$$\mathrm{WMD} = \sum \frac{d_i\, v_i}{V}$$

where d_i is the depth of a sampled layer (i. e. the mean of the upper and lower limit of the stratum), v_i is the abundance (n m^{-2}) in this layer and V is the total abundance (n m^{-2}) in the sampled water column. The 0-600 m series from the B0 and B1 cruises were standardized to 0-500 m by reduction of the 300-600 m layer with 1/3. This allows proper comparisons with the results of the 0-500 m sampling series during the B2 cruise. The WMD obtained from 0-300 m sampling, was used only if the species was epipelagic and non-migrating or present in the upper layer during night, when migrating — assuming that most of the population was present in the 0-300 m column at that time. The 500-1000 m hauls were not standard in the sampling program, therefore these were excluded from calculations of the WMD.

In the study area five regions were distinguished hydrographically and stations were pooled: the southern Red Sea (RS1, RS2), the Gulf of Aden (GA1, GA2), the northern Somali Basin (SI, OFZ, SB2), the equatorial Somali Basin (SB0, SB1, SB3, US0) and the Somali Current (US1, US1.5, US2). Note that station US0 (at 4°N) was assigned to the equatorial part of the Somali Basin. When this station was made in July, the upwelling conditions that prevailed there at the onset of the SW monsoon one month earlier, had disappeared by the northward propagation of the upwelling wedge (c.f. Schott *et al.*, 1990). Pooling of US0, SB1 and SB0 is based on the corresponding temperatures, silicate, nitrate and chlorophyll *a* concentrations in the surface waters in the period from 13 July to 3 August 1992, when these stations were made. Due to upwelling at US1 and US2 in the Somali Current, surface temperatures were about 5°C lower and silicate, nitrate and chlorophyll concentrations were considerably higher compared to US0 (c.f. Baars *et al.*, 1994).

The clustering program CLUSTAN (Wishart, 1978) was used to analyze the quantitative data from all samples in order to search for patterns in spatial and seasonal distribution of the euphausiids. Hierarchical classification based on a similarity matrix, made it possible to distinguish sample groups (clusters) that may delimit or represent different biotic communities. The raw data showed great variance in concentration within the same species from comparable samples, i. e. samples made from the same depths and during the same time of day during a cruise. This points to heterogeneous distributions, not uncommon in planktonic animals. Therefore, the species concentrations (number of individuals in 1000 m^3) were first logarithmically transformed [$y=\log(10x)+1$], reducing the weighting of abundant species with a high score and leaving the rare ones relatively unaffected. CLUSTAN was run, using the average-linkage method (Sokal and Mirchener, 1958) in combination with the Bray-Curtis coefficient. Species-grouping was found by inverse analysis of the results of the normal analysis. Species were distinguished as dominant for a cluster if present in ≥66.7% of the samples in that cluster. Species were distinguished as characteristic for a cluster (or a group of clusters) if in there, the average concentration was ≥75% of the total concentration in the data set.

Table IIa. Abundance of Euphausiaceae (n m^{-2}, 0-500 m unless otherwise indicated in italics) in the southern Red Sea, Gulf of Aden, Somali Current, Northern Somali Basin (NSB), and equatorial Somali Basin during the B0 and B1 cruises (onset and height of SW monsoon) by day (D) and night (N). Ommitted are the incomplete daytime series (0-100 m only) at SB2, SI, OFZ, and SB0 when no euphausiids were found. Values <0.01 denoted with 0.00. Numbers from series <500 m depth in italics.

	southern Red Sea						Gulf of Aden			Somali Current						NSB		equatorial Somali Basin			
Cruise	B0	B0	B0	B0	B0	B0	B1	B1	B1	B0	B1	B1	B1	B1	B1	B1	B1	B1	B1	B1	B1
Station	RS4	RS2	RS2	RS1	RS1	BEM	GA2	GA2	GA1	US2	US2	US2	US1.5	US1	US1	SB2	SI	US0	US0	SB1	SB1
Period	N	D	N	D	N	D	D	N	N	D	D	N	N	D	N	N	N	D	N	D	N
Range (0- x m)	500	500	500	500	500	*160*	500	500	*300*	500	500	*300*	*100*	500	500	*300*	500	500	500	*300*	500
Total of euphausiids	1.11	1.26	6.85	3.02	2.81	*0.71*	2.35	5.60	*5.73*	4.00	2.55	*8.96*	*1.34*	0.15	8.90	*2.11*	15.80	2.55	16.49	*1.77*	1.79
Number of species	5	5	5	5	5	5	11	16	11	15	7	11	12	5	13	9	13	22	18	6	15
E. diomedeae	0.47	0.05	3.35	0.02	0.01		0.95	2.27	*2.08*	0.15	0.17	*0.45*	*0.57*	0.03	0.70	*1.83*	11.90	0.42	13.72	*0.76*	0.17
E. sibogae	0.16	0.17	0.36	0.02	0.90	*0.05*	0.17	0.03	*0.57*	0.05	1.43	*7.29*	*0.06*	0.08	4.11	*0.02*	0.34	0.66	0.41		
S. abbreviatum	0.11	0.04	0.58	0.03	0.08		0.40	0.03		0.01		*0.03*	*0.06*		0.29		0.83	0.09			0.07
S. affine	0.20	0.71	1.54	2.94	1.77	*0.57*		0.01		0.13								0.02			
E. sanzoi	0.16	0.29	1.02	0.02	0.03	*0.01*				0.01	0.07	*0.06*	*0.05*		2.70						
S. longicorne							0.28	0.43	*0.49*	0.06		*0.03*	*0.03*		0.03		0.27	0.09	0.08		
N. gracilis							0.13	0.50	*1.50*	2.40	0.81	*0.30*	*0.12*	0.02	0.37		1.03	0.47	0.40		0.24
T. monacantha							0.01	1.14	*0.20*	0.13			*0.08*		0.09	*0.07*	0.40	0.01	0.18		0.19
N. tenella								0.05	*0.02*	0.34	0.00	*0.13*	*0.07*	0.01	0.11	*0.01*		0.03	0.17	*0.12*	0.09
S. maximum							0.11	0.12	*0.18*	0.02		*0.13*			0.02		0.02	0.01	0.20	*0.03*	0.04
N. flexipes							0.26	0.28	*0.25*	0.23		*0.41*	*0.13*		0.26	*0.06*	0.83	0.01	0.25		
T. orientalis							0.02	0.50	*0.40*	0.06	0.04	*0.14*			0.04		0.01	0.01	0.02		0.21
T. tricuspidata							0.01		*0.00*					0.01	0.09	*0.08*	0.02	0.06	0.33	*0.83*	0.55
N. microps										0.14			*0.11*		0.09	*0.02*	0.02	0.09	0.15	*0.01*	0.02
N. boopis							0.00	0.00		0.02	0.02	*0.01*						0.00	0.03	*0.02*	0.02
T. astylata								0.21	*0.03*				*0.03*			*0.02*	0.08	0.03	0.22		

Table IIa. (continued)

	southern Red Sea						Gulf of Aden			Somali Current						NSB		equatorial Somali Basin			
Cruise	B0	B0	B0	B0	B0	B0	B1	B1	B1	B0	B1	B1	B1	B1	B1	B1	B1	B1	B1	B1	B1
Station	RS4	RS2	RS2	RS1	RS1	BEM	GA2	GA2	GA1	US2	US2	US2	US1.5	US1	US1	SB2	SI	US0	US0	SB1	SB1
Period	N	D	N	D	N	D	D	N	N	D	D	N	N	D	N	N	N	D	N	D	N
Range (0- x m)	500	500	500	500	500	*160*	500	500	*300*	500	500	*300*	*100*	500	500	*300*	500	500	500	*300*	500
Total of euphausiids	1.11	1.26	6.85	3.02	2.81	*0.71*	2.35	5.60	*5.73*	4.00	2.55	*8.96*	*1.34*	0.15	8.90	*2.11*	15.80	2.55	16.49	*1.77*	1.79
Number of species	5	5	5	5	5	5	11	16	11	15	7	11	12	5	13	9	13	22	18	6	15
T. aequalis																*0.01*		0.06	0.04		0.04
S. robustum																					
E. paragibba								0.01					*0.04*					0.06	0.22		0.04
E. similis																		0.02	0.05		0.06
E. hemigibba																		0.01	0.02		
E. tenera								0.00										0.34			
T. pectinata																			0.01		
E. pseudogibba						*0.01*															
S. carinatum						*0.08*				0.27											
N. sexpinosum																	0.03				0.01
T. obtusifrons								0.01													0.05
S. elongatum																		0.02			
E. mutica																		0.05			

Table IIb. Abundance of Euphausiaceae (n m^{-2}, 0-500 m unless otherwise indicated in italics) in the southern Red Sea, Gulf of Aden, Somali Current, northern Somali Basin, and equatorial Somali Basin (ESB) during the B2 cruise (NE monsoon) by day (D) and night (N). Ommitted is BEM-D (0-170 m) where no euphausiids were found with RMT8. Values <0.01 denoted with 0.00. Numbers from series <500 m depth in italics.

	southern Red Sea				Gulf of Aden				Somali Current				northern Somali Basin				ESB
cruise	B2	B2	B2	B2	B2	B2	B2	B2	B2	B2	B2	B2	B2	B2	B2	B2	B2
Station	RS2	RS2	RS1	RS1	GA1	GA1	GA2	GA2	US2	US2	US1	US1	SI	SI	SB2	SB2	SB3
period	D	N	D	N	D	N	D	N	D	N	D	N	D	N	D	N	N
range from surface (m)	500	500	*300*	*300*	500	500	500	500	500	500	500	500	500	500	500	500	*100*
total of Euphausiaceae	1.99	6.05	*2.01*	*12.70*	2.29	6.93	8.03	4.67	3.48	5.05	3.87	4.60	5.00	15.60	4.78	5.41	*9.89*
number of species	5	6	6	7	11	10	9	14	15	17	12	17	15	11	17	14	11
Euphausia diomedeae	0.08	0.24	*0.00*	*0.04*	1.08	2.44	3.08	1.26	0.33	1.79	1.13	2.12	2.08	9.03	2.22	3.02	*7.62*
Euphausia sibogae	1.28	3.48	*1.89*	*11.00*	0.08	0.87	1.25	0.26	0.74	0.36		0.20	0.92	1.44	0.59	0.02	
Stylocheiron abbreviatum	0.00	0.73	*0.00*	*0.11*		0.74		0.05	0.01		0.15	0.06	0.02	1.82	0.18	0.36	*0.91*
Stylocheiron affine	0.55	1.31	*0.11*	*1.51*	0.12		0.09	0.02		0.08		0.07	0.01	0.42			*0.26*
Euphausia sanzoi	0.08	0.29	*0.00*	*0.01*											0.01		*0.09*
Stylocheiron longicorne			*0.00*	*0.02*	0.14	0.15		0.52	0.08	0.26	0.04	0.03	0.20	0.17	0.06		
Nematoscelis gracilis				*0.02*	0.10	0.69	0.83	0.61	0.95	1.13	0.66	1.02	0.84	1.58	0.86	0.12	
Thysanopoda monacantha		0.00			0.23	0.61	0.36	0.06	0.44	0.18	0.85	0.30	0.17		0.04	0.18	*0.23*
Nematoscelis tenella					0.02	0.01		0.09	0.30	0.33	0.30	0.26	0.03	0.07	0.31	0.67	*0.14*
Stylocheiron maximum					0.13	0.06	0.41	0.11	0.03	0.00	0.06	0.00	0.04	0.22	0.04	0.34	*0.09*
Nematobrachion flexipes					0.12	0.71	1.20	1.00	0.17	0.11	0.11	0.10	0.57	0.47	0.06	0.17	
Thysanopoda orientalis					0.25	0.64	0.71	0.59	0.18	0.45	0.39	0.20	0.04	0.35	0.13	0.17	
Thysanopoda tricuspidata					0.01			0.01	0.02	0.14	0.12	0.05	0.01		0.04	0.21	*0.11*
Nematoscelis microps							0.09		0.06	0.06		0.04	0.04	0.03	0.09	0.01	
Nematobrachion boopis									0.06	0.06	0.07	0.01	0.01		0.08	0.09	
Thysanopoda astylata								0.01	0.08	0.01		0.03	0.01			0.04	

Table IIb. (continued)

	southern Red Sea				Gulf of Aden				Somali Current				northern Somali Basin				ESB
cruise	B2	B2	B2	B2	B2	B2	B2	B2	B2	B2	B2	B2	B2	B2	B2	B2	B2
Station	RS2	RS2	RS1	RS1	GA1	GA1	GA2	GA2	US2	US2	US1	US1	SI	SI	SB2	SB2	SB3
period	D	N	D	N	D	N	D	N	D	N	D	N	D	N	D	N	N
range from surface (m)	500	500	*300*	*300*	500	500	500	500	500	500	500	500	500	500	500	500	*100*
total of Euphausiaceae	1.99	6.05	*2.01*	*12.70*	2.29	6.93	8.03	4.67	3.48	5.05	3.87	4.60	5.00	15.60	4.78	5.41	*9.89*
number of species	5	6	6	7	11	10	9	14	15	17	12	17	15	11	17	14	11
Thysanopoda aequalis											0.01						*0.15*
Stylocheiron robustum								0.10	0.04	0.08		0.10			0.09		*0.23*
Euphausia paragibba																	
Euphausia similis															0.01		
Euphausia hemigibba												0.02					
Euphausia tenera																	*0.06*
Thysanopoda pectinata										0.00						0.01	
Euphausia pseudogibba										0.01							
Stylocheiron carinatum																	
Nematobrachion sexpinosum																	
Thysanopoda obtusifrons																	
Stylocheiron elongatum															0.01		
Euphausia mutica																	

RESULTS

In total 29 species were collected. To obtain an impression of abundance, night time catches were used as species concentrate in the surface layers at night and the changes of net avoidance are lower. In the Red Sea proper only ten species were found, of which five were regular. In the Gulf of Aden apart from these ten, another 12 species occurred, whereas in the NW Indian Ocean proper, all 29 species were encountered (Tables IIa and IIb). In the Red Sea and the Indian Ocean *Euphausia diomedeae*, *E.sibogae*, were the most frequent and abundant species, followed by *Stylocheiron abbreviatum* and *S.affine* for both seasons. The abundances for the species at the various stations and the seasons sampled were very irregular, but, except for *E.diomedeae*, *E.sibogae* and perhaps *S.affine*, all species showed over all similar abundances between the seasons sampled. In the SW monsoon, total euphausiid catches were highest at the stations US0 (Somali Current) and SI (Great Whirl), caused by high concentrations of *E.diomedeae* (12-14 m^{-2}). During the NE monsoon, *E.diomedeae* also accounted for high catches at stations SI and SB3. In the SW monsoon, the density of *E.sibogae* peaked at stations US2 and US1 (4-7 m^{-2}) and was relative low at the other stations (0.03-0.9 m^{-2}), but the mean density was higher during the NE monsoon (2.2 *vs* 1.3 m^{-2}) in particular due to high values in the Red Sea (Table IIb). *S.affine* had its maximum densities in the Red Sea during both seasons (2.9 and 1.5 m^{-2} respectively). *E.sanzoi* was found in the Red Sea and the Indian Ocean, but absent from the Gulf of Aden. At station US1 in the Somali Current during the SW monsoon it was found in a relatively high concentration (2.7 m^{-2}). *Nb.flexipes* was abundant in the Gulf of Aden during the NE monsoon (0.7-1 m^{-2}), considerably higher than in the remaining area's. During the SW monsoon, the species did not show significant geographical differences. In the Somali Basin *N.tenella* attained maximum abundance during NE monsoon. In the Gulf of Aden its abundance was low and similar during both monsoons. *T.orientalis* was abundant in the Gulf of Aden during both monsoons (0.4-0.6 m^{-2}), but in the Somali Basin it was low during SW monsoon ($\leq$0.2 m^{-2}) and high during NE monsoon (0.2-0.4 m^{-2}).

The vertical distributions of 15 regularly found species were studied over 0-500 m —unless otherwise stated, and the weighted mean depths (WMD) given below refer to this range. Remarks on deep distribution are made if additional 500-1000 m samples were available. Ten species performed diurnal vertical migration (*E.diomedeae*, *E.sibogae*, *N.gracilis*, *N.microps*, *N.tenella*, *Nb.flexipes*, *T.orientalis*, *T.tricuspidata*, *T.monacantha,* and *T.astylata*), and 5 did not (*S.abbreviatum*, *S.affine*, *S.longicorne*, *S.maximum*, and *Nb.boopis*).

Stratification was found in day-night patterns for the above mentioned migrating species (Figure 3). Most clearly during night, depth preferences and migratory behaviour indicated by the WMD's, resulted in vertically grouping of species. *E.diomedeae*, *E.sibogae*, *T.tricuspidata*, and *T.astylata* were found during night in the upper 200 m predominantly. The WMD's ranged from 50 to 100 m and were regular for both seasons, however, *E.sibogae* was exceptionally deep at GA1 and GA2 during the NE monsoon. *E.diomedeae* was well concentrated in the upper layer throughout, and the over-all mean WMD was 75 m. In particular *T.tricuspi-data* and *T.astylata* preferred the surface layer (0-100 m), but were found down to 500 m in a single case each. The WMD's ranged from 50 to 75 m in *T.trcuspidata* and 50-150 m in *T.astylata* (Figure 3). *T.monacantha* and *N.microps* were found in the subsurface layers (100-200 m) mainly. The WMD's ranged from 100 to 200 m, except at US1 and SB2 during the SW monsoon (Figure 3), where both species were occurring more shallow (WMD about 50-100 m). *T.orientalis* was found at all depths >100 m, but 100-300 m was preferred. The WMD's were between 200 and 300 m (Figure 3); however, at US0 during the SW monsoon considerably lower (340 m). During both monsoons *N.gracilis* and *N.tenella* showed an irregular distribution pattern, and their WMD's ranged widely from 50 to 400 m (Figure 3). Generally the WMD of *N.gracilis* was between 200 and 300 m, but it was very shallow at US1 and US2 (75-90 m) during the SW monsoon and at SB2 during the NE monsoon (50 m). *Nb.flexipes* was found from 0-500 m during the SW monsoon, with a preference for 100-300 m. The WMD's ranged from 50 to 230 m. There was a tendency for a

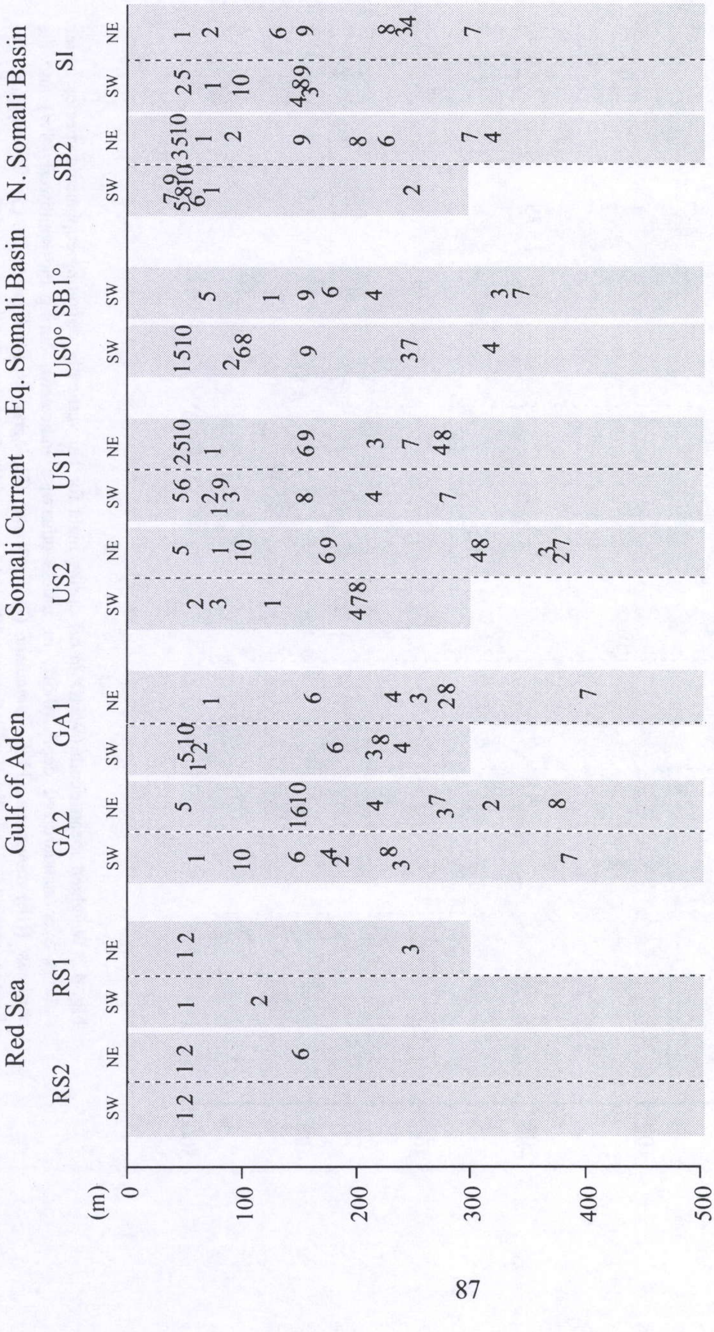

Fig. 3 Weighted mean depth (WMD in m) at daytime for ten vertically migrating euphausiid species at ten stations, during the southwest (SW) and the northeast (NE) monsoons. (1) *E.diomedeae*, (2) *E.sibogae*, (3) *N.gracilis*, (4) *T.orientalis*, (5) *T.tricuspidata*, (6) *T.monacantha*, (7) *N.tenella*, (8) *Nb.flexipes*, (9) *N.microps*, (10) *T.astylata*. Depth range standardized at 0-500 m, unless otherwise indicated. Lenght of grey bar represents sampled depth range. Stations are marked (°) for sampling during SW monsoon only.

shallow occurrence at nighttime at US1 (150 m), US0 (100 m) and SI (150 m), and the WMD was decreasing from the Gulf of Aden to the Somali Current and downstream in the northern part of the Somali Basin (Figure 3). During the NE monsoon, the species was not found in the upper 100 m, and preferred 200-300 m. The WMD's ranged from 220 to 380 m, being greater at every station compared to the SW monsoon (Figure 3).

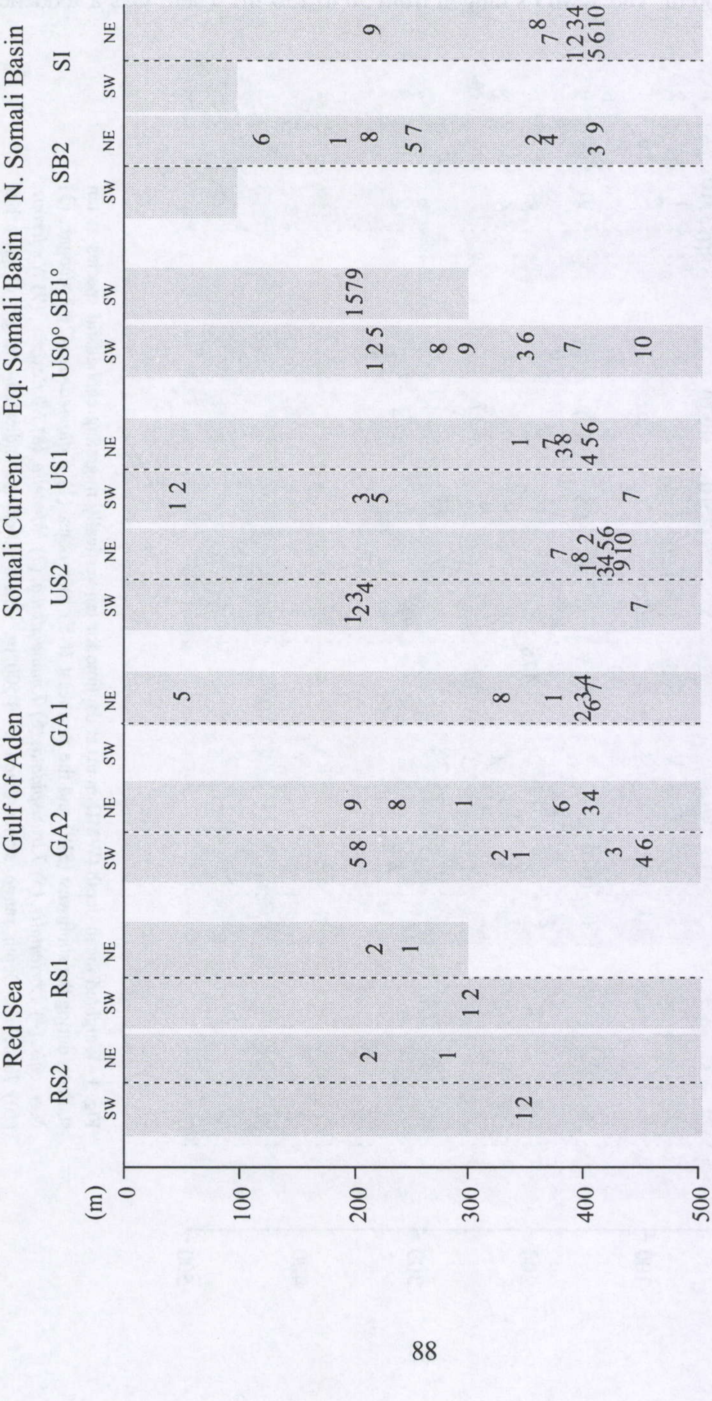

Fig. 4 Weighted mean depth (WMD in m) during night for ten vertically migrating euphausiid species at ten stations, over standardized depth (0-500 m, unless otherwise indicated), during the southwest (SW) and the northeast (NE) monsoons. (1) *E.diomedeae*, (2) *E.sibogae*, (3) *N.gracilis*, (4) *T.orientalis*, (5) *T.tricuspidata*, (6) *T.monacantha*, (7) *N.tenella*, (8) *Nb.flexipes*, (9) *N.microps*, (10) *T.astylata*. Stations are marked (°) for sampling during SW monsoon only. Lenght of grey bar represents sampled depth range.

The migrating species were found deeper during the day (Figure 4). All but *N.microps*, *T.astylata* and *T.tricuspidata* were also regularly found with the deep 500-1000 m samples made during the NE monsoon. Daytime distributions showed vertical differences related to the species' migratory range and seasonal response as well. *T.orientalis*, *T.monacantha* and *T.astylata* were practically always found deep (300-500 m) and the first two were also present in the 500-1000 m samples during NE monsoon. The WMD's ranged from 400 to 450 m, but *T.orientalis* was shallow at US2 (WMD=200 m) during the SW monsoon and *T.monacantha* was shallow at SB2 (WMD=120 m) in the NE monsoon. *N.gracilis* and *N.tenella* were staying deep also, except in the SW monsoon when *N.gracilis* occurred less deep at US1 and US2 and *N.tenella* occurred less deep at SB1 (all WMD=200 m). During the NE monsoon, *N.tenella* was found shallow at SB2 also (WMD=250 m). *E.diomedeae*, *E.sibogae* and *T.tricuspidata* were all staying from 100-400 m predominantly, their WMD's were ranging 200-400 m. During the NE monsoon, *T.tricuspidata* was absent from the 500-1000 m samples. In these three species seasonal differences were considerable. During the SW monsoon at daytime, *E.diomedeae* was deep in the Red Sea and the Gulf of Aden, but less deep in the Somali Current and the Equatorial Somali Basin (Figure 4). In contrast to this, during the NE monsoon at daytime *E.diomedeae* stayed shallow in the Red Sea and deep in the Somali Current (Fig 4). Generally, the daytime WMD for *E.sibogae* ranged from 300 to 400 m, but was much shallower in the Somali Current during the SW monsoon (130 m) and in the Red Sea during the NE monsoon (217 m) (Table III). For *T.tricuspidata* the daytime WMD was about 200 m during the SW monsoon, but shallow (50 m at GA1), mediate (250 m at SB2), or deep (400 m at US1, US2 and SI) during the NE monsoon.

The feeding pattern, as related with depth and time of day, was regular in *E.diomedeae*, *T.tricuspidata*, and *T.monacantha*. When found in the surface layers during night, the stomachs of these species were almost always completely filled. During the day the species were found deeper, with stomachs frequently empty or partially filled and contents digested. The feeding pattern in *N.tenella* and *Nb.flexipes* was less regular compared to the previous species. During both seasons at night, most stomachs were partially (50-100%) filled upon time of catch, whereas during the day — when found deeper, most stomachs still were partially filled and the remaining minority of stomachs were empty. Only occasionally deep-caught *Nb.flexipes* from 500-1000 m, had empty stomachs during the day. *N.gracilis* and *T.orientalis* were always found with partially filled stomachs (50-100%) disregarding the depth or time of day.

The abundant species that did not perform diurnal vertical migration, were ranked by increasing WMD below. *S.abbreviatum* was found in all areas predominantly above 300 m. The WMD ranged from 50 to 200 m (Figure 5). Throughout the whole column where *S.abbrevia-tum* was found, stomachs appeared to be empty in nearly all of the samples, disregarding season or time of day. During both seasons *S.affine* was apparently most abundant in the southern Red Sea, where it was found from 0 to 500 m, and in the additional 500-1000 m day and night samples during the NE monsoon as well. Here, the WMD ranged from 180 to 330 m (Figure 5). When *S.affine* was found in the other areas, concentrations were low — always less than 10 specimens in the sampled column. During both seasons and disregarding the time of day, in almost every sample *S.affine* was found with empty stomachs. *S.longicorne* was found below 100 m both during day and night, except at US0 (B1 cruise) when two specimens were found in the 0-100 m layer at daytime. The WMD's ranged from 150 to 300 m (Figure 5) and day-night differences were small. In many cases *S.longicorne* was found even shallower during the day than during night (Figure 5). In only a

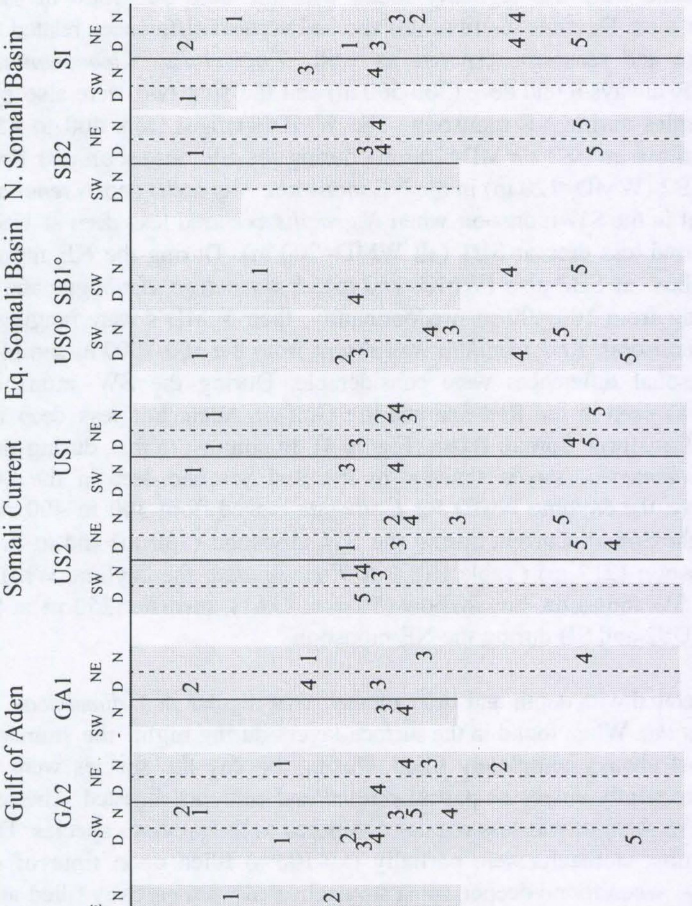

Fig. 5 Weighted mean depth (WMD in m) for day (D) and night (N), for five non vertically migrating euphausiid species at ten stations, during the southwest (SW) and the northeast (NE) monsoons. (1) *S.abbreviatum* (over-all mean WMD 106 m, standard deviation 46 m), (2) *S.affine* (mean 193 m, s.d. 84 m), (3) *S.longicorne* (mean 228 m, s. d. 38 m), (4) *S.maximum* (mean 281 m, s. d 79 m) and (5) *Nb.boopis* (mean 381 m, s. d 73 m). Depth range standardized at 0-500 m, unless otherwise indicated. Lenght of grey bar represents sampled depth range. Stations are marked (°) for sampling during SW monsoon only.

few cases (9 out of 41) filled stomachs were found without obviously preferred day or night feeding. Irrespective the of time of day, *S.maximum* occurred always below 100 m in all areas, except at GA1 during the SW monsoon, when it was found with a single specimen in the 0-100 m layer. In the NE monsoon it was found during night with the 500-1000 m samples as well (GA1 and US2). The average WMD was ranging from 175 to 412 m (Table III). During the SW monsoon about 95% of the animals caught at night had empty stomachs; whereas during the NE monsoon, this was the case in about 50% of the animals. *Nb.boopis* was never abundant — mostly less than 10 specimens in the sampled column, ranging from 100 to 500 m during the SW monsoon, and from 300 to 500 m during the NE monsoon. Occasionally it was also found with the 500-1000 m samples during cruise B2 (GA1, GA2, and US2 during night). In most cases, the WMD was about 400 m, except during the SW monsoon at GA2 (night) and US2 (day), when it was 200-250 m (Figure 5). During both seasons, *Nb.boopis* was equally found with empty or filled stomachs, irrespective of depth or time of day.

Table III. Weighted mean depth (m) of Euphausiaceae over standardized sampling depth (range from surface to 160, 300 or 500m) from stations in southern Red Sea, Gulf of Aden, Somali Current, northern Somali Basin (NSB) and equatorial Somali basin (ESB) during cruises B0 (onset SW monsoon), B1 (SW monsoon) — first part of Table — and cruise B2 (NE monsoon) — second part of Table — for day (D) and night (N). Southern Red Sea* and station US2* in Somali Current sampled during cruise B0.

Cruise B0/B1	southern Red Sea*					Gulf of Aden			Somali Current					NSB		ESB			
type of water	oligotrophic					oligotrophic			oli.	upwelling				downstr. upwelling		mesotrophic			
Station	RS1	RS1	RS2	RS2	BEM	GA1	GA2	GA2	US2*	US1	US1	US2	US2	SB2	SI	SB1	SB1	US0	US0
periode	D	N	D	N	D	N	D	N	D	D	N	D	N	N	N	D	N	D	N
range (m)	500	500	500	500	160	375	500	500	500	500	500	500	300	300	500	300	500	500	500
S.affine	181	208		200	84			53	100									201	
E.sanzoi	305	51		87	134				100		55	203	63						
E.diomedeae	305	51		52		55	331	62	222	50	74	203	121	68	76	203	113	209	52
E.sibogae	305	104		53	134	56	316	196	274	50	68	206	63	270	50			216	85
S.abbreviatum	139	99	153	116			133	53	100		55		201		95		120	65	
N.gracilis						210	402	226	351	144	87	201	83		157		310	346	229
N.tenella						238		374	353	450	251	451	201	50		203	322	374	231
S.maximum						238	206	271	353		203		201		227	203	333	355	254
T.orientalis						238	448	188	353		217	203	201		156		198	51	287
T.monacantha						172	448	146	353		55			67	113		175	355	105
Nb.flexipes						217	204	221	259		146		201	57	141			267	97
S.longicorne						238	206	227	246		194		201		156			196	263
T.tricuspidata						50	203			215	55			50	50	203	66	217	51
N.microps									353		71			50	156	203	152	282	149
Nb.boopis							448	251	353			203	201			203	399	449	373
T.astylata						50		99						50	94			449	51
T.aequalis														152			134	355	153
S.robustum																			
E.paragibba								183									51	374	76
E.similis																	197	374	240
E.hemigibba																		355	153
T.pectinata																			254
S.carinatum					52				100										
Nb.sexpinosus															227		152		
T.obtusifrons								53									205		
E.tenera								53										201	

Table III. (continued)

Cruise B2 type of water	southern Red Sea mesotrophic				Gulf of Aden mesotrophic				Somali Current mesotrophic				NSB mesotrophic			
Station	RS1	RS1	RS2	RS2	GA1	GA1	GA2	GA2	US1	US1	US2	US2	SB2	SB2	SI	SI
periode	D	N	D	N	D	N	D	N	D	N	D	N	D	N	D	N
range (m)	300	300	500	500	500	500	500	500	500	500	500	500	500	500	500	500
S.affine	220	173	193	182	49		199	332		223		246			50	254
E.sanzoi	250	205	368	63									408			
E.diomedeae	250	53	282	50	372	78	297	148	347	76	405	85	185	64	399	52
E.sibogae	230	53	217	50	405	285	408	318		54	405	382	359	91	398	73
S.abbreviatum	151	87	50	58		159		132	77	73	421		49	128	196	81
N.gracilis		247			405	256	408	275	381	218	421	367	408	51	400	242
N.tenella					405	403		268	367	242	376	381	248	301	376	305
S.maximum					130	403	219	247	402	249	421	253	212	228	348	349
T.orientalis					405	230	408	218	402	277	421	305	366	314	400	255
T.monacantha				153	405	153	380	159	402	162	421	177	126	221	400	
Nb.flexipes					327	284	238	284	378	277	400	307	212	201	362	223
S.longicorne	151	211			210	267		261	203	249	243	290	212		222	245
T.tricuspidata					49			49	402	53	421	54	254	51	400	
N.microps							199			154	421	178	408	148	219	154
Nb.boopis									402	411	421	381	408	399	400	
T.astylata								153		53	421	81		51	400	
T.aequalis									402							
S.robustum								398		112	202	400	212			
E.paragibba																
E.similis													408			
E.hemigibba										53						
T.pectinata												253		148		
S.carinatum																
Nb.sexpinosus																
T.obtusifrons																
E.tenera																

In the eastern Banda Sea, euphausiid samples were collected during the Snellius II Expedition in August 1984 (SE monsoon) and February/March 1985 (NW monsoon) (Van Couwelaar, 1994). Four stations were made during both monsoons, sampling strategies and gear specifications were principally the same as during the NIOP 1992-93 (c.f. Schalk 1987). Therefore a comparison could be made for the spatial and temporal distributions of the euphausiids in the Red Sea, the Indian Ocean and the Banda Sea by means of cluster analysis.

Of the 34 euphausiid species that were found with both expeditions, 28 were common. *S.insulare* and *N.atlantica* were unique for the Banda Sea; *Nb.flexipes*, *S.elongatum*, and *E.mutica* were found in the NW Indian Ocean only. The neritic *P.latifrons* was absent from the catches in the Red Sea and the NW Indian Ocean, although this species is not uncommon for this area. Cluster analysis was carried out with 199 samples and 34 species using logarithmically transformed data. In the resulting dendrogram, nine clusters (A to I) were distinguished — depicted in simplified form in Figure 6. After inverse analysis an ordered table was obtained to which the group of 17 samples was added (O) that contained no euphausiids at all (Table IV).

Table IV. Ordered table resulting from inverse analysis of species and clusters with samples from the Red Sea, the Gulf of Aden, the NW Indian Ocean (all NIOP B0-2 cruises) and the Banda Sea (Snellius II cruises). Average concentration (number of individuals per 1000 m3) of species in cluster. Numbers in bold: species present in ≥ 66.6 % of samples in cluster. Numbers underlined: average concentration of species in cluster or clusters >75% of total. Average concentrations <0.01 are denoted with 0.00.

Cluster	**O**	**A**	**B**	**C1**	**C2**	**C3**	**D**	**E**	**F**	**G**	**H**	**I**
mean minimum depth (m)	80	130	408	0	0	163	303	313	82	239	77	288
mean maximum depth (m)	220	300	732	100	100	306	595	429	197	351	235	518
mean number of species	0	1	2	2	2	3	3	5	6	8	6	8
number of samples (N=216)	17	1	7	4	1	33	2	7	35	41	8	60
S.abbreviatum				**1.16**		0.50		0.00	1.34	0.27	0.29	0.25
E.sanzoi						0.56			0.78	0.03	0.01	0.02
E.sibogae			0.00			5.45		0.02	1.86	0.00	0.39	**1.73**
S.affine			0.05		**0.13**	**3.11**		0.01	0.15	0.12	0.29	0.10
T.aequalis							0.06		0.05	0.00		0.02
T.orientalis			0.03	0.01				0.84	0.03	**1.00**		**0.64**
E.gibba								0.00		0.00		
T.monacantha			0.03			0.00		**0.17**	**0.80**	0.52	0.03	0.47
E.hemigibba									0.01	0.00		0.01
S.robustum									0.09	0.00		0.03
E.tenera									0.03	0.02		0.03
E.pseudogibba						0.01			0.43	0.30		
Nb.sexpinosus									0.00	0.00		0.00
N.microps			0.00		**0.13**			0.11	0.53	0.92	0.07	0.08
T.astylata								0.01	0.23	0.04		0.03
E.diomedeae						1.21	**0.14**	0.01	**22.31**	**2.01**	**1.47**	**1.28**
T.tricuspidata		**0.05**						0.01	**4.84**	0.53	0.01	0.03
E.paragibba			0.01						0.08			0.02
S.insulare									0.03			
P.latifrons									0.09			
N.tenella			0.02				0.07	0.04	0.07	**1.39**	0.06	**0.30**
S.maximum								0.01	0.03	**0.27**	0.43	0.15
T.cristata										0.00	0.01	
Nb.boopis			0.00					**0.11**	0.00	**0.55**		0.04
E.similis								0.03	0.04	**0.89**		0.01
N.atlantica										0.74		
T.obtusifrons									0.00	0.01		
T.pectinata										0.01		0.00
S.longicorne				0.02		0.01	0.04		0.02	0.20	**0.67**	**0.37**
Nb.flexipes							0.02	0.01	0.19	0.04	0.94	**0.69**
S.carinatum						0.02			0.01	0.02	0.17	0.00
N.gracilis			**0.20**	0.01					0.24	0.14	0.01	**1.84**
S.elongatum												0.00
E.mutica												0.01

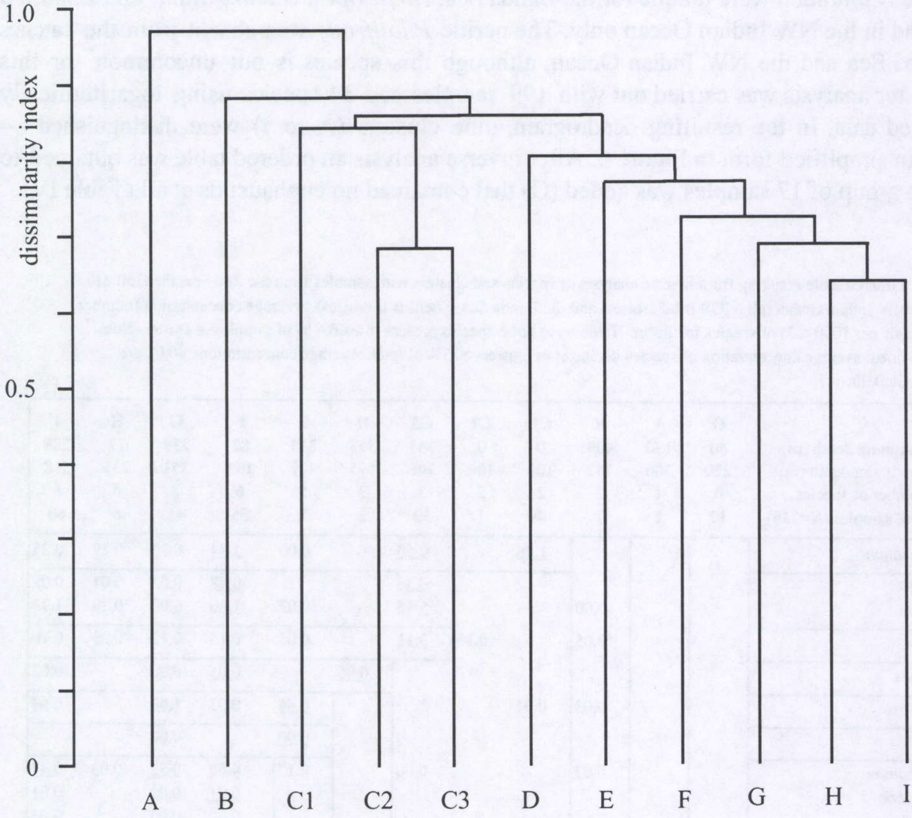

Fig. 6 Simplified dendrogram resulting from cluster analysis with all euphausiid samples from the eastern Banda Sea (Indonesia) during *Snellius II 1984-85*, and all euphausiid samples from the Red Sea, Gulf of Aden and Indian Ocean during *NIOP 1992-93*. The clusters are marked A to I and are linked at the dissimilarity level. See text for explanation of clusters.

- O (n=17). Samples without any euphausiids. All were made during the day from 0-100 m, disregarding the season or the area.

- A (n=1). A single sample made at US1 (B1 cruise) that contained only *T.tricuspidata*

- B (n=7). Samples made from depths predominantly >400 m during daytime. Six of them were made in the Somali Current and the Gulf of Aden. All the samples were poor in species (mean=2) and had *N. gracilis* in common, that was therefore the dominant species.

- C (n=38). Samples with a low mean number of species and sharing *E.sanzoi*, *E.sibogae*, *S.abbreviatum* and *S.affine*. Within cluster C, the following three subclusters were distinguished.

- C1 (n=4). Samples dominated by *S.abbreviatum*, made in the 0-100 m layer during the day. This cluster contained samples from the Banda Sea as well as the Indian Ocean.

- C2 (n=1) A single sample made at station SI, and similar to cluster C1, made from 0-100 m during daytime, and dominated by *S.affine* and *N.microps*. It was by the latter that this sample was not added to cluster C1, where the species was absent.

- C3 (n=33) Exclusively samples made in the Red Sea during both monsoons, plus two samples from the strait Bab el Mandab (BEM) during the onset of the SW monsoon. (The samples made at BEM during the NE monsoon contained no adult euphausiids, similar as two 0-100 daytime samples from the Red Sea that therefore belong to cluster O). The dominant and characteristic species for the Red Sea samples was *S.affine*, present during both monsoons. Other distinguishing species were *E.sibogae*, *E.similis*, and *S.abbreviatum*, however not dominant. Within cluster C2, two clusters could be distinguished at a lower linking level, C2.1 and C2.2. Inverse analysis of the samples and species in these subclusters, showed that both were dominated by *S.affine*, which was present in all the samples disregarding depth, time of day, and season (Table V). Cluster C2.1 (n=17), was dominated and characterized by *E.sanzoi*, *E.diomedeae*, *E.sibogae* and *S.abbreviatum*. It contained 64% of the 13 samples made during the NE monsoon (cruise B2) and sampled depths were either shallow (0-100 m) during the night, or mediate (200-400 m) during day or night. The other cluster, C2.2 (n=16), contained the rare *T.monacantha*, *E.pseudogibba* and *S.carinatum*, but except for *S.affine,* no dominant species were found. In this group, 60% of the 20 samples made during the onset of the SW monsoon (cruise B0) were gathered. The samples counted less species than those in cluster C2.1 (mean 2 *vs*. 4).

Table V. Ordered table from inverse analysis for all euphausiid species from the Red Sea samples in subclusters C3.1 and C3.2 (Table IV). Concentration in cluster expressed as mean number of specimens per 1000 m3. Bold: species is present in ≥ 66.7% of samples in cluster. Underlined: species's average concentration in cluster or clusters is > 75% of total. Average concentrations <0.01 are denoted with 0.00.

Cluster	**C3.1**	**C3.2**
mean Dmin (m)	142	185
mean Dmax (m)	289	324
mean number of species	4	2
number of samples (N=33)	17	16
S.affine	**3.14**	**3.09**
E.sibogae/distinguenda	**10.49**	0.10
E.diomedeae	**2.35**	0.01
E.sanzoi	**0.92**	0.18
S.abbreviatum	**0.87**	**0.10**
S.longicorne	0.01	
N.gracilis	0.01	
T.monacantha		0.00
E.pseudogibba		0.01
S.carinatum		0.05

- D (n=2) Two samples, both made in the Somali Basin at SB2, during the SW (100-200 m) and the NE monsoon (500-1000 m), having *E.diomedeae* in common.

- E (n=7) Mediate deep samples (300-600 m predominantly) irrespective the time of day or season. Six were made in the Banda Sea. The dominant species were *Nb.boopis* and

T.monacantha, present in all samples. There were no characteristic species for this cluster, that must be considered as a species poor variant of cluster G (see below).

- F (n=35) Two third of the samples in this cluster were made in the surface layer during night. This included all the samples made at the four Banda Sea stations from 0-100 m at night during both seasons (n=8), and with the exception of one, all the samples were made at the Indian Ocean stations from 0-100 m at night during both seasons (n=14). Additionally, this cluster contained Banda Sea samples also made during the night from various depths between 100 and 500 m (n=7). Disregarding the season, the samples in the surface layer during night, in both the Banda Sea and the Western Indian Ocean, were dominated by *T.monacantha*, *T.tricuspidata* and *E.diomedeae.* All are vertically migrating species, and attained their highest average concentrations in this cluster. *T.tricuspidata* and *E.diomedeae* were also characteristic species. *P.latifrons* and *S.insulare* were found in the Banda Sea only and were restricted to this cluster.

- G (n=41) Almost exclusively samples from Banda Sea stations (85%) that were equally made during both monsoons. Three fourth of the samples were made during the night. Surface samples (0-100 m) were absent, but all depth strata from 100-500 were present. The samples were dominated by *E.diomedeae*, *T.orientalis*, *N.tenella*, *E.similis*, and *Nb.boopis*, the latter two were also characteristic species. *N.atlantica* was restricted to this cluster, as it was found in the Banda Sea only.

- H (n=8) All daytime samples made from 0-300 m in the Banda Sea (n=2) and the Indian Ocean (n=6). The migrating *E.diomedeae* and the non-migrating *S.longicorne* were the dominant species; however, not characteristic. In the ordened table, *S.carinatum* had an average concentration of >67% in this cluster, but since it was found in one sample only, no significance was attached to this species.

- I (n=60) This cluster contained 27% of all the samples collected with the two expeditions. With one exception, all the samples in this cluster were made in the Indian Ocean and most were made from > 300 m during the night and from >200 m during the day. *N.gra-cilis* was the dominant and characteristic species. Only dominant species, with > 67% presence in the samples, were *N.gracilis*, *E.sibogae*, *E.diomedeae*, *Nb.flexipes*, *T.orien-talis*, *S.longicorne* and *N.tenella*. This cluster could be divided into 7 subclusters, but this did not reveal dominant and characteristic species for the two major subclusters that were found (with 12 and 27 samples respectively each).

All abundant species showed in general an excess of females to males. The over all sex ratio was 34.2, or 73% females to 27% males (n=625). If differentiated for season or time of day, the sex ratio was about the same. No species gave reason to assume a correlation of sex ratio and sampling depth, time of day or season. Ovigerous females or females with a ripe ovary were rare, as were spermatophore carrying females. In only 27 cases reproducing females were found, belonging to either *E.sibogae*, *N.flexipes*, *N.gracilis*, *N.microps*, *N.tenella*, *S.abbreviatum*, *S.affine*, *S.carinatum,* or *S.maximum*. They were encountered during both monsoons in the Red Sea and at the stations US1 and US2, but during the NE monsoon only at GA1, SB2 and SI. Reproducing females of *N.gracilis*, *N.microps*, *N.tenella*, *S.affine* and *S.carinatum*, were found during both monsoons. *E.diomedeae*, *E.sibogae* and *T.monacantha* were found active during the NE monsoon only and *Nb.flexipes* was active during the SW monsoon. In the Red Sea, *S.affine* was reproducing during both monsoons. The 10 samples from which the euphausiids could not be sexed due to damage were omitted, with the remaining 127, a cluster analysis was carried out with males and females of the species. The resulting dendrogram (not depicted) showed basically no differences with the one earlier presented. There were no species of which males or females were dominant and characteristic for any cluster. Therefore, based on the present data set and analysis method, there was no reason to assume spatial (vertical or geographical) or temporal segregation of the sexes. This was confirmed by the similar WMD's for males and females of the 14 most frequent species at stations with complete sample series (0-5(6)00 m) during day and night.

DISCUSSION AND CONCLUSIONS

During the present study, stocks were ranging from 0.5 to 16 euphausiids m^{-2} in the 0-200 m layer. This is low compared to the several hundred euphausiids per square meter as found in near-coastal catches (<200 m depth) over the SW Indian continental shelf (Mathew, 1980; Silas and Mathew, 1986; Mathew *et al.*, 1990); and also low compared to oceanic catches during the SW monsoon, producing 100-400 euphausiids m^{-2} from the upper 200 m in the Gulf of Aden and the Somali Current (Weigmann, 1970; Brinton and Gopalakrishnan, 1973) or 300-600 euphausiids m^{-2} over 0-300 m in the Somali Basin (c.f. Paulinose *et al.*, 1992). Different sampling techniques may account for these different results. All quoted literature figures come from vertical hauls made with Indian Ocean Standard Nets (mesh size 300-330 µm) or nets with comparable mesh, whereas during the present study an RMT8 with mesh size 4.5 mm was deployed in oblique hauls. Undersampling of small euphausiids by the RMT8 must be regarded as a main cause, demonstrated by the fact that greatest differences occurred for small epipelagic species like *E.diomedeae*, *E.sibogae* (c. q. *E.distinguenda*), *S.affine*, and *S.abbreviatum*. The large mesopelagic species showed relative small differences in numbers compared to the literature.

During the NE monsoon, when mixed layer conditions were all mesotrophic, mean stocks (0-500 m, day and night series) were very similar in the southern Red Sea, the Gulf of Aden, the Somali Current, and the northern Somali Basin (5.5-7.7 euphausiids m^{-2}). However, during the SW monsoon when trophic conditions were very different locally, mean stocks ranged from 3.0-4.5 in the oligotrophic Red Sea and Gulf of Aden to 4.0-8.9 euphausiids m^{-2} in the Somali Current and downstream the upwelling in the northern Somali Basin. The euphausiid abundance tended to be correlated with the trophic state of the surface layer: it was low under oligotrophic and high under mesotrophic conditions. Variation in abundance was large due to occasional high contributions of epipelagic *E.diomedeae* after upwelling at US0 and downstream upwelling at SI, and of *E.sibogae* in the upwelling of the Somali Current at stations US1 and US2.

In the Red Sea, the mean number of euphausiid taxa was nearly not related to oligotrophic or mesotrophic conditions in the surface layer, with five and six taxa respectively. For the Somali Current, greater differences were found in the number of taxa, being low under upwelling conditions (mean 9.6) and high when surface layers were mesotrophic (mean 11.2). In the Gulf of Aden, only a weak indication was found for a relative high stock and low number of taxa under mesotrophic conditions and low stock and high number under oligotrophic conditions. Thus, species diversity increases with decreasing trophic states.

Andersen *et al.* (1997) found similar results for euphausiids in and outside of the Mauritanian upwelling area off NW Africa.

Large scale distribution patterns for Indian Ocean euphausiids show major northern limits at ca. 10°S, 0° and 10°N (c.f. Mauchline and Fisher, 1969; Brinton and Gopalakrishnan, 1973, Brinton, 1975; Mauchline, 1980) coinciding with surface circulation patterns of the monsoon gyre system, or with low oxygen concentrations at subsurface depths north of 10°N (c.f. Wyrtki, 1973). In the present study, mesopelagic *Nb.boopis*, *Nb.flexipes*, *T.astylata* and *T.monacantha* were found in the Gulf of Aden (12°N), at their northern limit around 10°N, i.e. the southern border of the Arabian Sea — though *T.monacantha* was even found in the Red Sea once. Moreover, records from the Gulf of Aden of the mesopelagic *T.orientalis* (also found by Casanova, 1980), *T.obtusifrons*, and *S.robustum*, demonstrate an extension northward of their known northern limits at, or south of the equator. The epipelagic *E.mutica*, *E.similis*, *E.hemigibba*, have their northern limits at the equator (Brinton, 1975), but the incidental findings of these species between 0° and 8°N along East Africa's coast during the present study, can be explained as a northward extension matching with the Somali Current during SW monsoon.

The importance of the oxygen minimum zone (OMZ) in the Arabian Sea north of 10°N for zooplankton and micronekton distribution in the NW Indian Ocean has been recognized, e.g. for zooplankton biomass (Vinogradov and Voronina, 1961), copepods (Weikert 1980; Böttger-Schnack, 1996), euphausiids (Brinton and Gopalakrishnan, 1973; Gopalakrishnan 1974), and myctophid fish (Kinzer *et al.*, 1993). It was also pointed out that zooplankton can cope with low oxygen concentrations (Peterson, 1991) and possibly anaerobic metabolism exists in plankton and nekton, enabling life under suboxic circumstances (Childress, 1975, 1977, cited in US Globec, 1993). In the present study, euphausiids showed no avoidance of the low oxygen concentrations in the Gulf of Aden. Mesopelagic species were found by day in the deeper strata (300-500 m and 500-1000 m). There were no substantial differences in weighted mean depths (Table III) of mesopelagic euphausiids from the Gulf of Aden compared to these of the stations US0 and SB1 in the equatorial Somali Basin where no OMZ exists above 1000 m and where concentrations are always >43 μM (Table I). At station SI during both monsoons waters were well depleted from oxygen from 200 to 1000 m, and euphausiids were found in the deepest sampled strata during the B2 cruise when sampling was done to 1000 m depth. Epipelagic diurnally vertical migrating species also stay at low oxygen concentrations during daytime. In addition to this, in the Arabian Sea are more examples of vertically migrating micronekton crustaceans (Herring and Hargreaves, 1998; van Couwelaar *et al.*, 1997) and myctophid fish (Kinzer *et al.*, 1993) that are not hampered by low oxygen concentrations, because during the day they stay at greater depths in the OMZ. Though influences of the OMZ on euphausiid distribution have been published, the present study does not affirm these conclusions.

In the NW Indian Ocean as well as in the Banda Sea (Van Couwelaar, 1994), maximum euphausiid stocks were found at station B located downstream of the upwelling in the Banda Sea, at US0 after upwelling in the Somali Current at ca 4°N, and at SI downstream of the upwelling in the Great Whirl. In all cases euphausiid stocks could build up due to phytoplankton blooms. *E.diomedeae* and *T.tricuspidata* were always accounting for these high values. *E.sibogae* contributed also largely to the high stocks at the upwelling stations US1 and US2. *T.tricuspidata* was abundant after upwelling in the Banda Sea, but it was insignificant after upwelling in the NW Indian Ocean. In the Red Sea *E.sibogae* was the only species that exhibited a clear seasonality with higher stocks during the NE monsoon at both stations compared to the SW monsoon (Tables 2b *vs* 2a). These events clearly indicate a quick response by epipelagic species to upwelling related enhanced productivity, either by reproduction or by aggregation.

The non-migrating species were vertically segregated. Over all, *S.abbreviatum* was found in the surface layer (0-100 m), while *S.affine* was found from 100 to 300 m. Both species were abundant in the southern Red Sea. *S.abbreviatum* occurred predominantly above and in the discontinuity layer at about 50-100 m, that was marked by the thermocline and salinocline (Table I). *S.affine* stayed in and below this layer. Outside the Red Sea *S.abbreviatum* and *S.affine* were less abundant, but still displaying a vertical segregation, each occupying their depth zone similar as in the Red Sea. The epipelagic *S.longicorne* was rare in the Red Sea, but it was frequently found in the Gulf of Aden and the Indian Ocean. Where occurring together with *S.abbreviatum* and *S.affine*, *S.longicorne* was found below these. two species. The three *Stylocheiron* species are carnivorous or at least omnivorous (Mauchline and Fisher, 1969; Mauchline, 1980). The stomach contents consisted of fragments of various phytoplankton organisms, microzooplankton, and small crustaceans (most copepods, if recognizable), the composition was not typical for any of the species. Vertical segregation in these species was also found in the California Current (Brinton, 1967): *S.affine* occurred above the discontinuity layer, while *S.abbreviatum* occurred in and below, and *S.longicorne* occurred below the discontinuity layer. Note that *S.affine* occurred shallower than *S.abbreviatum*, opposite from the present study. The carnivorous mesopelagic *S.maximum* and *Nb.boopis* were found deep. Their stomach contents consisted predominantly of crustacean fragments (if detectable, most copepods). Over all, *S.maximum* occurred shallower than *Nb.boopis* — possibly the result of vertical segregation as to avoid food competition.

Vertical segregation was also found in diurnally vertical migrating species (Figure 3). During the night, *E.diomedeae*, *E.sibogae*, *T.astylata*, and *T.tricuspidata* stay in the surface layers mainly (0-100 m), whereas *N.microps* and *T.monacantha* were staying deeper (100-200 m). *T.orientalis* was found from 150 to 300 m, and *N.tenella* from 200 to 400 m. *Nb.flexipes* and *N.gracilis* were variable, ranging in vertical occurrence from 100 m to the deepest sampling limit. In the daytime distributions vertical segregation was apparent for the epipelagic species (*E.diomedeae*, *E.sibogae* and *T.tricuspidata*), but it was less evident for the mesopelagic species. A reason for this may have been that the sampling was not deep enough to cover full daytime distributions of the latter.

Under SW monsoon upwelling conditions, in the Somali Current *E.diomedeae*, *E.sibogae*, *N.gracilis*, *T.orientalis*, and *T.tricuspidata* were found shallower during the day, than during the NE monsoon when upwelling was absent. In the Red Sea, when the upper layers were mesotrophic during the NE monsoon, *E.diomedeae* and *E.sibogae* were also found shallower during daytime, compared to the onset of the SW monsoon when surface conditions were oligotrophic. Nighttime distributions did not show monsoonal effects, and the migrating species were in the surface and subsurface layers during night under all circumstances. In the Red Sea, the mesopelagic, non-migrating *S.abbreviatum* and *S.affine* also were found less deep during the NE monsoon compared to the onset of the SW monsoon. The populations of these epipelagic species tend to occur deeper during the day when surface conditions were oligotrophic, food is sparse in the surface layers. Nevertheless, in the shallow part of the Gulf of Aden (<1000 m depth), also with alternating oligotrophic and mesotrophic state of the surface layer, for *E.diomedeae* and *E.sibogae* this vertical shift in daytime distribution was not found.

During the SE monsoon in the Banda Sea, vertical distributions and migration patterns of species were irregular, compared to the NW monsoon when migratory species showed a more consistent pattern. During the SE monsoon, shallow distributions during daytime were recorded at the upwelling station A for *T.orientalis*, *Nb.boopis*, *T.orientalis* (mesopelagic and non-migrating) and *T.monacantha* (mesopelagic, migrating). Downstream upwelling, at station B, a shallower distribution during the day was found for *E.diomedeae*, *T.tricuspidata*, and *S.affine* (epipelagic) than in the NW monsoon.

In the upwelling areas of the NW Indian Ocean upward shifts in vertical distributions under upwelling conditions appeared to be more manifest, compared to the Banda Sea. This was evident by the number of species involved. Deviating depth distributions observed for euphausiids off NW Africa in the upwelling area at 20°N (Andersen *et al*., 1997), were correlated with eutrophic or mesotrophic surface layers, reducing vertical migration. The present study shows the same phenomenon, and even non-migrators showed such deviations in vertical occurrence. Andersen *et al*. (1997) related the observed reduced downward migration during the day to oxygen deficiency below eutrophic and mesotrophic surface layers, temperature and depth of the euphotioc zone. The present study fails to confirm the oxygen minimum as a barrier for downward migration. Epipelagic migrators during the day, and mesopelagic species, either migrating or not, stay under low oxygen concentrations at greater depths. Under oligotrophic circumstances organisms may stay at lower depths in order to save energy by decreasing the metabolic rate at lower ambient temperature (Schalk, 1988). Also, light attenuation is less when transparency is high in oligotrophic layers, and to escape from predators, organisms have to migrate deeper during the day. This need declines under meso- and eutrophic circumstances, when food is largely available and organisms can stay closer to the food resources, though the metabolic rate and risk of visual predation are higher.

To what extent the Red Sea, the NW Indian Ocean and the Banda Sea have different euphausiid faunas? The four major clusters of samples found, represented different euphausiid assemblages, but these were not necessarily regionally bound. The cluster C3 was the only one entirely basin linked, since it was confined to all samples from the Red Sea, regardless of depth, time of day or season. The Red Sea assemblage was characterized by a low number of species and a rather consistent species combination throughout space and time. It was dominated by the epipelagic, non-migrating *S.affine*, thriving well in the Red Sea. The cluster F represented both the assemblages in the surface layers during night in the Banda Sea and the Indian Ocean. It consisted of a majority of common epipelagic, diurnally migrating species. The frequent and highly abundant *E.diomedeae* and *T.tricuspidata* were typical for this layer, occurring together throughout the NW Indian Ocean and Banda Sea, even though *T.tricuspidata* was more abundant in the Banda Sea. Below 200 m euphausiid assemblages in the NW Indian Ocean and Banda Sea were different. The third cluster G represented the assemblage in these deeper layers of the Banda Sea. It concerned mesopelagic non-migrating species, mesopelagic migrating species during either night or day, and epipelagic migrating species at daytime. These species were common for both the Banda Sea and the Indian Ocean, but the specific abundances made this assemblage typical for the Banda Sea. The cluster I represented the assemblage in the sub-surface and intermediate layers of the NW Indian Ocean.

It was characterized by mesopelagic species, either migrating, or non-migrating, and migrating epipelagic species that occured deeper during the day. These species were common for both the Banda Sea and Indian Ocean — here again, specific combinations and abundances made this assemblage typical for the Indian Ocean. These last two assemblages (clusters G and I) can be regarded as each others counterparts for the NW Indian Ocean and the Banda Sea. Both have a similar depth distribution and host very much the same species, though in different combinations of abundances.

None of the clusters combined most of the samples taken during one particular season. It was apparent that in none of the seas were assemblages influenced seasonally to such an extent that it could be detected by cluster analysis. Neither the apparent seasonal (upwelling) related differences in the species' vertical distribution, were detected with cluster analysis; the possible signal for this was overruled in the first place by the main spatial pattern determined by species composition in the samples. The species concentrations also had a lesser influence: cluster analysis using binary data only (presence or absence of the species) indicated the same basic pattern as with the analysis presented here.

The Red Sea euphausiid assemblage was characterized by a low number of species , and a relative low total stock compared with the Banda Sea and the Indian Ocean. But for one species, *S.affine*, the stock was up to 10 times higher than elsewhere. The mesopelagic *T.monacantha* (for the Red Sea also recorded by Torelli, 1934, cited in Weigmann, 1970) and *S.longicorne* were found in the southern Red Sea during the NE monsoon with maximal surface inflow from the Gulf of Aden. The Hanish Sill, about 180 km NW of Bab-el-Mandab and maximum depth of about 100 m, is obviously an effective barrier keeping deeper living organisms from entering the Red Sea. Also, the hostility of this environment for low-temperature adapted species may play a role in stopping migrating species from settling in the Red Sea.

S.affine and *Sabbreviatum* from the present study showed smaller sized adults in the Red Sea compared to those in the Gulf of Aden. This size reduction may be related to the higher temperatures prevailing in the Red Sea, forcing animals to reach maturity at a smaller body size. Size reduction for Red Sea organisms was found in *S.abbreviatum* and *E.sanzoi* (Casanova, 1990), and in calanoid copepods (Schneider *et al*., 1994). Morphological differences were observed in populations of *S.affine* which have larger gills in the Red Sea than *S.affine* in the Gulf of Aden. This is explained as an adaptation to lower oxygen concentrations (Casanova, 1990). However, it may be well an adaptation to the higher oxygen demand of the animal under the high ambient temperatures that prevail in the Red Sea throughout the whole column. Morphological differences were found also in populations of myctophiid fish *Benthosema pterotum* from the Red Sea and Gulf of Aden (Dalpadado and Gjøsaeter, 1987). Although contact between the epipelagic faunas from the Red Sea and the Gulf of Aden is possible, it is likely that for common species separated populations occur in both seas due to the seasonally limited water exchange that restricts mixing of the population.

The seasonal differences in terms of concentrations appeared to be greatest in the upper stratum (0-100 m) during night, and small at greater depths. This is because monsoon related changes in the pelagic systems, are initiated in the upper part of the epipelagic, where organisms are usually herbivorous or at least omnivorous. This study shows that in the Indian Ocean epipelagic euphausiid species react more directly and strongly to seasonal differences than mesopelagic species. This was detected in the first place in the mixed layer. Below, the mesopelagic species appear to remain unaffected; this was demonstrated by rather constant abundances.

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CHAPTER 4

The distribution and biology of the swimming crab *Charybdis smithii* McLeay, 1838 (Crustacea; Brachyura; Portunidae) in the NW Indian Ocean

(with M. V. Angel and L. P. Madin)

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The distribution and biology of the swimming crab *Charybdis smithii* McLeay, 1838 (Crustacea; Brachyura; Portunidae) in the NW Indian Ocean

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Abstract—On seven cruises with the R.V. *Tyro*, R.R.S. *Discovery* and R.V. *Malcolm Baldrige* in the NW Indian Ocean between 1992 and 1995, the pelagic swimming crab *Charybdis smithii* was found in great densities during July–August (SW monsoon) and January (NE monsoon). Discrete depth sampling, using RMT1 + 8 and Mocness-10 gear, collected the species predominantly in the upper 200 m during night and day. Most of the crabs were concentrated above the thermo- and oxycline, both situated at around 150–200 m. In July–August the stock of crabs showed considerable variation, with maximum values of 1.9–2.4 crabs m^{-2} (0–500 m, night) found in the Southern Somali Basin, the Omani Basin and in the Central Arabian Sea. The maximum biomass (wet weight) of crabs was 12.7 g m^{-2} (0–500 m, day) off Somalia and in the Central Arabian Sea during the SW monsoon. In January stocks and biomasses were lower, with maximum values of 0.1 and 2.0, off Somalia at 7°N. The size–frequency distribution of all crabs found during the SW monsoon in the Somali Basin demonstrated the occurrence of smaller instars at the near-coast stations compared with the open ocean stations. During the NE monsoon there was a tendency for nearshore crabs to be larger than offshore. High concentrations of zoea and megalopa larvae of portunid crabs together with juvenile *C. smithii* were found in neuston samples off Somalia in May. Dense swarms of crabs occurred in the pelagic NW Indian Ocean in June–September (SW Monsoon). In October, crabs began to migrate onshore, where they characteristically formed surface swarms at night. Analysis of combined ship and literature data showed a 1 year life cycle for *C. smithii.* Aggregation of the crabs on the continental shelf precedes their breeding from about October to January (NE Monsoon). The larvae hatching in shelf waters disperse offshore and, after metamorphosis, form dense pelagic swarms from about July to August (SW monsoon). © 1997 Elsevier Science Ltd

INTRODUCTION

Most crab species are confined to neritic or benthic environments, but a few species have an adult pelagic stage in their life cycle during which they are to be found far offshore in the open sea. For example, the grapsid Columbus crab, *Planes minutus* (L., 1758) is found living in the neuston on bunches of sargassum weed, on the backs of sea turtles, and on floating objects. In the eastern Pacific Ocean, the galatheid Mexican red crab, *Pleuroncodes planipes* Stimpson, 1860, has been reported during summer in massive surface swarms as far as 700 km off Baja California (Kashkina and Kashkin, 1994), but in this species only the larval stages and the young adults are planktonic; older adults become benthic (Aurioles-Gamboa, 1992).

The true swimming crabs of the family Portunidae are predominantly living benthically despite their swimming capabilities. However, two portunid species regularly are found swarming in the pelagic environment. In the NE Atlantic, swarms of *Polybius henslowii* Leach, 1820, predominantly males, occur during the summer in slope waters off the Iberian Peninsula (Allen, 1968; Gonzalez-Gurriaran *et al.*, 1993). In the Indian Ocean *Charybdis smithii* McLeay, 1838 forms massive swarms at the surface at night far off East Africa during the intermonsoon from October to December (Della Croce and Holthuis, 1965; Losse, 1969; Rice, 1969), and off Oman during the NE monsoon (Daniel and Chakrapany, 1983). Less well known are the dense patches of crabs that occur in the upper layers during the SW monsoon (unpublished observations from R.R.S. *Discovery* during the International Indian Ocean Expedition in 1963). *C. smithii* is endemic to the western Indian Ocean, ranging from the shelf and slope waters off Natal and South Africa (Kensley, 1977; Branch, 1984), Tanzania and the Gulf of Aden (Stephenson and Rees, 1967a; Losse, 1969), the Arabian Peninsula, Pakistan, and India (Stephenson and Rees, 1967b; Daniel and Chakrapany, 1983; Balasubramanian and Suseelan, 1990), the western equatorial Indian Ocean (Stephenson, 1967), the Seychelles (Crosnier, 1984), and Madagascar (Crosnier and Thomassin, 1974).

The large swarms of *C. smithii* can have a major predatory impact in the upper water column. Merrett (1968), reporting on a long-lining survey conducted between 0° and 10°S in slope waters off East Africa, wrote: "Between the months of October and February throughout the survey area, damage to all baits is found to be considerable. Moreover, in several operations particularly inshore up to 300 hooks have been hauled with no bait remaining at all. This has occurred even when they have been left in the water for as little as three to four hours. During these same months a marked predominance of portunid crab *Charybdis* (*Goniohellenus*) *edwardsi* Leene and Buitendijk, 1949 (i.e. *C. smithii*), has been found in the stomach contents of all longline caught species. Live specimens of this crab have been taken on the surface at night at this time. It is, therefore, suspected that *Charybdis* is the cause of the bait damage, and the widespread effects suggest a considerable population in the area".

On oceanic cruises between 1992 and 1995, swarms of *Charybdis smithii* were encountered in the northwestern Indian Ocean during both SW and NE monsoons by the R.V. *Tyro*, R.R.S. *Discovery* and R.V. *Malcolm Baldrige*. In July and August during the SW monsoon the crabs were patchily distributed, often in particularly high concentrations in the upper 100 m. In January 1993, during the NE monsoon, large swarms were observed at the sea surface at night. Surprisingly, there have been no previous reports of these dense patches during the SW monsoon. When swarming, this species makes a substantial contribution to the standing crop of pelagic micronekton, constituting 50–90% of the displacement volume of the micronekton catch at times during the SW monsoon in the upper 200 m. At such times it must be playing an important, if not dominant, role in the pelagic ecosystem both as predators and as prey. The crabs swim continuously, and must have high metabolic demand. They are major dietary items for large pelagic fish such as tuna (Losse, 1969; Zamorov *et al.*, 1992).

The apparent importance of *Charybdis smithii* in the pelagic ecosystem, and its dramatic swarming behaviour synchronised with the monsoon regime, invite study of its seasonal distribution and life-history. In this paper we present data on the horizontal and vertical distribution of *C. smithii* gathered during cruises by the *Tyro*, *Discovery* and *Baldrige* in the NW Indian Ocean off Oman, Somalia and in the central Arabian Sea in 1992–1995, and discuss the life cycle and patterns of reproduction of this unusual crab.

General regional hydrography

The distribution of *Charybdis smithii* in the northwestern Indian Ocean is bound to be strongly affected by the monsoon cycle, which dominates the surface circulation (Wyrtki, 1973; Molinari *et al.*, 1990). North of the constantly westwards flowing South Equatorial Current (between about 10° and 20°S), the monsoon gyre changes current direction seasonally. During the NE monsoon (December–February), surface currents in the Arabian Sea are to the (north)west, fed by the North Equatorial Current at 0–10°N (Fig. 1). The southwest Somali Current merges with the East African Coastal Current, forming the eastward flowing Equatorial Counter Current at 0–10°S. During May–September, the strong tropospheric Findlater Jet blows from the Horn of Africa towards India, forming the core of the SW monsoon wind (Findlater, 1969). Both the Somali Current and the currents in the Arabian Sea reverse directions, now flowing predominantly northeast (Fig. 1). Flow in the eastern Arabian Sea is to the southeast, merging with the Equatorial Counter Current into the eastward flowing Indian Monsoon Current. During the SW monsoon, along the East African coast a series of smaller-scale clockwise gyres develops from about 0–10°N. Many eddies occur, off Oman and Somalia, where the Great Whirl at about 8°N is the largest and most persistent (Fig. 1).

There is a series of coastal upwelling centres along Somalia and the Arabian Peninsula (Fig. 1), and the eddies create filaments of upwelled water extending far into the western Arabian Sea (R.T. Barber and J. Kindle, personal communication, 1996). The upwelling induces high production in the surface layers, which in turn leads to high zooplankton biomass and high oxygen consumption in upper and subthermocline layers. High bacterial respiration in the subthermocline, and the old age of the water results in strong depletion of oxygen at depths generally below 100 m. In the southern Somali Basin during the SW monsoon, oxygen concentrations were reduced to about 1.0 ml l^{-1} from 600 to 1000 m, but above 500 m there was no serious oxygen depletion (*Tyro* station SB1, Fig. 2). In the Great Whirl further downstream a strong oxycline developed at 150–200 m with a minimum concentration of about 0.5 ml l^{-1} marking the top of an oxygen minimum zone (OMZ) ranging from 200 to 1200 m (*Tyro* station SI, Fig. 2). Off Oman during the SW monsoon an even stronger OMZ developed between 100 and 1250 m, with oxygen concentrations as low as 0.4 ml l^{-1} (*Discovery* station 12662, Fig. 2), and with a strong limiting effect on both pelagic and benthic communities. In general, in the NW Indian Ocean the oxygen concentration at 200 m depth decreases northward to values about 0.1 ml l^{-1} (Wyrtki, 1971). At *Tyro* stations US1, US1.5 and US2 in the Somali Current, during the SW monsoon the oxycline was between about 60 and 120 m at the top of an OMZ with oxygen concentrations of 1–2 ml l^{-1} down to 1000 m. At these same stations in the Somali Current, the thermocline was shallow (80 m) and not sharp; the surface temperatures were 18–22°C. Outside the upwelling area there was a strong thermocline at about 150 m depth (*Tyro* station SB1, Fig. 2). The thermocline, together with the oxycline and pycnocline, marked a boundary between different current speeds and directions. Apparently, during the NE monsoon the depth and value of the OMZ did not change significantly compared with the SW monsoon.

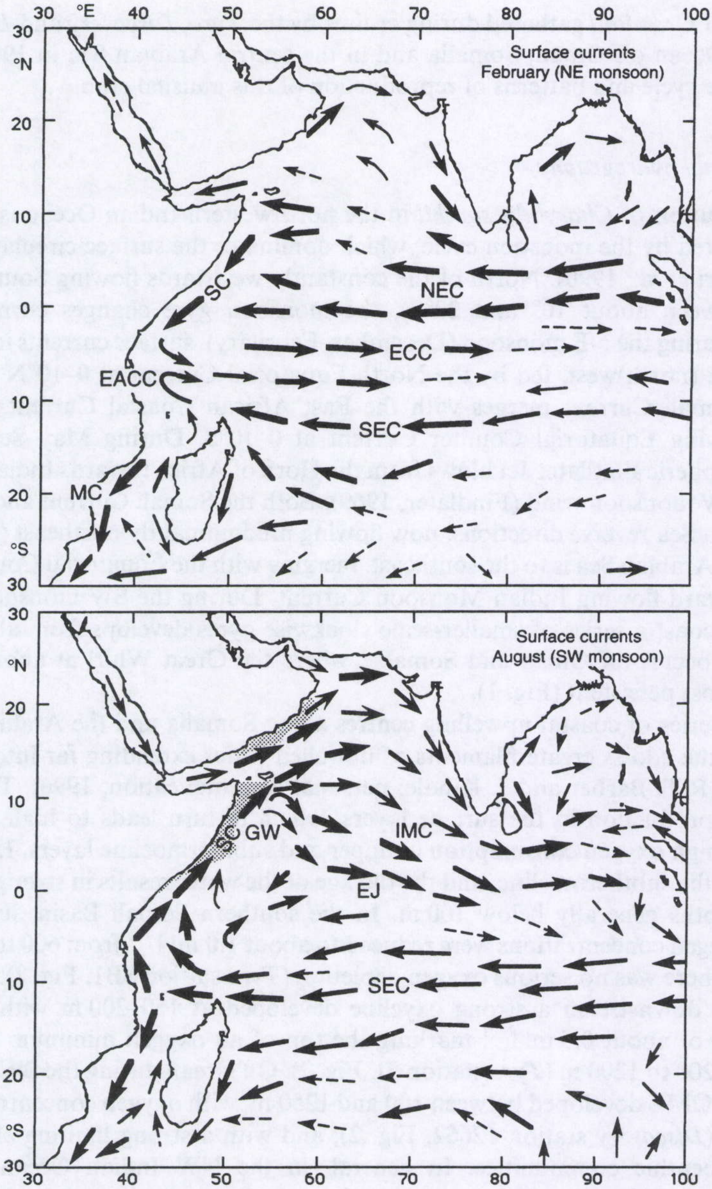

Fig. 1. The surface circulation pattern in the Indian Ocean during the NE monsoon in February (upper panel) and during the SW monsoon in August (lower panel). SEC, South Equatorial Current; ECC, Equatorial Counter Current; NEC, Northern Equatorial Current; SC, Somali Current; EACC, East Africa Coastal Current; GW, Great Whirl; IMC, Indian Monsoon Current. The Mozambique Current (MC) merges with southern branches of the SEC into the southward Agulhas Current (not depicted) along South Africa. Redrawn after Wyrtki (1973) and slightly adapted from Molinari *et al.* (1990). Stippled areas off Somalia and Oman have coastal upwelling during the SW monsoon.

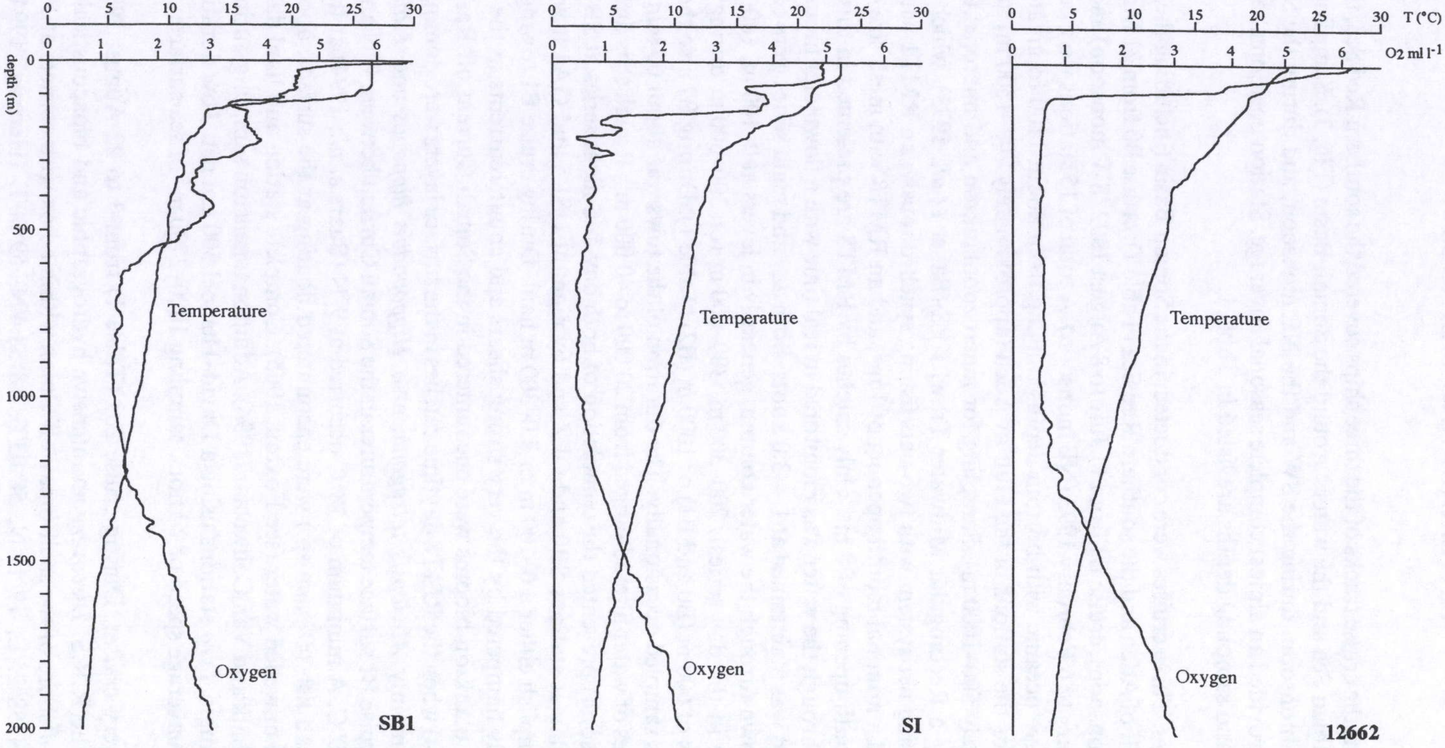

Fig. 2. Vertical oxygen and temperature profiles by CTD casts in the Somali Basin and off Oman during the SW monsoon. *Tyro* stations SB1 on 16 July (left panel) and SI on 31 July 1992 (middle panel). *Discovery* station 12662 (right panel) at 18°59′N, 58°26′E in the vicinity of station 12664 (Fig. 3) on 8 August 1994 (after Herring, 1994).

MATERIALS AND METHODS

Sampling

Taken together, the cruise tracks of the three ships covered the southern Red Sea, the Gulf of Aden, the Arabian Sea and the waters around the Somali Basin (Fig. 3). Sampling at the onset of the SW monsoon, during the SW and the NE monsoon, and during the SW–NE intermonsoon, provided an almost complete seasonal coverage. Station positions, sampling dates and times and sampling depths are listed in Table 1.

RV Tyro *cruises*. Three cruises were conducted, in the Somali Basin (including the Somali Current), the Gulf of Aden and the southern Red Sea (Table 1): cruise B0 from 21 May to 12 June 1992 (premonsoon), cruise B1 from 11 July to 8 August 1992 (SW monsoon) and cruise B2 from 11 January to 6 February 1993 (NE monsoon). A total of 15 stations were occupied (Fig. 3), most were oceanic with bottom depths ranging from about 1100 to greater than 4000 m, except for the stations in the Gulf of Aden (approximately 700–1500 m) and Red Sea (approximately 500–1000 m). Sampling for macrozooplankton and micronekton was undertaken using a Rectangular Midwater Trawl 1 + 8 (Baker *et al*., 1973), which has an opening and closing net system with two nets fishing synchronously; an RMT1 with mesh size 0.32 mm and a nominal mouth opening of 1 m^2, and an RMT8 with mesh size 4.5 mm an a nominal mouth opening of 8 m^2. Only catches by RMT8 are presented in this paper. The net's speed through the water was monitored in real time with a flowmeter mounted on the net frame, and was maintained at 1.4–3.0 knots. Both day and night series were collected systematically down through the water column, generally in layers at 0–100 m, 100–200 m, 100–300 m (only in the day series), 200–300 m, 300–600 m (or 300–500 m during B2) to maximum depths of 600 m (B0 and B1) or 1000 m (B2) (Table 1). During B2 also the 1000–1500 m layer was sampled occasionally. The duration of the tows was about 60 min during which the volumes of water filtered ranged from 20 000 to 40 000 m^3. Rough seas during the B1 leg (SW monsoon) prevented the completion of both day and night series at SB1, US2, SB2 and SI. By day at stations SB0 and OFZ and by night at US1.5 and GA1 it was only possible to accomplish either a 0–100 m or a 0–300 m haul. During cruise B1 towing below 100 m was greatly hampered by the very strong shears and countercurrents in the Somali Current. Intense plankton blooms were encountered in the Somali Current off Ras Hafun (Baars *et al*., 1994) when the RMT8 daytime catches in the surface layers were dominated by siphonophores (mainly *Abylopsis tetragona*, also *Hippopodius hippopus* and *Eudoxoides mitra*). During cruise B1 surface temperatures in the Somali Current between 7°N and 11°N were all below 20°C. A minimum of 18°C occurred at 9°N (Baars *et al*., 1994) at the same time as many dead fish (*Diodon* sp.) were encountered floating at the surface, apparently killed in the cold upwelled water (see Foxton, 1965). Complete station and haul data have been listed by Schalk and Van Couwelaar (1994). Additional neuston sampling during night was done at the main *Tyro* stations using a David–Hempel 500 µm net. Tow duration was 60–145 min at an average speed of 2 knots, sampling 1000–2700 m^2 of sea surface.

R.R.S. Discovery *cruises*. During cruise 209 (Table 1) from 3 to 22 August 1994 (SW monsoon) with the R.R.S. *Discovery* an intensive hydrographic and bioacoustical survey was carried out offshore of the shelf-break off Oman within a box with corners at 19°13′N, 59°23′E; 19°47′N 58°25′E; 19°12′N, 58°03′E; 18°38.4′N, 59°00′E (Herring, 1994). This survey marked the beginning of an intensive study of the flux processes at 19°N, 59°E,

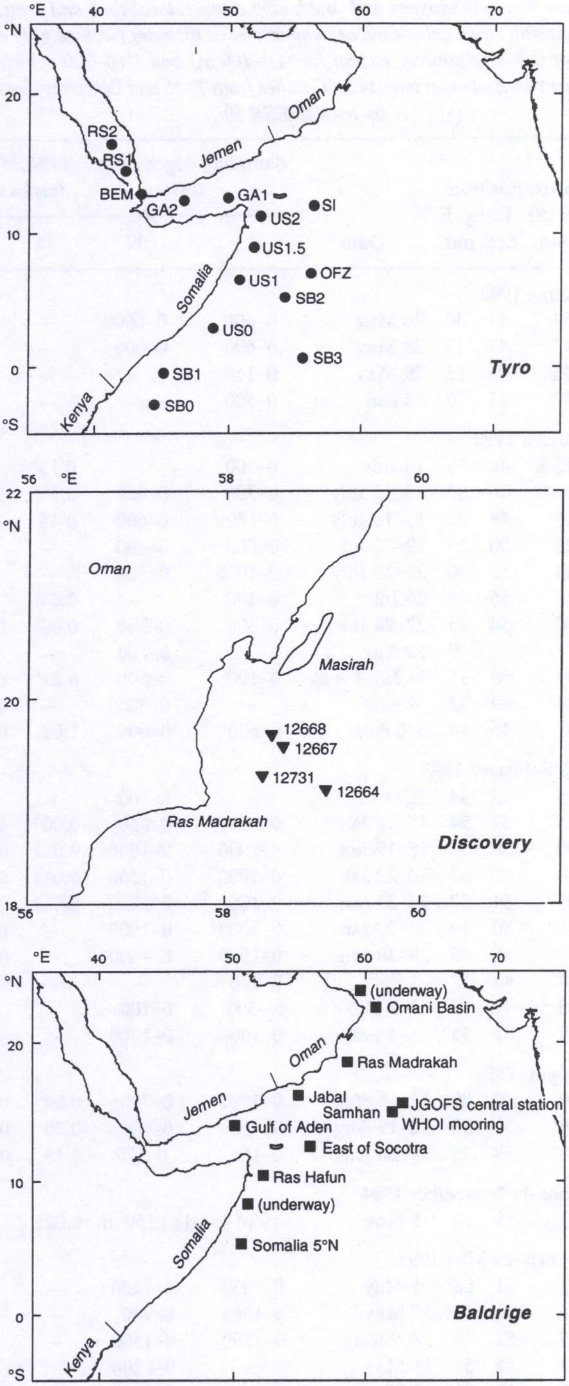

Fig. 3. Map of the study area with the RMT1 + 8 (*Tyro* and *Discovery*) and MOCNESS-10 (*Baldrige*) stations during cruises with the *Tyro* (upper panel), *Discovery* (middle panel), and *Baldrige* (lower panel) drawn with their codes at their approximate position.

Table 1. *Station data for the* Tyro, Discovery *and* Baldridge *cruises. local time and position were averaged from start and end of the tow.* C. smithii *stock calculated as number and as biomass (wet weight) of crabs during day (D) and night (N) in the 0–500 or 0–600 m column, except for ′ (0–100 m) and ‴ (0–300 m) where sampling depth was limited; – not found, + present with one specimen only. Catches from* Tyro *and* Discovery *by RMT 8, from* Baldridge *by MOCNESS 10*

Station	Approx. position Lat. N (S) deg.	min.	Long. E deg.	min.	Date	Sampling depth range (m) D	N	Number (crabs m^{-2}) D	N	Biomas (g m^{-2}) D	N
Tyro cruise B0, 21 May–12 June 1992											
RS2	15	54	41	30	26 May	0–600	0–600	–	–	–	–
RS1	14	47	42	15	28 May	0–600	0–600	–	–	–	–
BEM	12	45	43	12	29 May	0–160	–	–	–	–	–
US2	10	47	51	30	4 Jun	0–500	–	–	–	–	–
Tyro cruise B1, 11 July–8 August 1992											
SB0	02	15 S	44	56	14 July	0–300	–	0.13‴	–	0.54‴	–
SB1	00	06 S	46	00	15–15 July	0–300	0–600	0.11‴	2.36	0.30‴	3.80
US0	03	15	48	20	17–18 July	0–1000	0–600	0.45	1.14	1.02	2.23
US1	07	20	50	25	19–20 Jul	0–600	0–800	–	–	–	–
US2	10	44	52	00	21–22 July	0–1000	0–300	–	–	–	–
OFZ	07	33	55	59	26 Jul	0–100	–	0.64′	–	2.29′	–
SB2	06	00	54	25	27–28 Jul	0–600	0–300	0.08′	0.97‴	0.27′	3.07‴
US1.5	09	27	51	19	29 Aug	–	0–100	–	–	–	–
SI	12	02	56	15	31 Jul–1 Aug	0–100	0–600	0.21′	0.14	1.52′	1.18
GA1	12	26	49	47	4 Aug	–	0–300	–	0.01‴	–	0.03‴
GA2	12	07	46	40	5–6 Aug	0–600	0–600	1.03	0.01	0.19	0.27
Tyro cruise B2, 11 January–6 February 1993											
SB3	01	55	53	34	31 Jan	–	0–100	–	–	–	–
SB2	06	15	52	24	15–16 Jan	0–1500	0–860	0.007	0.05	0.11	0.98
US1	07	40	50	33	18–19 Jan	0–1000	0–1000	0.017	0.10	0.33	2.04
US2	11	00	52	02	20–22 Jan	0–1000	0–1500	0.011	0.07	0.26	1.52
SI	12	05	54	57	24–25 Jan	0–1000	0–1000	0.017	0.04	0.38	0.74
GA1	13	15	50	10	27–28 Jan	0–1000	0–1000	–	0.04	–	0.41
GA2	12	44	46	40	29–30 Jan	0–1000	0–1500	–	0.03	–	0.87
BEM	12	44	43	12	1 Feb	0–170	–	–	–	–	–
RS1	14	35	42	18	2–3 Feb	0.–300	0–100	–	–	–	–
RS2	15	58	41	35	3–4 Feb	0–1000	0–1000	–	–	–	–
Discovery cruise 209, 3–22 August 1994											
12664	19	00	59	00	12–16 Aug	0–1600	0–700	0.04	0.02	0.30	0.50
12667	19	30	58	30	18–19 Aug	0–400	0–400	0.30	0.05	0.75	0.32
12668	19	38	58	25	19–20 Aug	0–150	0–170	0.13	0.28	0.59	1.70
Discovery cruise 211, 9 October–11 November 1994											
12731	19	13	58	10	9 Nov	bottom trawl at 150 m		0.025		0.67	
Baldrige cruise MB9503, 27 April–24 May 1995											
Somalia 5°N	05	12	51	08	5 May	0–1430	0–1430	–	–	–	–
(underway)	08	41	51	12	7 May	0–1500	0–940	–	–	–	–
Ras Hafun	10	00	52	00	8–9 May	0–1500	0–1500	–	–	–	–
East of Socotra	11	40	54	51	11 May	–	0–1200	–	+	–	+
(underway)	13	03	57	03	12 May	–	0–1500	–	–	–	–
(underway)	14	43	59	50	13 May	–	0–1500	–	–	–	–
WHOI mooring	15	30	61	20	13–15 May	0–1000	0–1000	–	–	–	–

Table 1. (*continued*)

	Approx. position					Sampling depth range (m)		Number (crabs m^{-2})		Biomas ($g m^{-2}$)	
	Lat. N (S)		Long. E								
Station	deg.	min.	deg.	min.	Date	D	N	D	N	D	N
JGOFS central st.	16	00	62	00	15–16 May	0–1500	–	–	–	–	–
(underway)	16	27	60	09	18 May	–	0–1500	–	–	–	–
Ras Madrakah	18	56	58	14	19–20 May	0–1000	0–1000	–	–	–	–
Omani Basin	22	17	60	44	20–23 May	0–1000	0–1000	–	–	–	–
Baldrige cruise MB9506, 31 July–30 August											
(underway)	23	11	59	33	31 July	–	0–1000	–	–	–	–
Omani Basin	22	11	60	41	1–2 Aug	0–1000	0–1000	0.66	1.88	3.79	8.83
Ras Madrakah	18	44	57	59	5 Aug	0–1000	0–500	0.25	–	1.08	–
Jabal Samhan	16	46	55	27	7 Aug	0–1000	0–1000	0.76	0.88	7.53	7.12
Gulf of Aden	14	04	50	48	9 Aug	0–1000	0–1000	0.03	–	0.06	–
Ras Hafun	10	42	51	51	9–13 Aug	0–900	0–900	1.29	1.03	12.7	8.62
East of Socotra	12	48	55	19	14 Aug	–	0–1500	–	1.11	–	7.81
WHOI mooring	15	20	61	32	16–18 ug	0–1000	0–1000	1.88	0.46	9.43	2.59
JGOFS central st.	16	00	62	00	18–19Aug	0–1500	0–1500	2.19	1.71	12.7	7.63

continued on several succeeding cruises by the ship. Three midwater sampling stations were occupied: station 12664 at 19°N, 59°E; station 12667 over the slope; station 12668 over the shelf (Fig. 3). Midwater samples were collected using an RMT(1 + 8)M (Roe and Shale, 1979)—the multiple version of the RMT1 + 8 system used on the *Tyro*—allowing three consecutive pairs of macroplankton and micronekton samples to be collected. Each pair of nets was fished for 1 h with a towing speed of 2 knots maintained as close as possible, measured by a flowmeter mounted on the net and monitored in real time. Both day and night stratified samples were collected. In the upper 200 m, strata 50 m thick were sampled, and below 200 m the sampling strata were broadened to 100 m. The maximum depths of sampling were 1600 m at station 12664 (soundings 3300–3698 m), 400 m at station 12667 (soundings approximately 500 m), and 170 m at station 12668 (soundings approximately 195 m). At the shallowest station, catches were dominated by massive numbers of the scyphomedusan *Pelagia* sp. A preliminary account of the vertical distribution of biomass and its relation to the oxygen minimum has been given by Herring and Hargreaves (1997).

Another large sample of *Charybdis* was collected by a 3 m Agassizi trawl fished on 9 November 1994 (intermonsoon) at station 12731 during *Discovery* cruise 211 (Table 1) off Oman (Fig. 3). The trawl was towed at a speed of 1.5 knots on the bottom at a depth of approximately 150 m close to the shelf-break (Gage, 1995). It was on the bottom for 1 h and sampled approximately 8000 m^2 of the sea floor.

R.V. Malcolm Baldrige *cruises.* Two US GLOBEC Arabian Sea cruises were made in 1995 by the NOAA R.V. *Malcolm Baldrige* (Table 1). The first (MB9503) was during the start of the SW monsoon from 27 April to 24 May, and occupied stations off Somalia, in the central Arabian Sea, and off Oman. The second cruise (MB9506) during the SW monsoon from 31 July to 30 August, covered the same stations, with the addition of stations off Jabal Samhan and in the Gulf of Aden, and the omission of Somalia 5°N (Fig. 3). All stations were in oceanic waters, over bottom depths ranging from approximately 1100 to 4000 m. The sampling was conducted using a Multiple Opening–Closing Net Environmental Sensing System (MOCNESS-10) trawl. This device has five nets that can be tripped sequentially to make stratified samples. The first net was fished throughout the entire descent, and the remaining four were tripped at selected depths during the ascent. Each net has a mouth area of 10 m^2 and a mesh size of 3.0 mm. The MOCNESS-10 was equipped with a CTD that sends data on depth, temperature, conductivity, oxygen and operating parameters of the net (net speed and angle) to the ship in real time. Replicate pairs of day and night samples were made at most stations, to depths of 1000 or 1500 m. Volumes filtered by each MOCNESS net ranged from 3231 to 45 775 m^3. Additional sampling was done with a 500 µm David–Hempel neuston net fished during the night. Tow duration was in the order of 120 min at an average speed of 1.7 knots, sampling 1250–6000 m^2 of sea surface. This net collected large numbers of portunid larvae (zoeae and megalopae) at times during the cruise in May. A tow at the JGOFS central station made in August, collected a large number of apparently dead *Diodon* sp. (one fish per 800 m^2), indicating the large extension of upwelled water far into the Arabian Sea.

Biomass and meristic measurements

Crabs were usually picked out of the catches as soon as they came on board, not only to ensure that the crabs were preserved in good condition, but also to optimise the condition of the rest of the catch. The crabs were fixed and preserved in a 4–5% solution of formalin in seawater. On the *Tyro*, the displacement of the crabs was measured before preservation. On board the *Baldrige*, crabs were removed from formalin after a few days, and their meristic characters measured as described below. The displacement volume and the wet weight of crabs from *Discovery* samples were measured as soon as the material reached the laboratory, about 2 months after collection.

A series of meristic measurements were undertaken to look for evidence of morphological races in the three main areas sampled—the Somali Current, Gulf of Aden and off Oman. The characters measured with Vernier callipers to the nearest 0.1 mm were: carapace width (between the points of the lowest lateral carapace teeth); carapace length and thickness; length of the propodus and dactylus of both the chelipedes; length and width of the last segment of the swimming legs. The incidence of limb regeneration was noted.

RESULTS

Size–weight relationship

Measurements of the crabs showed a consistent ratio of carapace width to carapace length and thickness, indicating that growth of the carapace was isometric. Thus carapace width could be used as a reliable measure for the overall size of each animal. To establish the stock of the crabs as biomass, first the relation between the weight and the carapace width of *C. smithii* was calculated. Measurements of 368 crabs caught during the *Discovery* cruises were analysed by linear regression and showed a linear log–log relationship between carapace width and wet weight (formalin preserved animals):

$$\log(\text{wet weight}) = 3.098 \times \log(\text{carapace width}) - 0.873;\ r^2 = 0.984;\ p = 0.0001.$$

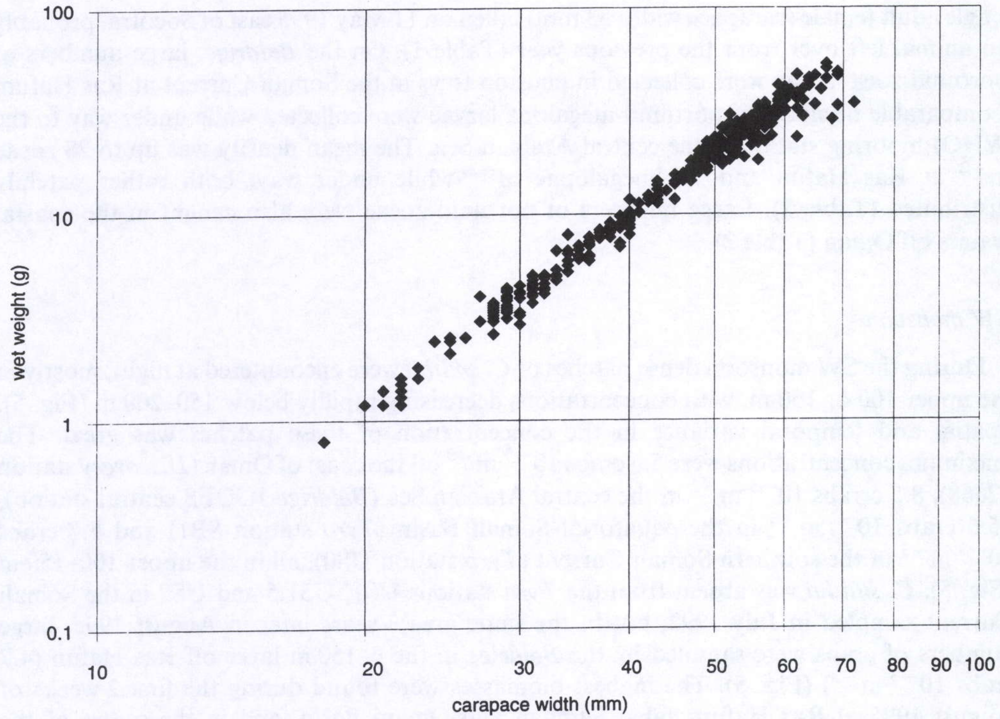

Fig. 4. The relation of the wet weight and the carapace width, on a log–log scale, for *C. smithii* from all *Discovery* samples off Oman during the SW and NE monsoon (cruises 209 and 211, respectively).

(see Fig. 4). A similar analysis of data from 74 crabs from the *Tyro* samples collected during both monsoons, gave very similar results:

$$\log(\text{wet weight}) = 3.132 \times \log(\text{carapace width}) - 0.922; \; r^2 = 0.992; \; p = 0.0001.$$

The first equation was used for calculating the wet weights of the remaining crabs in the *Tyro* samples and the crabs in the *Baldrige* samples, all of which had the carapace widths measured.

Seasonal occurrence

Charybdis smithii was absent from all hauls collected deeper than 600 m depth irrespective of season or time of day. No specimens were taken either in the southern Red Sea or at Bab el Mandab, the strait between the Gulf of Aden and the Red Sea, despite there being a strong subsurface inflow into the Red Sea during the SW monsoon and a surface inflow during the NE monsoon. Below, results are presented in seasonal order, beginning with the onset of the SW monsoon. The numbers of crabs per square metre in the 0–500 or 0–600 m water column (i.e. through the full depth range of the species) are listed in Table 1.

Onset of the SW monsoon

Adult *C. smithii* were absent from the Somali Current, off Oman, and the central Arabian Sea at the onset of the SW monsoon in early June 1992 and May 1995. There was only a single adult female (carapace width 53 mm) taken on 11 May 1995 east of Socotra, probably an animal left over from the previous year (Table 1). On the *Baldrige*, large numbers of portunid zoea larvae were collected in neuston tows in the Somali Current at Ras Hafun. Comparable numbers of portunid megalopa larvae were collected while under way to the WHOI mooring station in the central Arabian Sea. The mean density was up to 28 zoeae m^{-2} at Ras Hafun and 7.5 megalopae m^{-2} while under way, both rather patchily distributed (Table 2). Large numbers of portunid zoeae were also caught in the coastal waters off Oman (Table 2).

SW monsoon

During the SW monsoon dense patches of *C. smithii* were encountered at night, mostly in the upper 100 or 150 m, with concentrations decreasing rapidly below 150–200 m (Fig. 5). Spatial and temporal variance in the concentration of these patches was great. The maximum concentrations were 5.6 crabs 10^{-3} m^{-3} off the coast of Oman (*Discovery* station 12668), 8.5 crrabs 10^{-3} m^{-3} in the central Arabian Sea (*Baldrige* JGOFS central station), 15.6 crabs 10^{-3} m^{-3} in the equatorial Somali Basin (*Tyro* station SB1) and 5.7 crabs 10^{-3} m^{-3} in the southern Somali Current (*Tyro* station US0), all in the upper 100–150 m (Fig. 5). *C. smithii* was absent from the *Tyro* stations US1, US1.5 and US2 in the Somali Current sampled in July 1992, but in the same area 3 years later in August 1995, large numbers of crabs were sampled by the *Baldrige* in the 0–150 m layer off Ras Hafun (4.7 crabs 10^{-3} m^{-3}) (Fig. 5). The highest biomasses were found during the first 2 weeks of August 1995 at Ras Hafun, Jabal Samhan and Omani Basin, and in the centre of the Arabian Sea at the JGOFS central station (Fig. 6b), ranging from 7 to 9 g m^{-2} (*Baldrige* stations, Table 1). In the second half of July 1992 (3 weeks earlier in the season) lower biomasses were taken in the Equatorial Somali Basin, ranging from 2 to 3.8 g m^{-2} (*Tyro* stations SB1, US0 and SB2, Table 1). Diel vertical migration by the crabs was most obvious at the *Discovery* stations 12668 and 12667, where crabs were abundant in the 50–100 m layer by day and migrated up into the upper 50 m at night (Fig. 5). The biomass was higher at night, and increased from the oceanic station 12664 (0.5 g m^{-2}) to the shelf station 12668 (1.7 g m^{-2}).

During the SW monsoon, *C. smithii* contributed 92% of the total micronekton biomass (RMT8 sample) taken near the surface during the day at *Tyro* station SI, 81% at SB1 and about 60% in the upper 100 m at night at US0 and SB2. It contributed 27% of the total RMT8 biomass of *Discovery* station 12668 on the Oman shelf in August 1994, where the catches were dominated by swarming *Pelagia* sp., and about 10% at the other two stations. At all three stations the total catch of decapods in the upper 100 m both day and night was composed almost entirely of *C. smithii* (P. Herring, personal communication, 1995). The crabs accounted for about 50% in the total micronekton biomass in the 0–150 m layer during the day at Ras Hafun and in the central Arabian Sea (*Baldrige* stations). They constituted 28% and 37% in the 0–150 m layer at night at the Omani Basin and Jabal Samhan stations, respectively, and 25–43% in the 0–150 m layer at the two stations in the central Arabian Sea.

No crabs were taken deeper than 100 m off Oman by the *Discovery* in August 1994, when a very intense oxycline at 70 m co-occurred with a strong halocline capping a tongue of high-salinity Persian Gulf Water. Off Oman, records of acoustic backscatter using a 150 kHz ADCP showed multiple layers during the day. We suspect a layer at 65–70 m associated with

Table 2. Portunid larval (zoeae and megalopae) and juvenile stages in neuston samples with a 500 µm David Hempel net from Tyro *during* 1992 *and* 1993 *and* Baldrige *during* 1995. *Local time and position were averaged from start and end of the tow. Surface temperature and Chlorophyll concentration were sampled at a depth of* 3 m (Tyro) *and* 5 m (Baldrige). *Mean density of larvae and juveniles per sampled sea surface. Catches by day were not used for density calculations.* Baldrige *tows 4 and 29 failed due to stops of the ship. The zoeae, megalopae or juveniles respectively, are morphologically identical*

Station	Approx. position Lat. N		Long. E		Date	Surface temp.	Surface Chl.	Water type	Zoeae	Megalopae	Juv.
	deg.	min.	deg.	min.		(°C)	(mg m^{-3})		(ind 100^{-1} m^{-2}		
Tyro cruise B0 (1992)											
RS1	14	48	42	16	28 May	30.2	0.2	oligotrophic	130	68	
Tyro cruise B1 (1992)											
SB"	05	44	54	16	28 Jul	25.0	0.5	downstream upw.		3	
US1.5	09	26	51	19	29 Jul	18.1	0.7	upwelling		3	
SI	12	01	56	14	31 Jul	23.5	0.5	downstream upw.		1	
GA1	12	27	49	47	4 Aug	30.0	0.2	oliogotrophic	15	4	
GA2	12	10	46	59	4 Aug	29.7	0.2	oligotrophic		6	
Tyro cruise B2 (1993)											
SB3	01	57	53	34	13 Jan	26.5	0.3	mesotrophic		2	
SB2	06	20	52	23	15 Jan	26.9	0.3	mesotrophic		2	
US1	07	52	50	36	18 Jan	26.6	0.4	mesotrophic		0.1	
US2	10	55	52	01	20 Jan	26.0	0.4	mesotrophic		2	
SI	12	07	54	56	24 Jan	25.9	0.4	mesotrophic		27	
GA1	13	18	50	14	27 Jan	25.7	0.5	mesotrophic		86	
GA2	12	50	46	32	29 Jan	25.4	0.6	mesotrophic		86	
RS1	14	35	42	17	2 Feb	25.6	1.0	diatom bloom		94	
RS2	15	53	41	38	3 Feb	25.7	1.2	diatom bloom	1580	743	
Baldrige cruise MB9503 (1995)											
Somalia 5°N	05	00	49	04	4 May	30.0	<0.1	oligotrophic		1	
Somalia 5°N	05	00	49	05	4 May	30.0	<0.1	oligotrophic		1	
(underway)	06	40	50	07	6 May	30.0	<0.1	oligotrophic		2	
Ras Hafun	10	01	51	57	8 May	29.2	0.3	start upwelling	2829	27	
Ras Hafun	10	12	52	02	8 May	29.9	0.1	start upwelling	123	4	
Ras Hafun	10	01	52	16	9 May	29.3	0.8	start upwelling	47	6	
(underway)	11	39	54	50	10 May	30.0	<0.1	oliogotrophic	0.1		
(underway)	13	00	57	04	11 May	30.0	<0.1	oliogotrophic			
(underway)	13	00	57	04	11 May	30.0	<0.1	oliogotrophic	746		
JGOFS central st.	15	59	62	01	15 May	29.2	<0.1	oligotrophic		49	0.2
JGOFS central st.	16	00	61	59	16 May	29.2	<0.1	oligotrophic		24	
(underway)	16	24	60	17	17 May	29.2	<0.1	oligotrophic		1	
Ras Madrakah	18	55	58	12	19 May	27.3	0.5	start upwelling	403	28	
(underway)	21	58	59	54	20 May	27.5	0.3	start upwelling	17	20	0.01
Omani Basin	22	15	60	44	21 May	28.5	0.1	start upwelling		91	
Omani Basin	22	15	60	43	22 May	28.2	0.1	start upwelling		69	
Baldrige cruise MB9506 (1995)											
(underway)	23	09	59	34	31 Jul	30.5	0.1	oligotrophic	1	0.5	
Omani Basin	22	04	60	38	1 Aug	26.5	0.6	upwelling		6	
Ras Madrakah	18	43	58	00	5 Aug	21.3	0.4	upwelling		1	
Jabal Samhan	16	45	55	25	6 Aug	23.1	3.9	upwelling		9	
Jabal Samhan	16	46	55	26	7 Aug	22.3	5.0	upwelling		6	
(underway)	15	58	53	37	8 Aug	25.6	0.6	upwelling	5	5	
Gulf of Aden	14	01	50	40	9 Aug	29.0	0.5	downstream upw.			

Table 2. (continued)

Station	Approx. position Lat. N deg.	min.	Long. E deg.	min.	Date	Surface temp. (°C)	Surface Chl. ($mg\ m^{-3}$)	Water type	Zoeae	Megalopae	Juv.
									($ind\ 100^{-1}\ m^{-2}$)		
Gulf of Aden	14	04	50	51	9 Aug	28.6	0.1	downstream upw.			
Ras Hafun	10	40	51	49	11 Aug	22.2	3.0	upwelling		2	
Ras Hafun	10	43	51	52	12 Aug	22.5	1.8	upwelling		3	
(underway)	12	48	55	19	14 Aug	26.3	0.2	downstream upw.		2	
WHOI mooring	15	20	61	33	17 Aug	26.2	0.4	downstream upw.		7	
JGOFS central st.	15	59	61	58	18 Aug	26.2	0.2	doqnatream upw.		12	

the halo-oxycline was caused by the crabs. Trawl catches showed that myctophid fish and euphausiids were probably responsible for backscatter within the oxygen minimum layer itself.

Intermonsoon and NE monsoon

During the intermonsoon in November 1994, adult-sized crabs were sampled from the *Discovery* with a bottom trawl on the continental shelf off Oman, where oxygen levels at the bottom had risen, although they were still extremely low. The estimated density of *C. smithii* was 0.025 m^{-2}, assuming they were all caught at the bottom (Table 1). Crabs also were observed swimming at the surface. The biomass of crabs was 0.67 $g\ m^{-2}$ (Fig. 6c), but direct comparisons with the preceding sampling off Oman with the *Discovery* may be misleading because a different type of net was used.

During the NE monsoon the *Tyro* found lower stocks of larger crabs (Table 1). Maximum abundance was found at the stations US1 and US2, where concentrations were 0.60 crabs $10^{-3}\ m^{-3}$ in the 100–200 m layers at night, just subthermocline, and building up a stock of 0.07–0.10 crabs m^{-2} (Table 1). Although the deepest records of *C. smithii* were at these stations none occurred deeper than 300 m. Daytime concentrations were always very low compared with those at night, possible because of net avoidance by the crabs. During the NE monsoon in January 1993, biomass of *C. smithii* in the Gulf of Aden and the Somali Basin was lower than during the SW monsoon (Fig. 6b and d), ranging from 0.4 $g\ m^{-2}$ to 2.0 $g\ m^{-2}$, respectively (Table 1). Large surface swarms of *C. smithii* were seen in the Northern Somali Basin and in the Gulf of Aden (*Tyro* stations US2 and GA2) at night, but were absent during the day. Observations from the ship estimated concentrations to be about 1 crab per 10 m^2. In February 1993 the stock of *C. smithii* in the Gulf of Aden was about three times larger than during the preceding SW monsoon (Table 1), indicating this a concentration area.

Size–frequency distributions of crabs

The size–frequency distribution of 2447 juvenile, male and female crabs (65% of the total of crabs caught during all cruises), showed some clear peaks at 8, 22, 30, and 40 mm (Fig. 7). In the juvenile range only the 8 mm peak was distinct. If the peaks are assumed to represent the specific instars, then there were hints of other instars at 6, 12 and 14 mm; these juveniles also differed in appearance from the 8 mm specimens. Balasubramanian and Suseelan

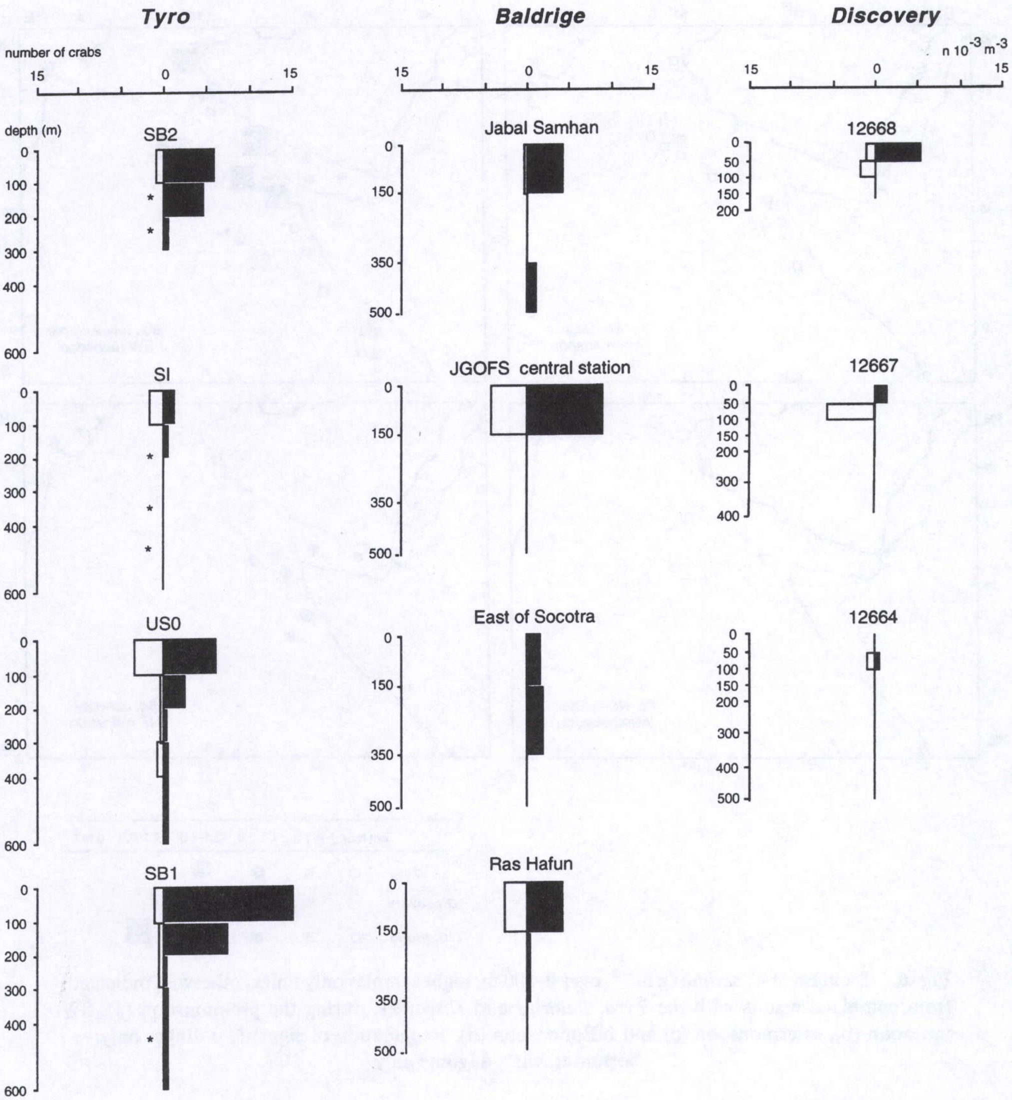

Fig. 5. Vertical distribution of *C. smithii* (number of crabs 10^{-3} m^{-3}) during the SW monsoon during day (open bars) and night (filled bars), at some stations of the *Tyro*, *Baldrige* and *Discovery* cruises. *, Sample lacking. The length of the vertical axes represents the sampled depth.

(1990) observed maxima at 11.5 mm and 13.5 mm in their material. If the size peaks at 5, 8.5, 13.5, 21.5, 29.5, 39.5, 48.5, 52.5 and 56.5 mm in Fig. 7 are related to successive instars then the incremental growth decreased from a factor of 1.7 to 1.07 during maturation. In Fig. 8 the growth increment plotted as a percentage of the carapace width on a log scale indicated a linear decrease. A similar plot of the pooled data shown in Fig. 7 implied that these estimates were not widely divergent from the observations. The absence of a clear peak at 56 mm might result from variability in moult increment increasing with the instar number (Hartnoll, 1982).

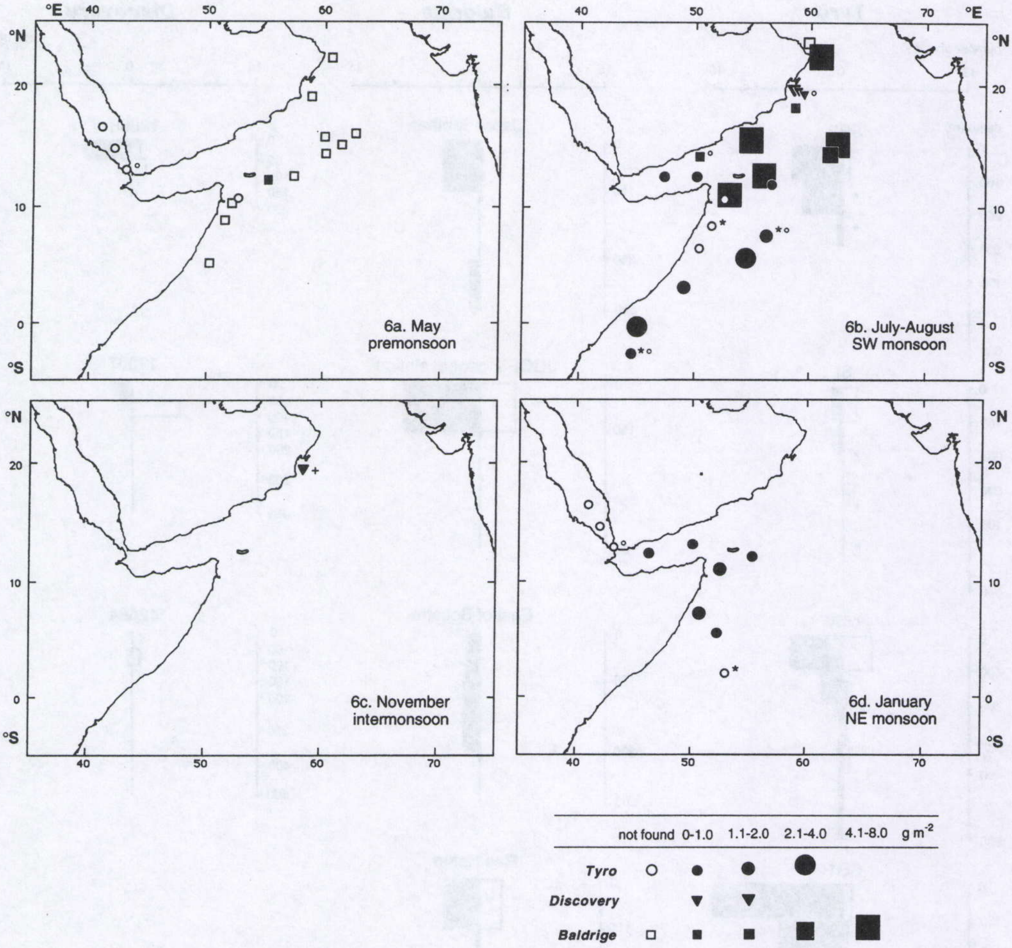

Fig. 6. Biomass of *C. smithii* (g m^{-2}, over 0–500 m, night samples only unless otherwise indicated) from combined results with the *Tyro*, *Baldrige* and *Discovery*, during the pre-monsoon (a), SW monsoon (b), intermonsoon (c) and NE monsoon (d). Explanation of signs: *, 0–100 m only; +, bottom trawl; °, daytime only.

The smallest crabs (5–6 mm) were found in neuston samples collected in May 1995 in the Arabian Sea (*Baldrige*, Table 2). In July 1992 small crabs ranging from 15 to 25 mm dominated RMT8 catches not far off the coast of Africa (*Tyro* stations SB1 and US0) together with few larger animals (25–40 mm); about 12–16 days later, and further offshore (stations SB2, OFZ and SI), larger crabs were collected (Fig. 9). Juvenile crabs of 7–12 mm were caught with the RMT8 in the Gulf of Aden in August 1992 (*Tyro* station GA2). The size–frequency distributions of crabs at the open ocean stations had a single maximum in contrast to the double peak seen from inshore collections, suggesting that the smaller crabs had moulted by the time they arrived offshore. It is unclear whether these crabs were produced from a single breeding event or several events, and had taken different lengths of time to arrive offshore. Crabs collected during the SW monsoon in August 1995 off Oman, in the Somali Current, and the central Arabian Sea (*Baldrige*) ranged from 18.9 to 53.9 mm

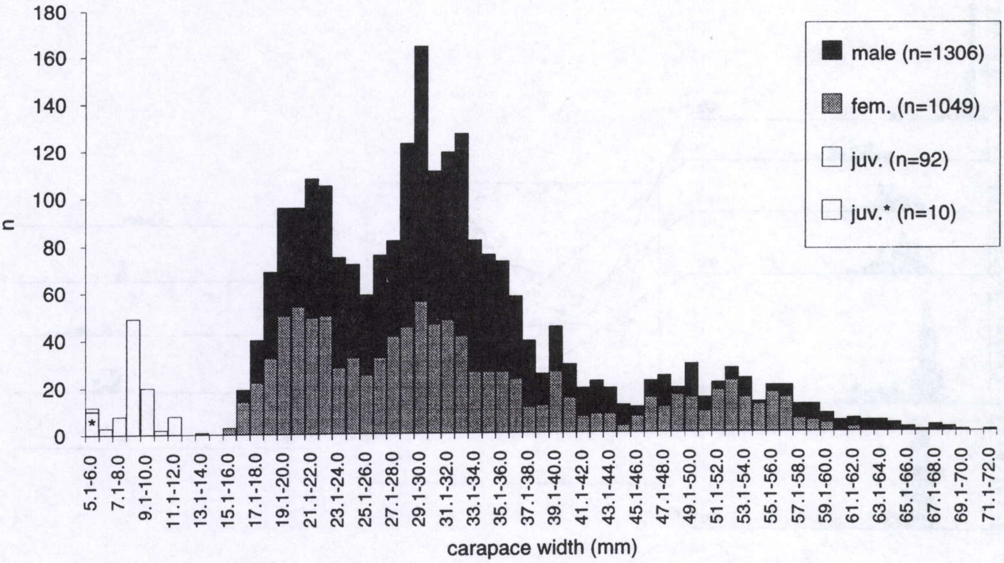

Fig. 7. Size–frequency distribution of carapace width (size class in mm along horizontal axis, numbers of crabs along vertical axis) for *C. smithii* (juveniles, males and females) in pooled samples with RMT8 (*Tyro* and *Discovery*), and MOCNESS-10 (*Baldrige*) gear during all cruises. *, Juveniles from David–Hempel neuston net (*Baldrige*).

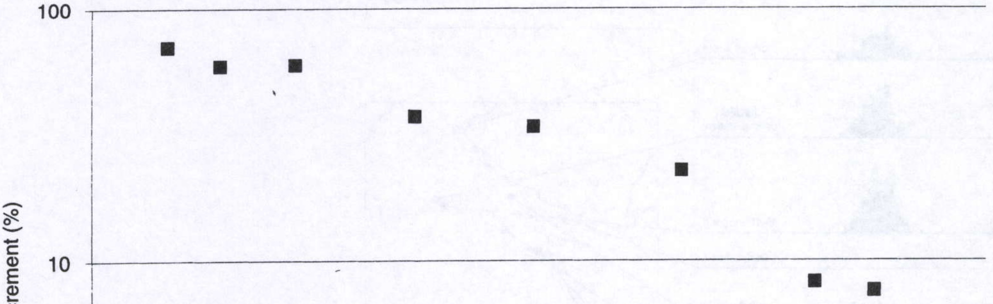

Fig. 8. Relation of log percentage moult increment and carapace width for *C. smithii*.

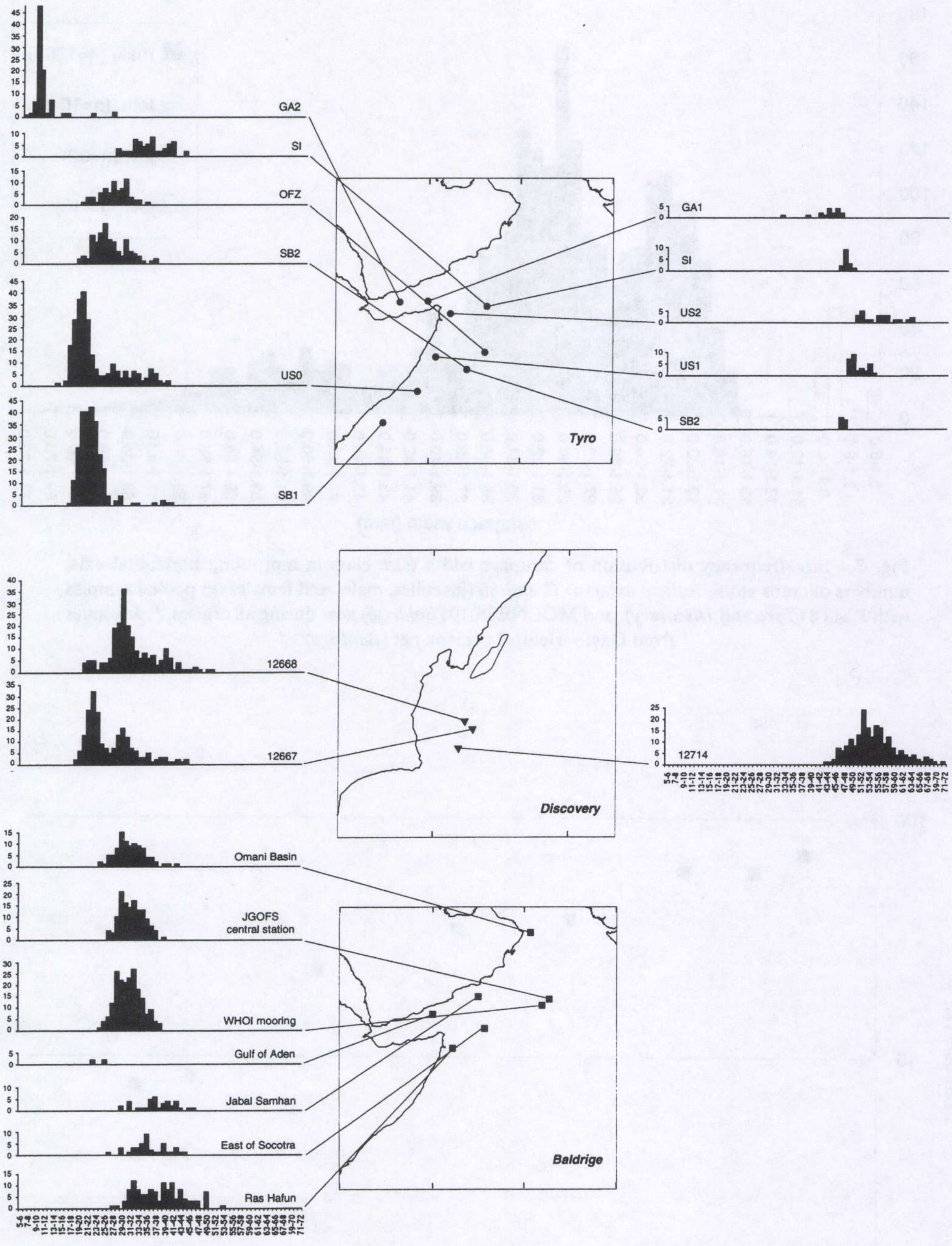

Fig. 9. Size–frequency distribution of carapace width (size class in mm along horizontal axis, numbers of crabs along vertical axis) for *C. smithii* (juveniles, males and females) at the *Tyro* (upper panel), *Discovery* (middle panel) and *Baldrige* (lower panel) stations, during the SW monsoon in July–August (left), during the intermonsoon in November and during the NE monsoon in January (both right). It should be noted that because of absence or relative low numbers of crabs in the catches, the following stations are omitted: *Tyro* GA1 (cruise B1) and SB3 (cruise B2), *Discovery* 12664 (cruise 209), and *Baldrige* Ras Madrakah (cruise MB9506).

in carapace width (Fig. 9; only data from large catches are illustrated). A peak at 30 mm was recognisable in the size–frequency distributions both at the WHOI mooring and at Ras Hafun; at the latter there was also a 41 mm peak, consistent with the stage size in Fig. 7. In January 1993 (*Tyro*) there was regional variation in the sizes, smaller crabs (32.5–46.2 mm) occurring in the Gulf of Aden and larger ones (50.4–63.5 mm; Fig. 9) in the Somali Current. However, the relatively small numbers of crabs caught at these stations might not be representative. The largest animals were found nearshore (stations US 1 and US2; Fig. 9). Those trawled from the bottom off Oman in November 1994 ranged in size from 43 to 71.7 mm (mean 54.8 mm). The peaks in the size–frequency distribution at 52 and 55 mm were made up of females (Fig. 9). The males showed a size peak at 59 mm, but as the male:female ratio was only 0.4, the male maximum was obscured in the overall size frequency distribution.

Larval and juvenile stages

Adults (carapace widths of 44–49 mm) collected during the *Tyro* B2 cruise in the Gulf of Aden in January 1993 were taken back to the Baltic Sea Research Institute at Warnemünde, Germany, where they were used by Mrs B. Meyer-Harms in laboratory breeding experiments. Copulation took place after the females moulted. The females laid eggs, carrying them on their pleopods beneath the abdomen. After 2–3 days the eggs were released, although normally egg-bearing females will carry the eggs until they hatch. The eggs were kept under aeration in two batches at 18°C and 24°C, and hatched after 4 weeks. Despite being fed with a diet of diatoms (*Odontella*) and freshly hatched *Artemia*, none of the larvae survived beyond the first zoeal stages (B. Meyer-Harms, personal communication,, 1995).

Zoea and megalopa larvae of portunid crabs were abundant in neuston samples collected in the Central Arabian Sea at 14°32′N, 59°48′E and in the Somali Current near Ras Hafun at 10°01′N, 51°57′E in May 1995 by the *Baldrige* using 500 µm mesh David–Hempel neuston net (Table 2). Portunid megalopae were also found in RMT8 samples from the 0–50 m layer off Oman at *Discovery* stations 12664 and 12668. We assume the megalopae were *C. smithii*. Comparison of the zoeae in the *Baldrige* neuston samples with the first zoeal stages hatched during the laboratory breeding experiments showed striking morphological similarity. However, the lack of distinctive characters made it uncertain whether or not they were conspecific.

Juvenile portunid crabs with carapace widths of 5–6 mm, presumed to be the smallest crab stage of *C. smithii*, were collected in the neuston during the first *Baldrige* cruise in the Central Arabian Sea at 14°32′N, 59°48′E (Table 2). Their meristic ratios were identical to juvenile *C. smithii* collected during the *Tyro* leg B1 in the Gulf of Aden (station GA2, carapace width 8–10 mm) and specimens collected in the southern Somali Current (station US0, with carapace widths of 12 mm and larger).

Loss of limbs and regeneration

In the pelagic *Discovery* material 20% of the specimens had lost either limbs or claws and had regeneration buds, so these losses had occurred before sampling; 21.9% of males ($n = 52$) and 17.8% of females ($n = 40$) were regenerating limbs (Table 3). Most (38 males and 27 females) had lost one or even both claws. There was a sexual disparity: males

Table 3. Summary of meristic data of C. smithii *in samples from the* Discovery *cruise 209, from 3–22 August 1994. Mean and standard deviation (SD) of ratios of character length to carapace width expressed as percentage for males and famales*

	Males			Females		
	Mean %	SD %	n	Mean %	SD %	n
Length	69.59	1.71	234	69.69	2.36	220
Thickness	35.80	1.32	229	36.27	2.80	218
Orbit	34.25	1.40	97	34.30	1.44	82
Telson	34.52	1.39	96	35.66	1.47	82
Left dactylus	33.23	2.40	73	32.52	1.95	60
Left propodus	66.28	2.81	66	63.42	3.00	60
Right dactylus	33.60	1.41	67	32.33	1.44	69
Right propodus	67.24	2.83	69	65.16	2.30	63
Paddle segt. of swimming leg	28.60	1.52	82	28.71	1.55	81
Left:right propodus	98.91	2.23	52	98.73	2.67	48

predominantly lost the right claw, and females the left. Regenerated claws were markedly slimmer and somewhat shorter than normal, and it was clear that loss of one or even two claws did not necessarily result in death (at least two specimens were found with a pair of abnormally slim claws indicating that both had been regenerated). Intraspecific fighting was seen between crabs at the surface at night, which may have resulted in the claw losses. Damage to the other legs may have resulted from unsuccessful attacks by predators. Not one example of regeneration of the swimming legs was noted, and presumably damage or loss of these would be fatal.

Meristic ratios

There were only trivial differences between the average ratios of the length of each of the body parts to the carapace width between samples collected from off Oman, in the Gulf of Aden, off Somalia, and from the southern Somali Basin. Thus there was no evidence that the swarms of *C. smithii* sampled at different stations belonged to separate discrete races. The length and thickness of the carapace and the length of the last segment of the fifth leg ("paddle") showed a constant linear relation with the carapace width in males and females of all sizes. However, some sexual dimorphism was found in the abdomen and in the propodus. The ratio of abdomen length to carapace width was constant in males, but in females greater than about 45 mm width, the abdomen was proportionally greater than in males of the same size or in smaller females and males (Fig. 10). In crabs greater than about 52 mm, the length of the left and the right propodus relative to the carapace width was proportionally greater in males than in females (Fig. 10). The lengths of the left and right propodus were not always 1:1 as expected (Table 4). In some cases, one of the propodes was longer than the other; probably because of loss of the cheliped and subsequent regeneration with the next moult. This occurred in more males than females, and equally with the left or right leg.

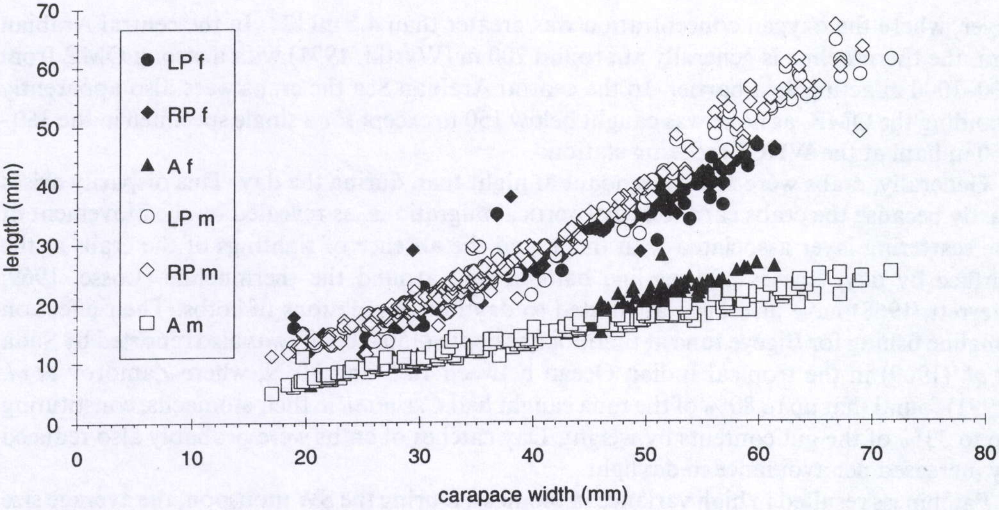

Fig. 10. **Relation of carapace width and length of abdomen (A), left propodus (LP), and right propodus (RP), in females (f) and males (m) of *C. smithii* from pooled samples during all cruises with *Tyro*, *Discovery* and *Baldrige*.**

DISCUSSION AND CONCLUSIONS

Crabs were not found deeper than 100 m off Oman in August 1994, where there was a very sharp oxycline at 70 m, suggesting that the crabs were avoiding the OMZ. In July 1992 and January 1993, the depth distribution of *C. smithii* was also correlated with oxygen concentration and the depth of the thermocline. During the SW monsoon in the Gulf of Aden and off Somalia the OMZ began at 50 m (GA2, US2) or 100 or 200 m (SI and SB2, respectively). At these stations the highest concentrations of crabs occurred in the upper

Table 4. *Regeneration of limbs in adult* C. smithii *males and females in samples from the* Discovery *cruise* 209, *from* 3–22 *August* 1994

Limb	Males n	Females n
Left claw	12	18
Right claw	21	4
Both claws	5	5
1 Walking claw	12*	6*
2 Walking legs	1	4
3 Walking legs	1	3
1 Claw + 1 Walking leg	4	1
1 Claw + 2 Walking legs	3	2
1 Claw + 3 Walking legs	3	0
Total of crabs	237	225
Total crabs regenerating	52	40
% of total	21.9	17.8

*Mostly the first walking leg

layer, where the oxygen concentration was greater than 4.5 ml l^{-1}. In the central Arabian Sea, the thermocline is generally at around 200 m (Wyrtki, 1971) with a strong OMZ from 200–1000 m acting as a barrier. In the central Arabian Sea the crabs were also apparently avoiding the OMZ, as none was caught below 150 m except for a single specimen in the 350–150 m haul at the WHOI mooring station.

Generally, crabs were more abundant at night than during the day. This disparity arises partly because the crabs carry out diel vertical migrations, as revealed by the movement of the scattering layer associated with them, and the absence of sightings of the crabs at the surface by day. Losses of long-line baits at and around the thermocline (Losse, 1969; Merrett, 1968) have also been attributed to daytime populations of crabs. Their effect on longline fishing for Bigeye tuna at thermocline depth (150–200 m) was also reported by Suda *et al.* (1969) in the tropical Indian Ocean between 10°S and 10°N, where Zamorov *et al.* (1991) found that up to 80% of the tuna caught had *C. smithii* in their stomachs, constituting up to 33% of the gut contents by weight. Day catches of crabs were probably also reduced by increased net avoidance in daylight.

Patchiness resulted in high variance in biomass. During the SW monsoon, the average size of the crabs sampled increased between late July (*Tyro* samples) and August (*Baldrige* and *Discovery* samples), so biomass also showed temporal variance. The absence of crabs in samples taken by the *Tyro* in the Somali Current during the SW monsoon, whereas in the same season 2 years later the *Baldrige* made large catches in the same area and in the same season, again points to spatial and temporal variance.

Once settled to the bottom, *C. smithii* appeared to be more tolerant of low oxygen concentrations. On the Oman shelf in November 1994 the top of the OMZ was at around 50 m and oxygen concentrations near the bottom at 150 m were 0.6–0.8 ml l^{-1} (Gage, 1995). However, the absence of egg-bearing females suggests that breeding activity may be inhibited until the bottom waters are reventilated with well-oxygenated water. Adult crabs were sparse on the sea bed (one crab per 40 m^2). If these adults had been recruited from pelagic populations as dense as observed in the same region in August, then there must have been a mortality of around 90% in the preceding 3 months. Considering the reports of large pelagic fish and squid feeding on the crabs, a loss of this magnitude may not be unreasonable. Bottom photographs and core and grab samples taken at similar depths on the same cruise showed the sea floor to be composed of a shelly fine sand, with foraminiferan populations dominated by *Uvigerina*, diverse macrofaunal populations of gastropods, bivalves and polychaetes, and megafauna including vescomyid bivalves (*Indocrassatella* sp.), gastropods, scaleworms and juvenile spider crabs (*Encephaloides* sp.). In deeper water, photographs often showed the bottom littered with empty carapaces of portunids. However, whether these carapaces were the result of predation or moulting could not be determined.

Off Somalia, dead crabs and parts of crabs were found in moored sediment traps deployed by the *Tyro* at 10°45′N, 51°56′E on the Somali continental margin and at 10°43′N, 53°34′E in the Somali Basin east of Socotra. The traps had a collection area of 1 m^2, protected with a 2.5 cm mesh grid. They were deployed at various depths from 1032 to 3047 m from 7 June 1992 to 28 February 1993. The quantities of crab remnants in the traps indicated a relatively minor contribution to the carbon sink during the SW monsoon (G. J. Brummer, personal communication, 1995), but later, when the primary production peak is passed and the crabs are larger, they may make a larger contribution to the carbon flux. Only small crabs or parts of crabs can pass through the protection grid on the sediment trap, so the samples may be underestimates. In any case, it is probable that dead crabs from patches of *C. smithii* can be an important part of the carbon flux.

Size distribution and growth

Samples collected off Oman during the SW monsoon in August revealed several peaks in the size–frequency. At station 12667 on the slope, there were two clear maxima of carapace width at 22 and 30 mm. At the shelf station 12668, the maximum at 22 mm was less defined, but that at 30 mm was clear (Fig. 9), with a possible third maximum at 40 mm. The ratios between these peaks were very similar, about 1.36. If these represent specific instars, and this size ratio remains consistent through all stages, then peaks in size frequency would be expected at 4.5, 6.3, 8.6, 11.7, 16, 22, 30, 41 and 56 mm (adult size). The maturation moult to adult size is subject to sexual dimorphism, and, as in most other portunids, further post-maturation moults may occur. The histogram of the pooled data in Fig. 7 suggests that these estimates are fairly close to the observations. Figure 7 is based on data for 2447 crabs (juveniles, females and males), i.e. most of the crabs caught by the three ships. The peaks expected at 4.5, 6.3, 11.7 and 16 mm are missing, possibly because the samples were collected when there were no crabs of these sizes in the water column, or because the neuston, where these small juvenile crabs can be expected in the first place, is missed by the pelagic gear. The juveniles in the neuston catches that fell into the 5.0–6.0 mm size class in Fig. 7 could represent either the expected 4.5 or 6.3 mm carapace width, considering a reasonable amount of variability. The expected peak at 56 mm is less clear, but this may result from variability in moult increment with higher instars (Hartnoll, 1982). The size–frequency distribution of the crabs caught off Oman in November 1994 suggests a peak between 52 and 57 mm. Thus, assuming the same populations were being sampled in the 83 days between 18–19 August and 9 November 1994, most of the crabs passed through at least two instars to reach adult size, and each of these late instars could last no longer than about 40 days. At that rate, the possible eight instars from the first crab stage to adult size would take a maximum of 320 days, and the life cycle is completed within a year.

These conclusions on stage durations are consistent with other data on *C. smithii*. Literature records show its distribution area situated in the NW Indian Ocean (Fig. 11), although the type locality is at Cape Town, South Africa. Carapace width data from the literature show an increasing size with time of year (Fig. 12). The smallest crabs (first instars) were recorded in February by Daniel and Chakrapany (1983) off Oman. Carapace widths ranging from 10 to 20 mm were reported for December, March and April in the SW Indian shelf waters by Balasubramanian and Suseelan (1990). At the same season, remarkably large crabs (about 70 mm) have been reported in the Gulf of Aden in March (Losse, 1969). Literature data show that the maximum size is 75 mm and that the large adults disappear after March (Fig. 12). This also indicates a 1 year life cycle for *C. smithii*, but it is difficult to deduce where and when reproduction occurs. The only records of ovigerous females are for January to March off Oman and SW India (Daniel and Chakrapany, 1983, Suseelan *et al.*, 1990); no other ovigerous females have been reported (Fig. 11). The presence of large non-breeding adults found with the *Discovery* off Oman in November suggests that breeding may occur there from December onwards. Juvenile crabs appear off India in December (Balasubramanian and Suseelan, 1990) so breeding must occur there earlier in November. Assuming that *C. smithii*, like several other *Charybdis* species, has six zoeal stages (Greenwood and Fielder, 1983), zoeal development may be completed in 21–27 days, but

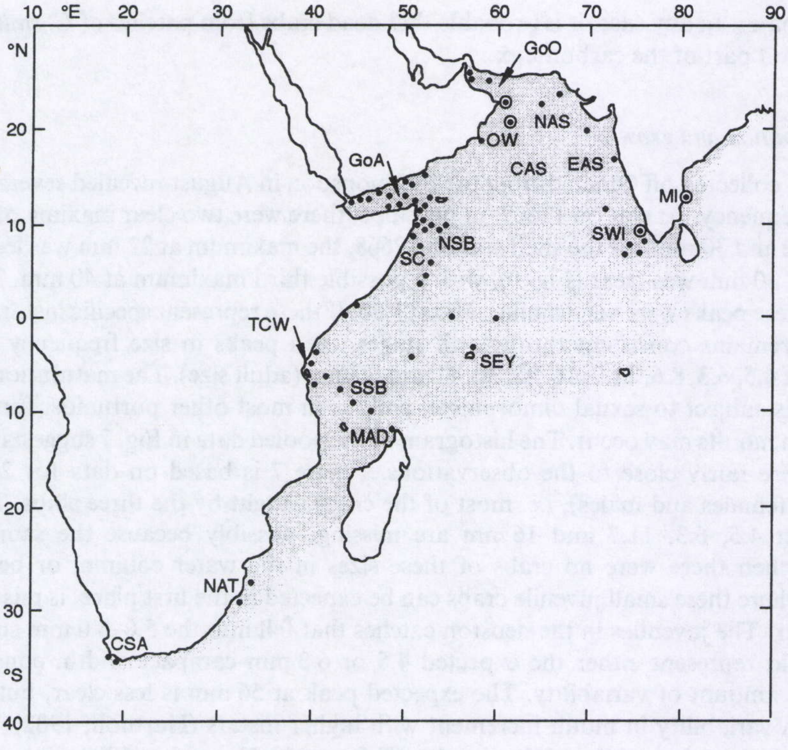

Fig. 11. ●, Records of *C. smithii* in literature used in this study; ○, records of ovigerous females. The probable distribution area is stippled, with the interpolated eastern limit matching the general surface current pattern. Topographical codes (from SW to NE): CSA, Cape South Africa; NAT, off Natal South Africa; MAD, Madagascar; SSB, southern Somali Basin; TCW, Tanzania coastal waters; SEY, Seychelles; SC, Somali Current; NSB, northern Somali Basin; GoA, Gulf of Aden; CAS, central Arabian Sea; OW, off Oman; GoO, Gulf of Oman; NAS, northern Arabian Sea; EAS, eastern Arabian Sea; SWI, off southwestern India; MI, off Madras, India.

there are no data on the duration of the megalopa stage.

Reproduction and life-history

Reproductive areas are known in the shelf waters off NE Oman and India (Fig. 11). Daniel and Chakrapany (1983) reported egg-bearing females (of *C. edwardsi*, a synonym of *C. smithii*) in the Northwestern Arabian Sea during January and February, and at deep water stations off Oman and in the shallow inshore waters of Madras (Bay of Bengal, East India) during January–March. Suseelan *et al.* (1990) reported that, in January 1988, 90% of all the females trawled from the bottom at depths of 130–382 m off SW India were ovigerous. Balasubramanian and Suseelan (1990) made no mention of any ovigerous females being amongst those caught in Isaac–Kidd Midwater trawls from along the western coast of India during either the 'postmonsoon' (October–January) or 'premonsoon' (February–May), even in samples collected near places where crabs were caught in bottom trawls. This suggests that copulation occurs, and egg-bearing adults are present during the breeding season, only on the bottom. In the same study, juvenile crabs (carapace width 12–

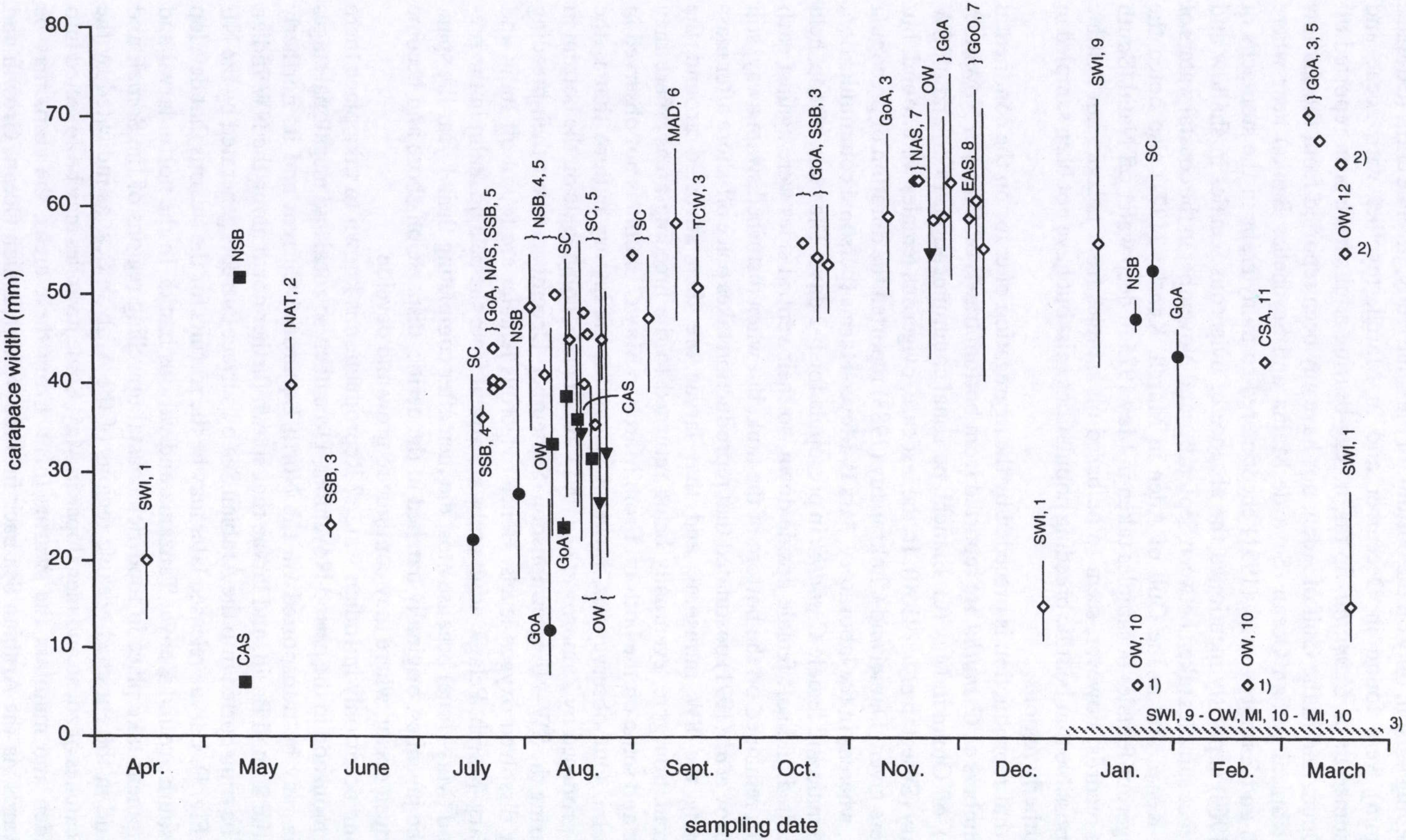

Fig. 12. Mean carapace width of *C. smithii* plotted to the sampling day, based on literature data (◇) and ship data from the present study (●, *Tyro*; ■, *Baldrige*; ▼, *Discovery*). Vertical lines indicate the size range. Remarks: (1) first instar, carapace width assumed to be 6 mm; (2) carapace width derived from mean body wet weight; (3) period with records of ovigerous females, no carapace width was given. For topographical codes, see Fig. 11. References: 1, Balasubramanian and Suseelan (1990); 2, Kensley (1977); 3, Losse (1969); 4, Stephenson (1967); 5, Stephenson and Rees (1967a); 6, Crosnier and Thomassin (1974); 7, Stephenson and Rees (1967b); 8, Sankarankutty and Rangarajan (1965); 9, Suseelan *et al.* (1990); 10, Daniel and Chakrapany (1983); 11, Branch (1984); 12, R.V. *Dr Fridtjof Nansen*, 1983 (G. Bianchi, personal communication, 1995).

during the breeding season, only on the bottom. In the same study, juvenile crabs (carapace width 12–20 mm) were found in December and in March, together with zoeae and megalopae assumed to be *C. smithii.* So far, no egg-bearing adults have been reported off East Africa, Oman and in the Gulf of Aden, nor have any been reported from the shallow banks of the tropical Indian Ocean (Saya de Malha and Seychelles Banks) near where Merrett (1968) and Zamorov *et al.* (1991) encountered so many crabs in the stomachs of tuna. Losse (1969) explicitly mentioned the absence of ovigerous females in shallow and deep water surface samples taken between September and November in the coastal waters of Tanzania and Kenya and in the Gulf of Aden in March. Kensley (1977) also noted the absence of ovigerous females in samples taken in May 1975 in deep water off Natal (South Africa). These records, however, seem to be based on samples from pelagic, not benthic trawls, so it is possible that benthic breeding populations exist but have not been sampled in these more southerly regions.

We assume that reproduction is preceded by the aggregation of crabs on the continental shelf. Large numbers of *C. smithii* are reported from bottom trawls off Oman in November (present study), off Oman in May (G. Bianchi, personal communication, 1995) and off SW India in January (Suseelan *et al.*, 1990). In the last case, ovigerous females were found, but no size data were given. Daniel and Chakrapany (1983) reported the duration of precopula to be 2–3 days, whereas in the laboratory, Mrs B. Meyer-Harms (personal communication, 1995) observed male and female *C. smithii* in precopula for 1–2 days. The male, on top, held the freshly moulted and soft female upside down, so their ventral sides were against each other. The crabs remained on the bottom of the tank, but when disturbed swam away, still coupled. Zamorov *et al.* (1991) postulated that reproduction takes place off-shore after mass migration during the SW monsoon, and that larvae are then advected around the monsoonal circulation gyre, eventually being returned to the breeding areas where they metamorphose and settle on the bottom. From March to May *C. smithii* is not observed in the pelagic realm. Our observations, however, suggest a life-history pattern that is the reverse of that proposed by Zamorov *et al.* (1991). Adult crabs congregate on the bottom in shelf waters during the SW–NE intermonsoon (September–December) where their breeding is regulated by dissolved oxygen levels. Hence ovigerous females are found off India and Oman in January–March. Pelagic adult crabs are absent from the pelagic realm in the pre-monsoon period (May–June) because most die then after completing their 1 year life span. At this time, the juveniles, originally hatched in the neritic, disperse off-shore and become pelagic in the open ocean, where they continue to grow and develop.

Does breeding occur only in Indian waters? Reproduction is known to take place there during the NE monsoon in the period November–December, so zoeal and megalopal stages from SW India may be transported via the North Equatorial Current and its northerly branches into the Somali Basin, and larvae that spawn further north along the NW Indian shelf may also be transported into the Arabian Sea by surface currents generated by the NE Monsoon (see Fig. 1). Larvae released later may be the recruits for the swarms that develop further to the south around Kenya, Tanzania and various banks. In the north, larval and juvenile development take place in food-rich coastal upwelling regions of the Somali and Omani coast and in the enriched oceanic regions of the Arabian Sea, as indicated by the dense neuston catches of zoeae and megalopae in May. Some juveniles may be advected into the Gulf of Aden and maintain the swarms there. From these areas, the crabs may be advected eastwards via the Arabian Sea back into the western Indian Ocean. Growth and development rates would show considerable regional variation as a result of the different temperature and nutritional regimes that the larvae and crab swarms encounter. For example, zoeal stages have been found in the southern Red Sea (Table 2), but adult *C. smithii* are absent from this area. However, it seems more likely that the spawning populations maintain the vast swarms of this portunid at shelf and slope depths throughout the NW Indian Ocean. The scenario of westward transport of larval stages is not consistent, however, with the collection, from the *Baldrige*, of zoea larvae off Somalia and megalopae further to the east. Possibly these larval stages were the offspring of breeding populations of crabs on the African shelf, which have not yet been sampled.

The occasional swarms and individual adults encountered south, in the Mozambique Channel, off Natal, and off South Africa seem likely to be expatriates (Fig. 11). Mass stranding of *C. smithii* along the shores of the Cape Peninsula, South Africa, under unusually warm water conditions in February 1983 (Branch, 1984), may have been caused by the temperature shock when the crabs in the warm Agulhas Current encountered colder Atlantic water. All animals stranded were sexually mature with a mean carapace size of 42.7 mm, 62% were female. Recently, mass strandings of *C. smithii* have been reported from a 500 km stretch of coastline in South Africa. Crabs were first noticed near East London at the end of January 1996, and near Port Elizabeth in the beginning of February 1996. In this event most crabs were male (B. Newman, personal communication, 1996). These crabs usually wash up every year, in December–February, usually after very strong onshore winds. On several occasions swarms have reached as far as Cape Town (Branch *et al*., 1994). On 2 March 1996, a gravid female of *C. smithii* was reported from the Bushmans River Beach, South Africa (approximately halfway between Port Elizabeth and East London), but this record remains unconfirmed (B. Newman, personal communication, 1996).

A major unresolved question about the life-history of *C. smithii* is: what is it that limits this species, with such effective dispersion capabilities, to the waters of the Western Indian Ocean? Why has pelagic swarming evolved only in the Indian Ocean in *C. smithii* and to a lesser degree in the upwelling system off the Iberian Peninsular in the portunid *Polybius henslowi* (Allen, 1968)? Are this regions where countercurrent systems allow the swarms to return to their original waters? Are there separate populations of the species associated with the various gyres in the NW Indian Ocean? The development of basin-scale simulation models of the circulation and productivity in the Indian Ocean offers opportunities to explore the relationship between the distribution pattern and the life cycle of *Charybdis smithii*. This crab may be a crucial species, whose feeding, growth and moulting influences fluxes of energy and material through the coastal and oceanic upwelling system of the Indian Ocean, strongly linking pelagic and benthic systems at some times of year. It appears to be able to flourish both inside and outside the upwelling systems, but the populations inhabiting such contrasting ecosystems show no phenotypic signs of genetic divergence.

In summary, our data indicate that *Charybdis smithii* has a 1 year life cycle. The crabs aggregate on the continental shelf before mating from about October to January (NE Monsoon), when ovigerous females are found in the waters off India. It remains unresolved whether or not they occur in other shelf regions. Large adult crabs are not found after April and may die after reproducing. The larvae hatch in the shelf waters and disperse out towards oceanic waters through May. Dense swarms of pelagic crabs are found in June–September (SW Monsoon) in the NW Indian Ocean. In October, crabs start to return to the shelf waters, where they form nocturnal swarms.

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CHAPTER 5

Summary and conclusions

CHAPTER 5, SUMMARY AND CONCLUSIONS

Chapter 1 presents the results of a study of the spatial and seasonal variations in zooplankton and micronekton biomass from the Somali Basin, the southern Red Sea and Gulf of Aden. During the SW monsoon of 1992 mean zooplankton biomasses (displacements of RMT1 samples over 0-300 m depth during night) were low in the southern Red Sea and the Gulf of Aden (14-17 ml m^{-2}) and high in the upwelling area of the Somali Current (38 ml m^{-2}) and downstream of the upwelling in the Great Whirl (21-36 ml m^{-2}). In the equatorial Somali Basin zooplankton biomasses were low compared to the Somali Current and the northern Somali Basin. During the NE monsoon of 1993, primary production was high in phytoplankton blooming in the southern Red Sea and the Gulf of Aden, and there the mean zooplankton biomass doubled to 24-40 ml m^{-2} compared to the preceding season. In the northern Somali Basin the mean phytoplankton carbon production during the NE monsoon was about two-thirds compared to the SW monsoon, but zooplankton biomasses were higher than might be expected from the lower primary production and no statistically significant differences were found between the mean values for both seasons. The mean macrozooplankton and micronekton biomass (displacements from RMT8 samples over 0-300 m depth during night) were also not significantly different from SW to NE monsoon for the southern Red Sea pooled with the Gulf of Aden (5.8 *vs.* 6.8 ml m^{-2}), and for the Somali Basin (8.0 *vs.* 7.8 ml m^{-2}). However, there were seasonal differences in the composition of the micronekton. Biomasses of mesopelagic fish and large crustaceans were higher in the southern Red Sea during the SW monsoon, and higher in the Somali Current during the NE monsoon.

Chapter 2 treats the seasonal and spatial distribution of Euphausiacea from the Banda Sea. With upwelling during the SE monsoon, surface layers became locally nutrient enriched. Total euphausiid stocks were high downstream of the upwelling (37.8 euphausiids m^{-2} over 0-500 m depth during night) but were considerably lower and heterogeneously distributed elsewhere (1.6-6.6 euphausiids m^{-2}). In the relative poor NW monsoon season, stocks were fairly high and more homogeneously distributed (4.1-8.1 euphausiids m^{-2}). *Euphausia diomedeae*, *E. pseudogibba*, *Thysanopoda tricuspidata*, *T. monacantha* and *Nematoscelis microps* were the most abundant species during both seasons. The local high stock during the SE monsoon was due to a rapid response of the epipelagic, herbivorous *E. diomedeae* and *T. tricuspidata* to increased phytoplankton biomass. The day-night depth distribution pattern of the euphausiid population in the upper 500 m was generally the same in both seasons, with comparable migration ranges. However, some species showed a somewhat upward shifted depth distribution in the nutrient enriched period. Especially for mesopelagic and bathypelagic species food resources were then favorable in the upper layers, as indicated by rare shallow records of mesopelagic *T. cristata*. Analyses of stomach contents showed that the diurnal vertically migrating species feed mainly at night while the non-migrating species feed continuously.

In Chapter 3 the spatial and temporal variations in the distribution of euphausiids were studied off Somalia, in the Gulf of Aden and southern Red Sea during the SW and NE monsoons. In both seasons *E. diomedeae*, *E. sibogae*, *Stylocheiron affine* and *S. abbreviatum* were the most abundant of the 29 species found. During the SW monsoon, maximum stocks (over 0-500 m depth at night) were 16 euphausiids m^{-2} in the Somali Current after passing of the first upwelling at *ca* 4°N, and 16 euphausiids m^{-2} in the Great Whirl downstream of the second Somali upwelling at *ca* 7°N. The epipelagic *E. diomedeae* accounted for more than 60% of these high values. During the NE monsoon, when upwelling was absent, still high stocks were found in the Somali Basin (maximum 15 euphausiids m^{-2}), comparable to the preceding season. Also, the relative abundance of *E. diomedeae* dropped. The very small seasonal difference in euphausiid stock in the Somali Basin was concordant with the absence of significant seasonal differences in zooplankton biomass. Diurnally vertically migrating species such as *E. diomedeae* and *E. sibogae* reduced the downward daytime migration in the Somali Basin during SW monsoon and in the Red Sea during NE monsoon.

Pooled data from euphausiid samples made during NIOP in the NW Indian Ocean and the Red Sea, and similarly made during Snellius II in the eastern Banda Sea, were subjected to cluster analysis. Twelve clusters of samples were established, and after inverse analysis four main euphausiid assemblages were distinguished, based on 78% of all the samples. None of the assemblages were typical for either one of the monsoons. One assemblage was confined to the southern Red Sea, where *S. affine* was the characteristic dominant species. The Red Sea contains no endemic species or species that do not occur in the other two basins. The second assemblage was typical for the upper layer (from surface to ca 150 m) in both the Banda Sea and the NW Indian Ocean during night, where *E. diomedeae* and *T. tricuspidata* were characteristic dominant. Although *T. tricuspidata* was more abundant in the Banda Sea than in the NW Indian Ocean, the combination of the two species was so strong that with cluster analysis no difference was found between the two seas at this level. The remaining two assemblages were predominant for midwater (200-600 m) in the NW Indian Ocean and the Banda Sea respectively. They consisted of non-migrating species and of the diurnally vertically migrating species during daytime.

Chapter 4 discusses the distribution and biology of the pelagic swimming crab *Charybdis smithii*, an endemic species for the western Indian Ocean and known from shelf waters from the Bay of Bengal to South Africa. The study is based on pooled data on *C. smithii* collected by RV *Tyro*, RRS *Discovery* and RV *Malcolm Baldrige* on seven cruises in the NW Indian Ocean during SW and NE monsoons in the years 1992-1995. All ships collected *C. smithii* in July-August (SW monsoon), when crabs occurred in dense patches, predominantly concentrated above the thermo- and oxycline at 150-200 m. The data show considerable variation in the stock of crabs, with maximum of 2.0-2.5 crabs m^{-2} (over 0-500 m depth during night) in the Somali Basin, the Omani Basin, and in the central Arabian Sea. Carapace width of all crabs found in this season ranged from 14 to 56 mm with a mean of 28 mm. The large variation in stocks and sizes is due to the different years and localities of sampling. Spatial variation in size was evident in samples from the Somali Basin during the SW monsoon. The mean carapace width increased from 22 to 35 mm along the Somali Current going into the Great Whirl. There was a tendency for smaller crabs to occur at the near-coastal stations. This may point to the start of juvenile development in African neritic waters during early SW monsoon. During the NE monsoon, stocks and biomasses of crabs were considerably lower compared to the SW monsoon. The crabs were bigger than in the preceding season, with mean carapace width of 53 mm, and a maximum of 72 mm. Remarkable vast, nocturnal surface swarms of large crabs, also reported in the literature, were observed in the Somali Basin and Gulf of Aden.

Based on the size distribution of all crabs and literature data, the duration of the life cycle of *C. smithii* was estimated at one year. From about November to February (NE Monsoon) crabs aggregate on the continental shelf for mating. The larvae hatch in the shelf waters and disperse offshore. From May to September (SW monsoon) crabs grow, become adult, and form dense pelagic swarms in the NW Indian Ocean. In October-January, crabs leave the open ocean for the shelf waters, making use of the NE monsoon surface currents and displaying characteristically surface swarming during night. Arriving at the shelf, the crabs aggregate at the bottom for mating. Ovigerous female and juvenile *C. smithii* are only known from the SW Indian coastal waters, records from Africa and Arabia are lacking.

The first obvious conclusion from the above studies is that different euphausiid faunas exist in the Red Sea on one hand and the Indian Ocean and Banda Sea on the other. Though, as demonstrated in Chapter 3, the Red Sea contains no species not occurring in the other two basins, its fauna is unique because of a low number of species and dominance of the epipelagic *Stylocheiron affine* in concentrations apparently not attained elsewhere (this fauna is represented with assemblage C3 in Fig. 1). The high temperature and salinity from surface to the bottom in the Red Sea may be the reason for the existence of a special fauna. Apparently, few species could adapt to this environment. The Hanish Sill may also effect the composition of the Red Sea pelagic fauna and change the euphausiid community. Located just north of Bab el Mandab, this sill leaves ca. 100 m of water and acts as a barrier for deep living Indian Ocean species.

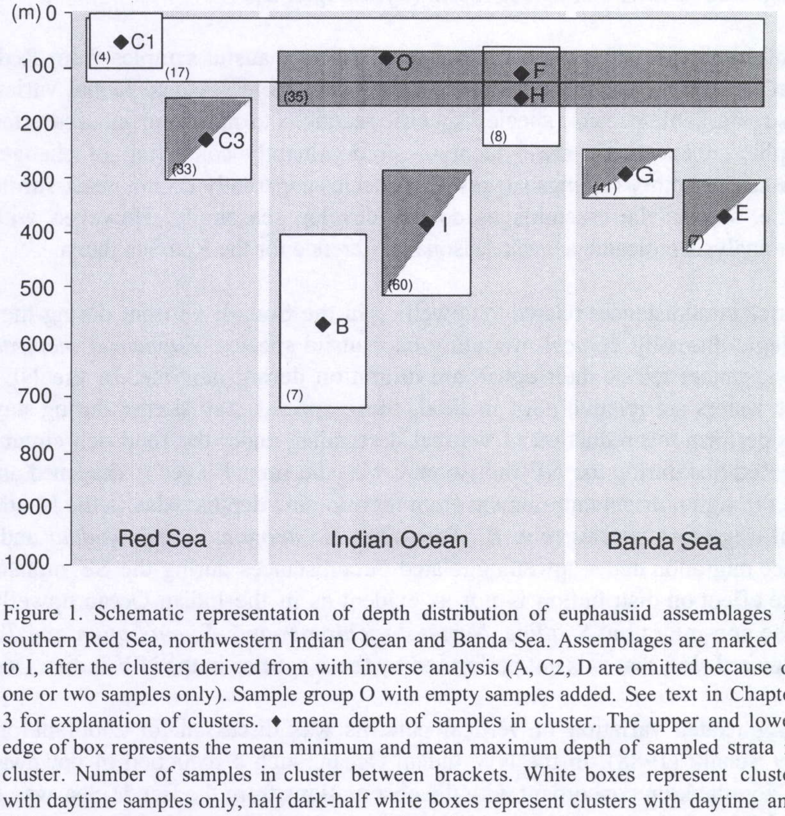

Figure 1. Schematic representation of depth distribution of euphausiid assemblages in southern Red Sea, northwestern Indian Ocean and Banda Sea. Assemblages are marked B to I, after the clusters derived from with inverse analysis (A, C2, D are omitted because of one or two samples only). Sample group O with empty samples added. See text in Chapter 3 for explanation of clusters. ◆ mean depth of samples in cluster. The upper and lower edge of box represents the mean minimum and mean maximum depth of sampled strata in cluster. Number of samples in cluster between brackets. White boxes represent cluster with daytime samples only, half dark-half white boxes represent clusters with daytime and night samples, dark box represents cluster with predominantly night samples.

Monsoon related reversing flow of surface water between Red Sea and Gulf of Aden results in exchange of epipelagic faunal elements, and the Red Sea holds an impoverished euphausiid fauna, derived from the Indo-West Pacific fauna without endemic euphausiid species. Still, there are infraspecific meristic differences between euphausiids from the Red Sea and Gulf of Aden.

Morphological differences have been found in various groups, not only euphausiids (see Beckmann, 1984 for zooplankton; Delpadado and Gjøsaeter, 1987 for myctophiid fish). This variation may have a genetic basis, but it might also be due to the extreme temperature, salinity and oxygen concentrations in the Red Sea, which could effect growth.

The euphausiid faunas of the Banda Sea and northwestern Indian Ocean are similar and different at the same time, having more than 95% of the euphausiid species in common. In particular, diurnal vertical migration patterns of euphausiids correspond because of similar species' behaviour. However, relative concentrations and the combinations of species are different, leading to faunal differences. In the upper layer of the NW Indian Ocean as well as the Banda Sea, during night euphausiid assemblages are similar, dominated by two epipelagic diurnally vertically migrating species: *Euphausia diomedeae* and *Thysanopoda tricuspidata* (assemblage F in Fig. 1). Below this layer, in both basins the assemblages are different in species composition and abundance, and therefore to a certain extend typical for the area. The deeper assemblages in the Indian Ocean and Banda Sea (I and G in Fig. 1 respectively) consist of non-migrating species during night and day, and diurnally vertical migrating species during the day — the latter are present in the assemblage above ca 150 m during night. (*c.f.* Chapter 3).

An important conclusion after cluster analysis of the euphausiid samples from Red Sea, NW Indian Ocean and Banda Sea, is that in none of the basins were seasonal faunal variations detectable. This is remarkable because species' specific reactions to monsoon induced effects (upwelling and trophic enhancement) are evident — predominantly consisting of changes in abundance. These contradictory findings suggest that species apparently do not react similarly and at the same time, so that the assemblages do not develop seasonally. However, within-sample group cluster analysis indicated a weak seasonal difference for the Red Sea fauna.

Under food-rich circumstances related to upwelling in the Somali Current during the SW monsoon, epipelagic diurnally vertical migrating euphausiid species (*Euphausia diomedeae* and *E. sibogae*, for instance) reduce their downward migration during daytime. In the NE monsoon, when surface waters are relative poor in food, these species stay deeper during daytime. The same species perform this reduction of vertical descending under the food-rich circumstances in the southern Red Sea during the NE monsoon, when the mixed layer is deepened and becomes mesotrophic through nutrient entrainment from thermocline depths. Also in the Banda Sea diurnally vertical migrating species (*e.g. E. diomedeae*, *E. sibogae*, *T. tricuspidata* and *T. monacantha*) reduce migration under upwelling related circumstances during the SE monsoon (Chapter 2), but the effect on distribution is not as evident as in the Indian Ocean upwelling. In the Banda Sea the non-migrating *S. affine*, *Nematobrachion boopis*, *S. maximum* and *T. orientalis* showed an upward shift that was not performed by these species in the NW Indian Ocean.

The upwelling related variation in vertical patterns was discussed for zooplankton from the Banda Sea by Schalk (1988). In the NW Indian Ocean, such a reduction in downward daytime migration of zooplankton concordant with the observations from the Banda Sea was found only in the Gulf of Aden during the NE monsoon, and to a limited extent. Compared to the (oligotrophic) SW monsoon, the migratory range for zooplankton in the southern Red Sea was small during the NE monsoon under mesotrophic conditions; even though the daytime depth of zooplankton biomass was not significantly shallow. Staying deep at low temperature during the day enables the animal to save energy. However, the downward move is limited as too long a migratory path will cost too much energy during upward migration. Therefore a balance is found between energy requirement and food uptake at shallower depth if large amounts of food are available.

In the Red Sea, *Euphausia diomedeae* and *E. sibogae*, for instance, undertake diurnal vertical migration under homothermal conditions of about 21°C below the thermocline. This excludes for these euphausiids (and for other organisms) the advantage of energy savings by deep daytime migration. Still, the animals have to balance between energy requirements (determined by temperature) and supplies, and therefore stay at shallower depth during daytime compared to other low-food situations outside the Red Sea. Avoidance of visual predators is another reason for diurnal vertical migration, and this may drive vertical migration even when energy saving can not be achieved.

Euphausiids in the permanent upwelling area in the NE Atlantic Ocean off NW Africa (Mauritania) show a similar reduction of the migration amplitude under mesotrophic and eutrophic conditions in the upper layer compared to the adjacent area where upwelling is absent and surface waters are oligotrophic. Here, this phenomenon may be attributed to increased light attenuation, allowing euphausiids to stay at shallower depth without risk of visual predation, and it is possibly forced by oxygen depletion below the thermocline under meso- and eutrophic con-ditions (Andersen *et al.*, 1997). Although the thermogradient was sharp during the SW monsoon in the upwelling area in the NW Indian Ocean, and the depth of the thermocline varied from 100 to 200 m between both seasons, temperature differences at the critical daytime depth were only several degrees. There was thus no indication found for temperature determining seasonal differences in daytime depth. The light attenuation coefficient in the mixed layer of the Somali Basin — in particular the upwelling area, was similar during both monsoon, Chlorophyll biomass, however, during NE monsoon was 50 % less compared to the SW monsoon (see Veldhuis *et al.*, 1997). Still seasonally different daytime depths were found for the euphausiid species with reduced downward migration; this indicates that light attenuation was not primarily determining the daytime depth.

From the vertical distributions of macrozooplankton and micronekton biomass (RMT8 samples), no indications were found for reduced vertical migration. An important observation was that vertical migration by micronekton is not hampered by severely decreased oxygen concentrations (<1 ml l^{-1}) generally found between 100 and 800 m depth.

This study considers thee monsoonal influences on the ecosystem from different angles. As described in Chapter 1, and recapitulated here in Table 1, zooplankton (>340 μm) gives a clear seasonal response in the southern Red Sea and the Gulf of Aden, with a strong increase in biomass from SW monsoon (oligotrophic) to NE monsoon (mesotrophic). This seasonality is also observed in both biomass and carbon production of bacterioplankton (Wiebinga *et al.*, 1997) and phytoplankton (Veldhuis *et al.*, 1997) and in the zooplankton >200 μm (Baars *et al.*, 1994). In contrast, in the Somali Current and the northern Somali Basin, these parameters decreased from SW to NE monsoon (Table 1). Nutrient concentrations in the upwelling area of the Somali Current and primary production were high during the SW monsoon compared to the NE monsoon. Due to short residence time of the surface water in the northern Somali Current during the upwelling period (according to Molinari *et al.* [1990] surface current speed can be >1m s^{-1} in August), primary production was under its potential (*c.f.* Veldhuis *et al.*, 1997) and the not consumed nutrients washed out in to the ocean. Here, at much lower NO_3 concentrations, chlorophyll *a* biomass and primary production were as high as, or even higher than in the

Table 1. Average temperature, nitrate concentration, phytoplankton biomass (chlorophyll *a*), phytoplankton and bacterioplankton carbon production, and biovolume (displacement) of zooplankton (vertical nets, 200 µm mesh, day and night catches pooled; RMT1, 340 µm mesh, night catches) and micronekton (RMT8, 4.5 mm mesh, nicht catches) from southern (s) Red Sea, Gulf of Aden, Somali Current, northern (n.) and equatorial (eq.) Somali Basin during SW and NE monsoon. Calculated from 1) Wiebinga *et al.* (1997) and 2) Veldhuis *et al.* (1997); adapted from 3) Baars (1998).

				Biomass	Production		Biomass		
							Zooplankton		Micronekton
	depth (m)	mixed layer		0-150	mixed layer	0-300	0-150/200	0-300	0-300
		Temp. 1) °C	Nitrate1) µM	Chl. *a*2) mg m^{-2}	Phytoplankton2) mg C m^{-2} d^{-1}	Bacterioplankton1) mg C m^{-2} d^{-1}	200 µm3) ml m^{-2}	340 µm ml m^{-2}	4.5 mm ml m^{-2}
SW monsoon	s. Red Sea	30	0.05	24.0	789	115		14.0	9.0
	Gulf of Aden	30	0.05	20.1	513	88	22.0	17.5	7.0
	Somali Current	21	13.10	32.0	1493	115	42.0	33.3	6.3
	n. Somali Basin	25	5.00	43.4	942	191		28.5	7.3
	eq. Somali Basin	26	0.50	32.3	1170	138	18.0	18.0	6.5
NE monsoon	s. Red Sea	26	0.70	60.0	943	224		23.9	6.4
	Gulf of Aden	26	0.95	40.0	1419	223	53.0	40.2	9.1
	Somali Current	26	0.65	24.3	660	98	25.0	25.1	6.9
	n. Somali Basin	26	0.50	29.5	902	134		24.6	4.6

Somali upwelling. This explains the high zooplankton biomass downstream from the upwelling in the Great Whirl. Also, this paradox probably was due to large mesh sizes that did not retain the small size (herbivorous) zooplankton fraction present during SW monsoon, and thus biomass including mesozooplankton was underestimated.

The average zooplankton biomass in the northern Somali Basin and the Somali Current was similar during both monsoons and this poses questions as to whether the Somali upwelling event is the most important for secondary production in the NW Indian on a one year basis. Obviously, upwelling and off-shore advection of nutrients during SW monsoon are the source for the high productivity in the NW Indian Ocean, but winter cooling substantially creates high production in the NE monsoon. Compared to the Somali upwelling, the upwelling off Oman provides a much higher contribution. Model studies showed that off shore transport with filaments from the Omani upwelling area is of great importance for enrichment of the central Arabian Sea (Keen *et al*., 1997). The high zooplankton biomass during NE monsoon in the Somali Basin could be linked by advection (see current directions and speeds and zooplankton concentrations in the model of McCreary *et al*. [1996]) to the high zooplankton stock in the eastern Arabian See created after winter cooling (Madhupratap *et al*., 1996). It has been demonstrated (Baars, 1998) that the high zooplankton biomass in the Somali Basin during the NE monsoon was less paradoxical. The over-all primary production is lower during the SW monsoon than always assumed. Because the primary production during the NE monsoon is considerable, the seasonal differences in primary production are less extreme. This explains the moderate seasonal differences in zooplankton biomass.

The seasonal variation of micronekton biomass (large crustaceans and mesopelagic fish from RMT8 samples) in the southern Red Sea, was opposite to that of zooplankton biomass (RMT1 samples) (Chapter 1). Biomasses of both mesopelagic fish and large crustaceans were much higher at the onset of the SW monsoon in June (when zooplankton biomass was low) than during the NE monsoon in January, when high zooplankton biomasses co-occurred with diatom blooms. In the Somali Basin, biomasses of mesopelagic fish and large crustaceans were highest during the NE monsoon. In both cases this suggests that growth in large crustaceans and mesopelagic fishes is linked to the monsoon and reproduction is synchronized with the productivity at lower trophic levels, so that the larval stages can profit from abundant food resources. In contrast to the micronekton, the biomass of siphonophorans and salps in the Red Sea increased from SW to NE monsoon, when food resources became favourable for these predators and filter feeders (medusans were very few during SW monsoon and absent during NE monsoon). Siphonophorans, salps and medusans were abundant in the Somali Basin during the SW monsoon, but decreased towards the NE monsoon, and medusan numbers in the Gulf of Aden doubled from the SW to the NE monsoon (S. van der Spoel, personal communication). These facts demonstrate the quick response in growth and reproduction of the herbivorous and carnivorous gelatinous plankton to favourable food conditions.

The swimming crab *Charybdis smithii*, treated in Chapter 4, is without doubt one of the most intriguing species found during this study. It is an example of a pelagic species with a distant-neritic distribution who's life-cycle is linked to the monsoon cycle, like the copepod *Calanoides carinatus*. Breeding takes place at the southwestern Indian shelf during the SW-NE intermonsoon. The findings of many portunid zoeae and megalopae of supposedly *C. smithii* in the Somali Current in May suggest that breeding may also take place at the African shelf. This crab is reported as a major food item for yellowfin tuna (*Thunnus albacares*) in the Indian Ocean

(Zamorov *et al*., 1991). Yellowfin tuna is a migratory fish, and hooking-rates in the NW Indian Ocean north of the equator are lowest during the SW monsoon and catches are restricted to south of 7°N. From NE monsoon to the SW pre-monsoon, yellowfin is caught all over the NW Indian Ocean up to 15°N and hooking-rates are at the maximum in this period (Suda, 1973). In this period *C. smithii* crabs are large and their stock and biomass is low compared to the SW monsoon. Heavy predation by yellowfin tuna might explain the low concentration of crabs during the NE monsoon. Absence of yellowfin tuna north of 5°N and low hooking-rates during the SW monsoon coincides with high stocks and biomasses of smaller crabs. Evident is the time lap of about six months between maximum yellowfin concentrations and upwelling in the Somali Current. From field and lab observations of the crab's behaviour, from stomach content analysis (Chapter 4), and literature data on the crab as food item I conclude that *C. smithii* is an important member of the ecosystem, both as a vigorous predator and as prey. The species invites further study, not only to discover its breeding areas, but also to elucidate its potentially high contribution to the carbon sink through dead body rain on the ocean bottom.

Of the different Indian Ocean zoogeographical zones, the Red Sea was conspicuous regarding the impoverished euphausiid fauna and the absence of the pelagic crab *C. smithii* — to mention the investigated taxa. *Charybdis* species that occur in the Red Sea are *C. omanensis* Leene 1938 and *C. acutidens* Türkay 1986 — the latter deep living species is only known from the Red Sea (Türkay, 1986). None of these species are really pelagic. The northern Somali Basin and the Somali Current were not distinguished in holding different euphausiid faunas, neither were the Arabian Sea water mass (0-500 m) and Red Sea-Persian Gulf water mass (500-1000 m). Records of *T. orientalis*, *T. obtusifrons* and *S. robustum* in the Gulf of Aden, three mesopelagic species that have their normal northern limits at the equator (Brinton, 1975), indicated that the northward increasing oxygen deficit is not a barrier. The boundaries between the zoogeographical zones are no barriers for many species that are transferred in and out the zones depending on the prevailing current (*e.g.* the Somali Current transporting species from the zone south of 10°S into the Arabian Sea during SW monsoon, and the current from the Gulf of Aden into the Red Sea).

Monsoon related changes were most effective in the mixed layer, covered by the 0-100 m sample, which often included the thermo- and pycnocline as well. Samples from this stratum displayed the greatest variation in biomass, number of species and dominance of one or more species. Below this stratum, the response of the system was generally less evident, and concerned only moderate differences in abundance of species (as in euphausiids) or in zooplankton biomass. This indicates the meaning of the pycnocline as a border for vertical plankton distribution. The shear between the mixed layer and the layers below, as often observed at this depth in particular in the Somali Current, adds more effect to this vertical boundary.

Euphausiids appeared to be poor ecological indicators. However, three species showed an ecological response to favourable circumstances: *S. affine* in the Red Sea, of *E. diomedeae* in the Somali upwelling and of *T. tricuspidata* in the Banda Sea. Seasonal upwelling is no barrier for the distribution of euphausiids in the NW Indian Ocean. Moreover, the regular alternation of surface currents maintains a continuous long-time mixing that creates a vast habitat for innumerable pelagic organisms without spatial diversification. Where it prevails in the Indian Ocean, the system of reversing monsoon currents, favours the formation of separate faunas. On the present scale differences are small and concern abundances, more than species composition. The present study showed different faunas for the Indian Ocean and the Banda Sea, however, on a smaller within-basin scale substantial differentiation was absent. An example of large scale morphological differentiation is found in *Stylocheiron longicorne* that that is distinguished with a North-Indian Ocean (Brinton, 1975); its distribution pattern is concordant with the northern monsoonal gyre north of ca. 5°N.

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SAMENVATTING

(Dutch summary)

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Inleiding

Dit onderzoek betreft de verspreiding in ruimte en tijd van *zoöplankton* en *micronekton* in zeeën die onder invloed verkeren van de moesson. Moessonsystemen behoren tot de troposferische circulatie tussen ongeveer 30°N en 30°Z en hun bestaan is beperkt tot de noordelijke Indische Oceaan en de Oost-Aziatische wateren. Hier heersen twee moessons: de India-Moesson en de Australisch-Aziatische, of Oost-Aziatische Moesson. Moessonwinden ontstaan door het verschil in luchtwarmte boven zee en land en hebben als belangrijke eigenschap dat de richting ieder halfjaar omkeert met de wisseling van zomer en winter. (Zie Figuur 1 in de Engelse inleiding van dit proefschrift). Moesson komt van het arabische *mausim*, dat seizoen betekent. De zeestromen van de noordelijke Indische Oceaan zijn sterk gekoppeld aan de moessonwind en veranderen dus ook ieder halfjaar van richting. Samenhangend hiermee wisselt de hoeveelheid nutriënten in de bovenste laag van de oceaan (0 tot *ca* 100 m). Dit is een belangrijk kenmerk van de hier bedoelde zeeën, die in het algemeen dus een seizoen met een hoge en een seizoen met een lage productie kennen.

Zoöplankton is de verzamelnaam voor vrijzwemmende dierlijke organismen met onvoldoende vermogen om zich onafhankelijk van de grote waterbewegingen te verplaatsen; nekton is de naam voor de vrijzwemmende dieren die wel krachtig genoeg zijn om dat te kunnen — bijvoorbeeld grote garnalen, vissen en zoogdieren. De meeste zoöplanktonten zijn klein, tot *ca* 5 mm, maar volgens de definitie behoort een kwal ook tot het zoöplankton. In de praktijk betreft micronekton vooral de kleinere en langzaam zwemmende vissen (tot *ca* 10 cm) en de grotere kreeftachtigen (vanaf *ca* 3 cm).

De biomassa van het zoöplankton en micronekton, de Euphausiacea (een orde van de kreeftachtigen) en de zwemkrab *Charybdis smithii*, zijn als onderwerp gekozen om te onderzoeken hoe het pelagische ecosysteem waar zij deel van uitmaken, op verschillende organisatieniveaus reageert op de effecten van de moesson. Daartoe zijn de horizontale en verticale verdeling en indien van toepassing, de soortsamentelling en de concentratie van de soort in de noordwestelijke Indische Oceaan, de zuidelijke Rode Zee en de Bandazee onderzocht tijdens twee achtereenvolgende moessons.

Van de drie grote oceanen — de Indische, Atlantische, en Grote Oceaan — is de Indische Oceaan uniek omdat hij in het noorden door land is afgesloten en omdat ten noorden van 10°Z het patroon van alle zeestromen om het halve jaar verandert door de afwisseling van de Zuidwest- en de Noordoost-Moesson. Van juni tot september waait de krachtige ZW-Moesson van de Hoorn van Afrika over de noordwestelijke Indische Oceaan naar India — om precies te zijn, over het Somalibekken, de Golf van Aden en de Arabische Zee. Deze wind drijft zeestromen aan, waarvan de noordoostelijke Somalistroom langs Afrika en de oostelijke Moessondrift in de Arabische Zee de kenmerkendste zijn (Fig. 1). De zuidelijke Rode Zee bevindt zich ook in de invloedssfeer van de moesson. Door de ZW-Moesson stroomt water uit de Rode Zee en met de NO-Moesson is er een ingaande stroom. Gepaard aan de ZW-Moesson vindt sterke opwelling plaats langs de kusten van Somalië en het Arabisch schiereiland en in geringere mate langs de zuidwestkust van India (*coastal upwelling*). Met opwelling komen met koud water van grote diepte, grote hoeveelheden nutriënten in de bovenlaag terecht. Deze nuriëntenrijkdom maakt

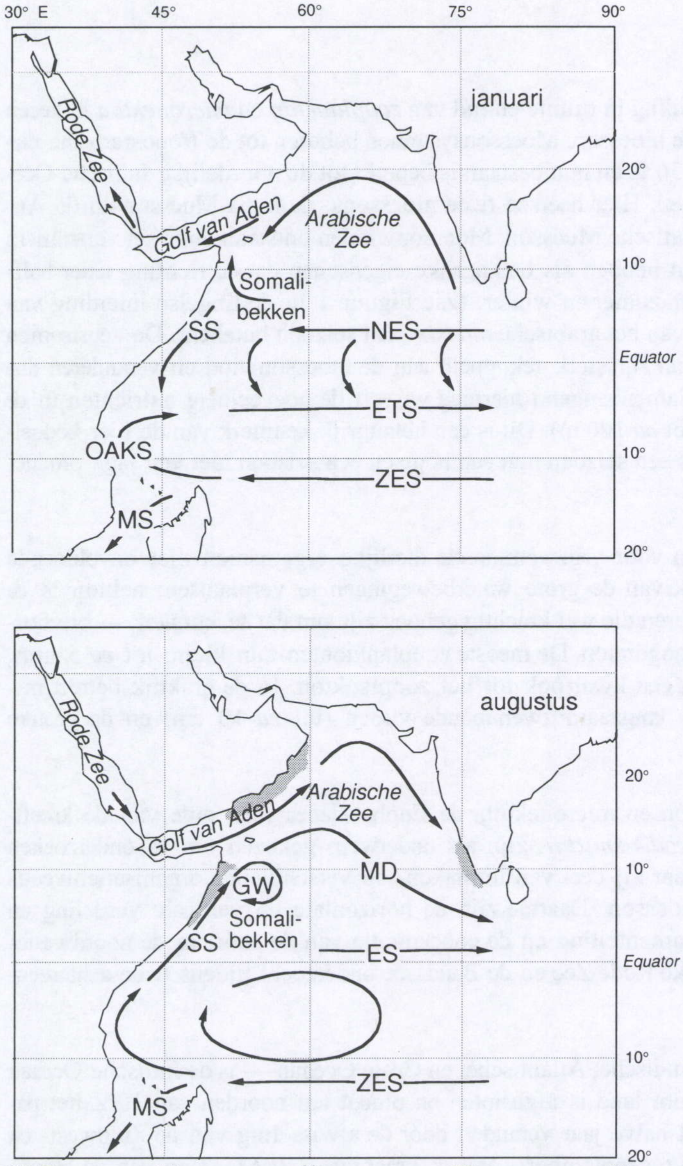


Fig. 1. Schematische weergave van de zeestromen in de noordwestelijke Indische Oceaan in januari tijdens de Noordoost-Moesson (boven) en in augustus tijdens de Zuidwest-Moesson (onder). SS - Somalistroom, GW - Grote Wervel, MD - Moessondrift, ES - Equatoriale stroom, NES - Noord equatoriale stroom, ETS - Equatoriale tegenstroom, ZES - Zuid equatoriale stroom, OAKS - Oost-Afrikaanse kuststroom, MS - Moçambiquestroom. De gebieden met opwelling aan de kust tijdens de ZW-Moesson, zijn in grijs weergegeven. (Naar Molinari *et al.*, 1990 en Wyrtki, 1973)

fytoplanktonbloei mogelijk. Voor zover de nutriënten niet meteen benut worden, worden ze over grote afstand vervoerd tot ver in de Arabische Zee en dragen daar bij aan een hoge productie in de bovenlaag. Een andere oorzaak van nutriëntverrijking is oceanische opwelling (*open-ocean upwelling*), waarbij door de wind aangedreven verticale circulatie, diep water naar boven komt. Toch zijn vooral de vele kleine, van de Arabische kust afgaande oppervlaktestromen, de belangrijkste bron van nutriënten en van planktonbiomassa in de centrale Arabische Zee (Keen *et al.*, 1997).

De Bandazee in Indonesië ligt tussen de Grote Oceaan en de Indische Oceaan, net onder de evenaar en bevindt zich in de invloedssfeer van de Australisch-Aziatische moesson die afwisselend zuidoost en noordwest is (zie Figuur 3 in de Engelse inleiding). In de oostelijke Bandazee vindt tijdens de ZO-Moesson (van juni tot september) opwelling plaats waardoor de oppervlaktewateren mesotroof (matig voedselrijk) worden. De opwelling speelt zich af boven de rand van het continentaal plat en in de open oceaan, daarom betreft het slechts de bovenste 300 m en is het effect van de opwelling op de bovenlaag matig. Gedurende het andere seizoen, de NW-Moesson van december tot april, is er geen opwelling en zijn de wateren oligotroof (voedselarm).

De betekenis van de moesson voor pelagische systemen werd onderzocht in de Bandazee tijdens de Indonesisch-Nederlandse Snellius II Expeditie in 1984-85, en in de noordwestelijke Indische Oceaan met het Nederlandse Indische Oceanprogramma (NIOP) in 1992-93. Beide expedities werden uitgevoerd met het Nederlandse onderzoekschip *Tyro* en omvatten elk twee opeenvolgende moessons. Op de oostelijke Bandazee zijn twee vaartochten gemaakt: in augustus 1984 (ZO-Moesson) en in februari-maart 1985 (NW-Moesson). Op de noordwestelijke Indische Oceaan zijn drie vaartochten gemaakt: in mei-juni en juli 1992 tijdens het begin en het hoogtepunt van de ZW-Moesson, en in januari 1993 tijdens de NO-Moesson.

Zoöplankton en micronekton werd bemonsterd met een *Rectangular Midwater Trawl* (RMT) 1+8. Dit vistuig werkt met twee netten tegelijkertijd. Het RMT1 heeft een opening van 1 m^2 en maaswijdte 0,34 mm en verzamelt zoöplankton. Het RMT8 heeft een opening van 8 m^2 en maasswijdte 4,5 mm en vangt het miconekton, hoofdzakelijk bestaande uit middelgrote en grote kreeftachtigen, kleine vissen en gelatineus plankton (kwallen, salpen, siphonophoren). De monsters werden overdag en 's nachts genomen in lagen van 100 of 200 m dik, van het zeeoppervlak tot 1000 m diep.

Hoofdstuk 1

De verspreiding van de biomassa van het zoöplankton en het micronekton in het Somalibekken, de zuidelijke Rode Zee en de Golf van Aden werd onderzocht met betrekking tot ruimte (horizontaal en verticaal) en tijd (dag-nacht en seizoen). Tijdens de ZW-Moesson was de gemiddelde zoöplanktonbiomassa (het biovolume van RMT1-monsters van 0 tot 300 m diepte 's nachts) laag in de Rode Zee en de Golf van Aden (14-17 ml m^{-2}) en hoog in het opwellingsgebied van de Somalistroom (38 ml m^{-2}) en stroomafwaarts van de opwelling (21-36 ml m^{-2}). In het equatoriale deel van het Somalibekken was de zoöplanktonbiomassa laag vergeleken met de rest van het Somalibekken. In de zuidelijke Rode Zee en de Golf van Aden was tijdens de NO-Moesson de primaire productie hoog in een fytoplanktonbloei, en de zoöplanktonbiomassa was verdubbeld tot 24-40 ml m^{-2} ten opzichte van het voorafgaande seizoen. In het noordelijke Somalibekken was de primaire productie gedurende de NO-Moesson ongeveer één derde lager vergeleken met de ZW-Moesson, maar de zoöplanktonbiomassa was veel hoger dan werd verwacht op basis van de lagere primaire productie. Het beeld van een afwisselende rijke en arme staat op alle trofische niveaus van het pelagische systeem, zoals dat in de Bandazee werd vastgesteld tijdens Snellius II, was niet van toepassing op het systeem in het Somalibekken. De seizoensvariatie in de primaire productie was paradoxaal veel groter dan in het zoöplankton. Er was zelfs geen significant statistisch verschil tussen de gemiddelde biomassa in beide seizoenen. Er was geen verschil tussen de gemiddelde biomassa van macrozoöplankton en micronekton (het biovolume van RMT8-monsters van 0 tot 300 m diepte 's nachts) tijdens de ZW- en de NO-Moesson in de samengevoegde zuidelijke Rode Zee en de Golf van Aden (5,8 *vs* 6,8 ml m^{-2}), en evenmin in het Somalibekken (8,0 *vs* 7,8 ml m^{-2}). Toch was er een seizoensverschil in de samensteling van het micronekton. De biomassa van mesopelagische vissen en grote kreeftachtigen was hoog in de Rode Zee gedurende de ZW-Moesson en hoog in de Somalistroom tijdens de NO-Moesson. Hoge biomassa van het micronekton valt dus samen met lage primaire productie.

Hoofdstuk 2

In dit hoofdstuk zijn de horizontale en verticale verspreiding van de Euphausiacea in de Bandazee onderzocht. Tijdens de ZO-Moesson was de bovenlaag plaatselijk verrijkt met nutriënten als gevolg van opwelling. Stroomafwaarts van de opwelling was de *stock* (het bestand) hoog (37,8 euphausiiden m^{-2} van 0 tot 500 m diepte, 's nachts), maar elders aanzienlijk lager en heterogeen verdeeld (1,6-6,6 euphausiiden m^{-2}). Gedurende de betrekkelijk arme NW-Moesson was de stock toch tamelijk hoog en minder heterogeen verdeeld (4,1-8,1 euphausiiden m^{-2}). *Euphausia diomedeae*, *E. pseudogibba*, *Thysanopoda tricuspidata*, *T. monacantha* en *Nematoscelis microps* waren in beide seizoenen de meest abundante soorten. De hoge stock stroomafwaarts van de opwelling tijdens de ZO-Moesson was het gevolg van een snelle reactie door de epipelagische, herbivore *E. diomedeae* en *T. tricuspidata* op de verhoogde fytoplanktonbiomassa. Het patroon in de verticale verspreiding van de euphausiiden in de bovenste 500 m zowel overdag als 's nachts, was vrijwel gelijk in beide seizoenen, met vergelijkbare migratieafstanden. Sommige soorten echter, vertoonden een wat ondiepere verspreiding in de nutriëntrijke periode. Speciaal voor mesopelagische en bathypelagische soorten zijn dan de voedselrijkdommen in de bovenste lagen aantrekkelijk, zoals blijkt uit vondsten van de zeldzame en mesopelagische *T. cristata* op geringere diepte dan elders in zijn verspreidingsgebied. Analyse van maaginhouden toonde aan dat de dagelijks verticaal migrerende soorten zich vooral 's nachts voeden en dat de niet-migrerende soorten voortdurend eten.

Hoofdstuk 3

Dit hoofdstuk gaat over de verdeling in ruimte en tijd van Euphausiacea in het Somalibekken, de Golf van Aden en de zuidelijke Rode Zee tijdens de ZW- en de NO-Moesson. In beide seizoenen waren *Euphausia diomedeae*, *E. sibogae*, *Stylocheiron affine* en *S. abbreviatum* de meest abundante van de 29 gevonden soorten. Tijdens de ZW-Moesson bedroeg de maximum stock (van 0 tot 500 m diepte 's nachts) 16,0 euphausiiden m^{-2} in de Somalistroom na afloop van de opwelling. Stroomafwaarts van de opwelling was in de Grote Wervel (Fig. 1) de stock eveneens 16,0 euphausiiden m^{-2}. De epipelagische *E. diomedeae* maakte 60% uit van deze hoge stocks. Tijdens de NO-Moesson is er geen opwelling, maar in het Somalibekken werden nog steeds hoge stocks vastgesteld (maximum 15,0 euph. m^{-2}). *E. diomedeae* was minder abundant ten gunste van andere epipelagische soorten. Het zeer kleine seizoensverschil in de stock van euphausiiden in het Somalibekken viel samen met de afwezigheid van een significant seizoensverschil in de biomassa van het zoöplankton. Soorten die dagelijks verticaal migreren, zoals *E. diomedeae* en *E. sibogae,* verminderden de neerwaartse migratie in het Somalibekken tijdens de ZW-Moesson en in de Rode Zee tijdens de NO-Moesson.

De euphausiidenmonsters van het *Netherlands Indian Ocean Programme* werden samengevoegd met euphausiidenmonsters uit de Bandazee, die op dezelfde wijze genomen zijn tijdens de Snellius II-expeditie. De gegevens werden aan een clusteranalyse onderworpen. Twaalf clusters werden vastgesteld en na inverse analyse zijn vier grote *assemblages* (groep individuen van bepaalde soorten en in bepaalde concentraties) onderscheiden, die samen op 78% van alle monsters berusten. Geen van deze assemblages was typisch voor een van de seizoenen. Eén was beperkt tot de Rode Zee, met *S. affine* als de karakteristiek-dominante soort. De tweede assemblage was typisch voor de bovenlaag (van 0 tot *ca* 150 m) in zowel de Bandazee als de noordwestelijke Indische Oceaaan gedurende de nacht, waarin dan de dagelijks verticaal migrerende *E. diomedeae* en

Thysanopoda tricuspidata karakteristiek-dominant zijn. Ofschoon *T. tricuspidata* meer abundant was in de Bandazee dan in de Indische Oceaan, was de combinatie met *E. diomedeae* zo sterk dat met clusteranalyse op dit niveau geen verschil werd gevonden tussen de twee zeeën. De twee overgebleven assemblages waren elk overwegend typisch voor de middendiepten (200-600 m) van de noordwestelijke Indische Oceaan en de Bandazee. Zij bevatten niet-migrerende soorten en de dagelijks migrerende soorten overdag.

Hoofdstuk 4

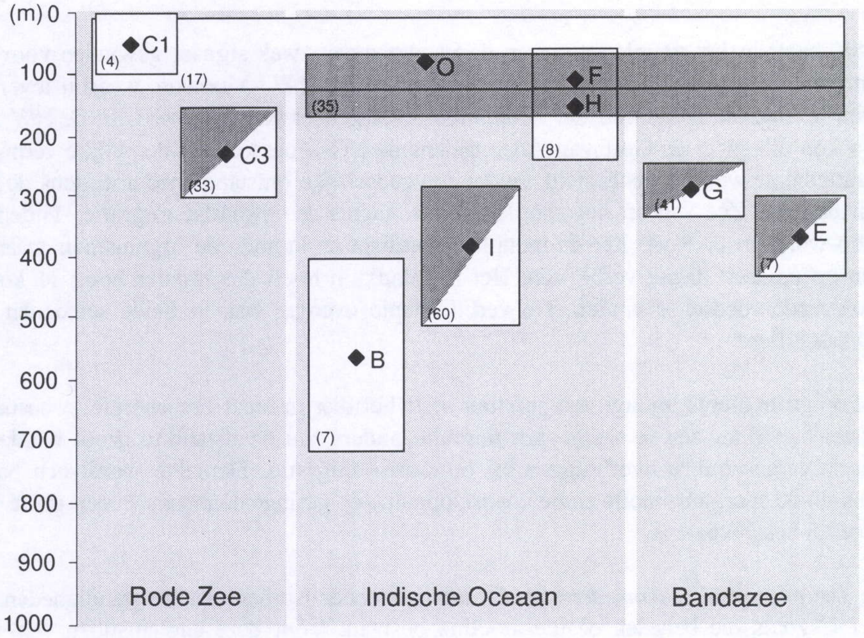
In dit hoofdstuk wordt de verspreiding en de biologie van de pelagische zwemkrab *Charybdis smithii* behandeld. *C. smithii* is een endemische soort in de westelijke Indische Oceaan, en bekend van de continentale zeeën vanaf de Golf van Bengalen tot aan Zuid Afrika. Dit onderzoek is gebaseed op samengevoegde gegevens die verkregen zijn met zeven vaartochten door de onderzoekschepen *Tyro*, *Discovery* en *Malcolm Baldrige* op de noordwestelijke Indische Oceaan tijdens de ZW- en NO-Moessons van de jaren 1992-95. Alle schepen verzamelden *C. smithii* in juli-augustus (ZW-Moesson). De krabben kwamen voor in dichte scholen, vooral geconcentreerd boven de thermo- en oxycline (beiden tussen 100 en 200 m gelegen). De hoeveelheid krabben variëerde aanzienlijk, en de maximale concentraties waren 2,0 tot 2,5 krabben m^{-2} (van 0 tot 500 m diepte, 's nachts) in het Somalibekken, het Omanibekken en in de centrale Arabische Zee. De carapaxbreedte van alle krabben die in dit seizoen gevonden zijn, variëerde van 14 tot 56 mm en was gemiddeld 28 mm. De grote variatie in de stock en de afmeting van de krabben was het gevolg van verzamelen in meerdere jaren en op verschillende plaatsen. Ruimtelijke variatie in de grootte van de krabben was duidelijk waarneembaar in monsters uit het Somalibekken tijdens de ZW-Moesson. Van ZW naar NO in de richting van de Somalistroom tot in de Grote Wervel nam de carapaxbreedte toe van 22 tot 35 mm. Er was een tendens naar het voorkomen van kleinere krabben dicht bij de kust. Gedurende de NO-Moesson waren de stock en de biomassa van *C. smithii* aanzienlijk kleiner dan in de ZW-Moesson. De gemiddelde carapaxbreedte was 53 mm, het maximum was 72 mm. In de Golf van Aden en het Somalibekken werden 's nachts uitgestrekte krabbenzwermen op het zeeoppervlak gezien, een van de weinige feiten die van deze krab in de literatuur bekend zijn.

Op grond van de grootteverdeling van alle krabben en gegevens uit de literatuur, werd de duur van de levenscyclus van *C. smithii* geschat op een jaar. Van ongeveer november tot februari (NO-Moesson) verzamelen de krabben zich op het continentaal plat voor de voortplanting. De krabbenlarven komen in de kustwateren vrij en verspreiden zich naar de open oceaan. Van mei tot september (ZW-Moesson) groeien de krabben, worden volwassen en vormen dichte pelagische scholen in de oceaan. Van october tot januari verlaten de krabben de open ocean en gaan naar de continentale zee, gebruikmakend van de oppervlaktestromen, waarbij ze 's nachts in typische zwermen aan het zeeoppervlak komen. Aangekomen op het continentaal plat, verzamelen de krabben zich op de bodem voor copulatie. Eierdragende vrouwtjes en juveniele *C. smithii* zijn alleen bekend van de kustwateren van Zuidwest-India; tot dusverre ontbreken gegevens uit Afrika en Arabië.

De eerste duidelijke conclusie die uit het vorengaande getrokken kan worden is dat in de Rode Zee aan de ene kant en in de Indische Oceaan en de Bandazee aan de andere kant, verschillende euphausiidenfauna's voorkomen. Ofschoon, zoals in Hoofdstuk 3 is aangetoond, de Rode Zee geen soorten kent die in de andere twee zeeën niet voorkomen, is de fauna in de Rode Zee uniek gezien het geringe aantal soorten en het belang van de epipelagische *Stylocheiron affine* in dichtheden die elders niet bereikt worden. Deze fauna is met assemblage C3 in Fig. 2 weergegeven. Van het zeeoppervlak tot aan de maximaal *ca* 2000 m diepe bodem zijn temperatuur en saliniteit hoog, respectievelijk 21°C en meer dan 37‰. Dit is de redenen voor het bestaan van een typische fauna. Kennelijk hebben slechts weinig soorten zich aan deze omgeving kunnen aanpassen. Bovendien heeft de Hanishdrempel een selectief effect op de samenstelling van de pelagische fauna. Deze drempel ligt net ten noorden van de Bab el Mandab, de smalle zeestraat die de Rode Zee verbindt met de Golf van Aden. Omdat er maar 100 m water boven deze drempel staat, is het voor diep levende soorten in de Indische Oceaan een barrière om de Rode Zee binnen te trekken. De stroomrichting van het oppervlaktewater tussen de Rode Zee en de Golf van Aden keert met de moesson om. Daarmee worden epipelagische faunaelementen tussen de twee zeeën uitgewisseld. Toch is de euphausiidenfauna in de Rode Zee een verarmde Indo-West Pacifische fauna zonder endemische soorten. Voor bepaalde meristische kenmerken (lichaamsverhoudingen) bestaat er binnen een soort verschil tussen populaties in de Rode Zee en de Golf van Aden. Door beperkte uitwisseling kan genetische variatie zijn ontstaan die dus in de morfologie tot uiting komt. Morfologische vershillen zijn ook bij andere groepen dan euphausiiden vastgesteld (zie Beckmann (1984) voor zoöplankton; Delpadado en Gjøsaeter (1987) voor Myctophidae of lantaarnvissen, een familie mesopelagische vissen). Deze variatie kan een genetische basis hebben, maar kan ook het gevolg zijn van negatieve effecten op de groei door de extreem hoge temperatuur en saliniteit en de lage zuurstofconcentratie, die onder de thermo- en oxycline op *ca* 100 m zo kenmerkend zijn voor het pelagische milieu in de Rode Zee.

De euphausiidenfauna's in de Bandazee en de NW Indische Oceaan zijn verschillend en tevens gelijk en hebben >95% van alle gevonden soorten gemeen. In het bijzonder bestaat er overeenkomst in het verticale verdelingspatroon door overeenkomstig gedrag in dagelijkse verticale migratie. Niettemin, door combinaties van soorten in verschillende dichtheden ontstaan toch aparte fauna's. In de bovenste laag (van het zeeoppervlak tot *ca* 150 m) van zowel de NW Indische Oceaan als de Bandazee komt dezelfde assemblage voor die gedomineerd wordt door twee epipelagische, dagelijks verticaal migrerende soorten: *Euphausia diomedeae* en *Thysanopoda tricuspidata* (assemblage F in Fig. 2). Onder deze laag zijn in beide zeeën de assemblages verschillend door combinaties van soorten in verschillende dichtheden en derhalve typisch voor het gebied. Zowel in de NW Indische Oceaan (assemblage I) als in de Bandazee (assemblage G) betreft het op deze diepte (>200 m), assemblages van dagelijks verticaal migrerende soorten gedurende de dag ('s nachts komen deze soorten omhoog en vormen de assemblage in de bovenlaag) en soorten die niet verticaal migreren en dus altijd op hun diepte verblijven. Omdat het verticale verspreidingspatroon sterk overeen komt, kunnen deze twee assemblages als elkaars tegenhanger gezien worden (Hoofdstuk 3).

Een belangrijke conlusie na clusteranalyse van de euphausiidenmonsters van de Rode Zee, NW Indische Oceaan en Bandazee, is dat er in geen van deze zeeën tijdens de ene moesson een andere fauna aanwezig was dan tijdens de andere moesson — althans, op het niveau van similariteit dat gesteld was voor het onderscheiden van alle twaalf clusters (<30%). Dit is opmerkelijk, omdat



Figuur 2. Schematische weergave van de diepte van euphausiidenassemblages in de Rode Zee, Indische Oceaan en de Bandazee. De assemblages zijn aangegeven met B t/m I, gelijk aan de clusters waarvan zij afgeleid zijn na inverse analyse (A, C2 en D zijn overgeslagen wegens slechts een of twee monsters). De groep O met alleen lege monsters is toegevoegd. Zie Hoofdstuk 3 voor uitleg van de clusters. ◆ = gemiddelde diepte van de monsters in het cluster. De boven- en onderrand van de rechthoek komt overeen met de gemiddelde minimum- en maximumdiepte van de monsters in het cluster. Het aantal monsters in het cluster tussen haakjes. Wit stelt dagmonsters voor, donker stelt nachtmonsters voor.

soorten wel reageren op de veranderingen die met de moesson samengaan (opwelling en trofische verrijking), voornamelijk met populatiegroei. Inverse analyse van subclusters uit de Rode Zee, toonde een zwak seizoensverschil aan dat tot uiting kwam door een hoger aantal en hogere concentratie van soorten tijdens de rijkere NE-Moesson. Zoals gezegd, dit verschil was niet sterk genoeg om ten opzichte van de clusters uit de NW Indische Oceaan en de Bandazee tot een significant verschil te leiden.

Onder voedselrijke omstandigheden in de Somalistroom als gevolg van opwelling tijdens de ZW-Moesson, blijkt een aantal epipelagische, dagelijks verticaal migrerende soorten (bijvoorbeeld *E. diomedeae* en *E. sibogae*) overdag de neergaande migratie te beperken (Hoofdstuk 3). In de NO-Moesson, wanneer de bovenlaag betrekkelijk voedselarm is, verblijven deze zelfde soorten overdag veel dieper. Ook in de zuidelijke Rode Zee tijdens de dan voedselrijke NO-Moesson, verblijven deze soorten minder diep overdag dan onder voedselarmere omstandigheden. In de Bandazee verminderen *E. diomedeae*, *E. sibogae*, *T. tricuspidata* en *T. monacantha* eveneens de neerwaartse migratie na opwelling tijdens de ZO-Moesson (Hoofdstuk 2), maar het effect op de verticale verspreiding is hier niet zo duidelijk als onder de opwelling in de Indische Oceaan. In de Bandazee was de diepte van de niet-migrerende *S. affine*, *Nematobrachion boopis* en *T. orientalis* onder opwellingomstandigheden minder dan in het andere seizoen. Een dergelijk verschil was bij deze soorten in de Indische Oceaan niet duidelijk waarneembaar.

Schalk (1988) heeft in het zoöplankton van de Bandazee een zwak signaal gevonden voor verminderde migratie onder voedselrijke omstandigheden tijdens de ZO-Moesson, waarbij tevens de activiteit van het metabolisme van het zoöplankton als geheel verhoogd was. In de NW Indische Oceaan kon alleen in de Golf van Aden tijdens de NO-Moesson een dergelijke vermindering in migratiediepte worden vastgesteld. Onder de voedselrijke omstandigheden tijdens de NO-Moesson in de Rode Zee verkort het zoöplankton 's nachts de opwaartse migratie. Tijdens de NO-Moesson wordt in de Rode Zee de menglaag verdiept en kunnen de organismen waar het zoöplankton op predeert dieper verblijven. Het zoöplankton hoeft dus minder hoog te komen om toch voldoende voedsel te vinden. De verblijfdiepte overdag was in beide seizoenen niet significant verschillend.

Een verblijf op grote diepte bij lage temperatuur stelt het dier in staat om energie te besparen. Er is echter een beperking aan de neergaande migratie, anders zou de afstand te groot worden en te veel energie vergen om te overbruggen bij opwaartse migratie. Derhalve wordt een balans gevonden tussen de energiebehoefte en de voedselopname op geringe diepte als er een grote hoeveelheid voedsel beschikbaar is.

In de Rode Zee migreren *E. diomedeae* en *E. sibogae* onder isothermale omstandigheden van ongeveer 21°C zoals die beneden de thermocline bestaan. Voor deze euphausiiden (en voor andere organismen) bestaat er op iedere diepte onder de thermocline geen voordeel in energiebesparing door een verblijf op grotere diepte overdag. Toch moet het organisme de balans vinden tussen energiebehoefte (die door ondermeer de temperatuur bepaald wordt) en voedselvoorraad, en verblijft daarom overdag ondieper vergeleken met andere voedselarme omstandigheden buiten de Rode Zee. Het vermijden van zichtpredatoren is een andere reden voor het ondernemen van dagelijkse verticale migratie die daarom ook in de Rode Zee nog steeds uitgevoerd wordt, ook als energiebesparing niet behaald kan worden.

In het gebied met permanente opwelling in de noordoostelijke Atlantische Oceaan tegenover Mauritanië (NW Afrika), is onder mesotrofe en eutrofe omstandigheden bij euphausiiden ook een verkleining van de migratieamplitude vastgesteld (Andersen *et al.*, 1997). In dit geval is de verhoogde demping van het licht (vanwege veel fytoplankton in de bovenlaag onder deze voedselrijke omstandigheden) als mogelijke oorzaak van dit verschijnsel verondersteld. Hierdoor kunnen de euphausiiden ondieper verblijven zonder een verhoogde kans op visuele predatie. Ook is voorgesteld dat de euphausiiden overdag minder diep migreren ter vermijding van het lagere zuurstofgehalte onder de oxycline, dat samengaat met een hogere productie in de bovenlaag (Andersen *et al.*, 1997).

Alhoewel in de opwelling van de Somalistroom tijdens de ZW-Moesson, de thermogradiënt scherp was en de diepte van de thermocline verschoof van 100 m tijdens de upwellling naar 200 m tijdens de NO-Moesson, was op de verblijfdiepte overdag, het temperatuursverschil tussen beide seizoenen maar enkele graden. Daarom is het onwaarschijnlijk dat de geringere verblijfdiepte veroorzaakt is door het met opwelling omhoog komen van kouder water. De demping van het licht in de menglaag van het Somalibekken (in het bijzonder in de opwelling) was in beide seizoenen practisch gelijk (Veldhuis *et al.*, 1997). Omdat onder deze omstandigheden toch diepteverschil bestaat tussen beide seizoenen, is de lichtdemping niet een hoofdfactor.

In de verticale verspreiding van biomassa van het macrozoöplankton en micronekton zijn geen aanwijzingen gevonden voor verminderde migratie. Gezien de heterogeniteit van deze groepen zal een eventueel seizoensverschil bij dagelijks verticaal migrerende soorten, gemakkelijk overschaduwd worden. Opvallend is dat micronekton in de neerwaartse migratie kennelijk niet gehinderd wordt door het geringe zuurstofgehalte (<1 ml l^{-1}) in de zuurstofminimumzone, die in de Arabische Zee alom aanwezig is van *ca* 100 tot *ca* 800 m. Dit is niet alleen bij mesopelagische vissen vastgesteld, ook euphausiiden en decapoden (kreeftachtigen) zijn in staat om althans een deel van het etmaal door te brengen onder zuurstofarme omstandigheden op een diepte van meer dan *ca* 500 m.

De invloed van de moesson op het ecosysteem is vanuit verschillende invalshoeken onderzocht. Zoals in Hoofdstuk 1 beschreven is en hier in Tabel 1 kort is samengevat, vertoont het zoöplankton (RMT1-monsters, 340 µm) in de Rode Zee en de Golf van Aden een duidelijk seizoensritme met een lage biomassa in de SW-Moesson (oligotroof) en een hoge biomassa in de NO-Moesson (mesotroof). Deze periodiciteit bestaat er ook in de biomassa en productie van bacterioplankton (Wiebinga *et al.*, 1997) en fytoplankton (Veldhuis *et al.*, 1997) en in het zoöplankton groter dan 200 µm (Baars *et al.*, 1994). Vergeleken met de Rode Zee en de Golf van Aden, was in de Somalistroom en het noordelijk Somalibekken de periodiciteit in deze parameters tegenovergesteld: hoge waarden tijdens de ZW-Moesson en lage waarden in de NO-Moesson. Omdat de nutriëntconcentraties in de opwellingperiode hoog waren, was de primaire productie ook hoog. Door de korte verblijftijd van het oppervlaktewater in de Somalistroom [volgens Molinari *et al.* (1990) is in augustus de gemiddelde stroomsnelheid maximaal *ca* 1 m s^{-1}] blijft de primaire productie onder de maat (zie Veldhuis *et al.*, 1997) en de nog niet benutte nutriënten spoelen uit in de oceaan. Het gevolg hiervan is dat in de Grote Wervel stroomafwaarts van de opwelling, bij lagere nutriëntconcentraties, de chlorofylbiomassa en primaire productie toch even groot zijn als, of groter zijn dan in de Somalistroom (zie Veldhuis *et al.*, 1997). Dit verklaart de hoge zoöplanktonbiomassa in het Somalibekken tijdens de ZW-Moesson.

Toch was de gemiddelde zoöplanktonbiomassa (340 µm) in het Somalibekken tijdens de NO-Moesson niet lager dan tijdens de ZW-Moesson. Het is de vraag hoe bepalend de opwelling bij Somalië op jaarbasis is voor de secundaire productie in de NW Indische Oceaan. Vanzelfsprekend is deze via de koppeling aan de primaire productie voor een groot deel gerelateerd aan opwelling, maar de productie in het upwellingsgebied van de Somalistroom is door de korte verblijftijd van het oppervlaktewater onder de maat. De opwelling bij Oman lervert een veel grotere bijdrage aan de productie (zie Baars, 1998). Modelstudies hebben aangetoond dat het kustafwaartse transport in de bovenlaag nog belangrijker is voor de rijkdom van de Arabische Zee (Keen *et al.*, 1997. Dit alles speelt zich af tijdens de ZW-Moesson. De betrekkelijk hoge zoöplanktonbiomassa in het Somalibekken tijdens de NO-Moesson zou met horizontale aanvoer [zie het model van McCreary *et al.* (1996)] kunnen zijn ontstaan uit de hoge zoöplanktonbiomassa die weliswaar op zeer grote afstand, "stroomopwaarts" opgebouwd wordt als gevolg van *winter cooling* in de oostelijke Arabische Zee tijdens de NO-Moesson (Madhupratap *et al.*, 1996). [Door winter cooling wordt het temperatuurverloop tussen de menglaag van 0 tot *ca* 50 m en de thermocline op ca 100 m minder sterk. Omdat hierdoor de dichtheid van het water boven de thermocline gelijkmatiger is, kan het makkelijker mengen en wordt de menglaag dieper. Dit heeft een nutriëntverrijking als gevolg].

Tabel 1. Gemiddelden van: temperatuur, nitraatconcentratie, fytoplanktonbiomassa (chlorofyl *a*), koolstofproductie door fytoplankton en bacterioplankton, biovolume van zoöplankton (verticaal net, 200 µm maaswijdte, dag- en nachtvangsten samengevoegd; RMT1, 340 µm maaswijdte, nachtvangsten) en micronekton (RMT8, 4,5 mm maaswijdte, nachtvangsten) in de zuidelijke (z.) Rode Zee, Golf van Aden, Somalistroom, noordelijk (n.) en equatoriaal (eq.) Somalibekken, tijdens de ZW- en NO-Moesson. Berekend uit 1) Wiebinga *et al.* (1997) en 2) Veldhuis *et al.* (1997); en overgenomen uit 3) Baars (1998).

				biomassa	productie		biomassa		
							zoöplankton		micronekton
	diepte (m)	menglaag		0-150	menglaag	0-300	0-150/200	0-300	0-300
		temp.[1] °C	nitraat[1] µM	chl. *a*[2] mg m^{-2}	fytoplankton[2] mg C m^{-2} d^{-1}	bacterioplankton[1] mg C m^{-2} d^{-1}	200 µm[3] ml m^{-2}	340 µm ml m^{-2}	4.5 mm ml m^{-2}
ZW-Moesson	z. Rode Zee	30	0,05	24,0	789	115		14,0	9,0
	Golf van Aden	30	0,05	20,1	513	88	22,0	17,5	7,0
	Somalistroom	21	13,10	32,0	1493	115	42,0	33,3	6,3
	n. Somalibekken	25	5,00	43,4	942	191		28,5	7,3
	eq.Somalibekken	26	0,50	32,3	1170	138	18,0	18,0	6,5
NO-Moesson	z. Rode Zee	26	0,70	60,0	943	224		23,9	6,4
	Golf van Aden	26	0,95	40,0	1419	223	53,0	40,2	9,1
	Somalistroom	26	0,65	24,3	660	98	25,0	25,1	6,9
	n. Somalibekken	26	0,50	29,5	902	134		24,6	4,6

Het is inmiddels aangetoond (Baars, 1998) dat de hoge zoöplanktonbiomassa in het Somalibekken tijdens de NO-Moesson niet zo paradoxaal is. Tijdens de ZW-Moesson is de productie veel lager en het seizoensverschil in primaire productie is dus minder extreem dan altijd werd aangenomen. Een meer technische oorzaak van deze paradox is de grote maaswijdte van het RMT1-net, waardoor het kleine (herbivore) mesozoöplankton niet verzameld werd, ofschoon het er dankzij de hoge productie in de ZW-Moesson wel was. In dit seizoen is de totale zoöplanktonbiomassa dus onderschat.

De seizoensvariatie in de biomassa van zowel mesopelagische vissen als grote kreeftachtigen (micronekton uit RMT8-monsters) is tegenovergesteld aan die van de zoöplanktonbiomassa (RMT1-monsters). In de Rode Zee is aan het begin van de ZW-Moesson in juni de biomassa van het zoöplankton laag en die van het micronekton hoog. Tijdens de ZO-Moesson in januari, toen een hoge zoöplanktonbiomassa samenging met een bloei van diatomeeën, was de biomassa van het micronekton juist laag. Dezelfde koppeling doet zich voor in het Somalibekken, maar dan met hoge micronektonbiomassa tijdens de NO-Moesson. In beide gevallen toont dit aan dat de groei van mesopelagische vissen en grotere kreeftachtigen gekoppeld is aan de moesson en dat de voortplanting afgestemd is op de hoge productie op lagere trofische niveaus (fytoplankton en zoöplankton) zoadat de larven en juvenielen kunnen profiteren van het grote voedselaanbod. In het Somalibekken zijn — in tegenstelling tot het micronekton — siphonophoren, salpen en medusen (kortweg het gelatinueze plankton) juist abundant tijdens de ZW-Moesson en zij nemen af in de NO-Moesson als de biomassa van het fytoplankton en zoöplankton laag is. In de Rode Zee nam de biomassa van siphonophoren en salpen toe van de ZW- naar de NO-Moesson als dan het micronekton laag is. Het aantal medusen in de Golf van Aden verdubbelde van de ZW- naar de NO-Moesson (Van der Spoel, pers. com., 1998). Deze feiten laten zien hoe snel het herbivore en carnivore gelatineuze plankton reageert met enorme groei en snelle voortplanting in tijden van gunstig voedselaanbod.

Ongetwijfeld is de zwemkrab *Charybdis smithii* (Hoofdstuk 4) een van de meest intrigerende soorten die met dit onderzoek gevonden zijn. Het is een voorbeeld van een pelagische soort die een aan de kustwateren gebonden verspreiding heeft en waarvan de levenscyclus gekoppeld is aan de moessons, net zoals de copepode *Calanoides carinatus*, die ook in de NW Indische Oceaan voorkomt. De voortplanting vindt plaats op het continentale plat van Zuidwest-India in de periode tussen de ZW- en NO-Moesson. Aangenomen dat de vele zwemkrablarven die tijdens het begin van de ZW-Moesson in de Somalistroom gevonden zijn, tot *C. smithii* behoren (de identiteit van zulke jonge dieren is niet tot op de soort vast te stellen), zou de voortplanting ook op het Afrikaans continentale plat kunnen gebeuren. De krab is een belangrijk prooidier voor de geelvintonijn, *Thunnus albacares* (Zamorov *et al*., 1991). Geelvintonijn is een noord-zuid migrerende soort; in de NW Indische Oceaan komt de soort in de ZW-Moesson ten noorden van 7°N niet voor. Tijdens de NO-Moesson en tot aan de start van de ZW-Moesson komt de geelvintonijn voor tot 15°N en de vangsten zijn in deze periode maximaal (Suda, 1973). In deze periode zijn de zwemkrabben groot, maar is hun stock en biomassa laag vergeleken met de ZW-Moesson. De afwezigheid van geelvintonijn ten noorden van 7°N en de lage vangsten gedurende de ZW-Moesson, gaan samen met hoge dichtheden van kleine krabben. Predatie door geelvintonijn zou de lage concentratie van krabben tijdens de NO-Moesson kunnen verklaren. Uit gedragswaarnemingen gedaan op zee en in het laboratorium, uit analyse van de maaginhoud en uit literatuurgegevens, moet geconcludeerd worden dat *C. smithii* een belangrijk lid is van het ecosysteem, zowel als een duchtig predator als een prooi. De soort verdient nader onderzoek, ook om uit te vinden hoe groot z'n aandeel is in het koolstofverlies door dode krabben die op de bodem van de oceaan terecht komen.

Van de verschillende zoögeografische zones van de Indische Oceaan springt de Rode Zee er uit gezien de verarmde euphausiidenfauna en de afwezigheid van bijvoorbeeld de zwemkrab *C. smithii*. In de Rode Zee zijn wel twee andere *Charybdis*-soorten bekend: *C. omanensis* Leene 1938 en *C. acutidens* Türkay 1986. De laatste, diep levende soort, is vooralsnog alleen uit de Rode Zee bekend. Geen van deze soorten is echt pelagisch. Ook andere groepen tonen het beeld van een aparte fauna in de Rode Zee, maar vallen buiten het bereik van dit onderzoek. Aan de hand van de onderzochte groepen, kon horizontaal geen onderscheid gevonden worden tussen de Somalistroom en de rest van het Somalibekken; evenmin konden eigen fauna's voor de Arabische Zee-watermassa (0-500 m) en de watermassa van de Rode Zee-Perzische Golf (500-1000 m) aangetoond worden. Vondsten van *T. orientalis*, *T. obtusifrons* en *S. robustum* in de Golf van Aden — mesopelagische soorten waarvan de noordgrens bij de evenaar ligt (Brinton, 1975), laten zien dat het noordwaarts toenemend zuurstoftekort hier nog geen barrière is. In de Arabische Zee ontbreken diepe euphausiidensoorten ten noorden van ca 15°N (Brinton, 1975). Het zuurstoftekort is daar zo groot geworden dat er alleen maar epipelagische soorten kunnen voorkomen die 's nachts in de bovenlaag vertoeven, waar dankzij de primaire productie de zuurstofconcentratie voldoende is. De zoögeografische grenzen in de Indische Oceaan zijn geen belemmeringen voor vele soorten, die met de heersende stromingen in en uit de zones vervoerd worden. Voorbeelden hiervan zijn soorten die met de Somalistroom vanuit de zuidelijke zone (die in het noorden bij 10°Z stopt) in de Arabische Zee gebracht worden.

De veranderingen in het systeem die met de moessons te maken hebben, zijn het meest effectief in de menglaag, die telkens binnen het bereik viel van het RMT-monster van 0 tot 100 m; ook de thermocline en pycnocline werden veelal met dit monster bemonsterd. Monsters van deze laag vertoonden de grootste variatie in biomassa, in soortaantallen en de dominantie van een of meerdere soorten. Monsters dieper dan 100 m vertoonden veel minder variatie. Dit duidt de betekenis van bijvoorbeeld de pycnocline als grenslaag, waarbij verschil in dichtheid (soortelijk gewicht van het water) en vaak ook tegengestelde stroomrichting van de menglaag en de laag daaronder (*shear*), van belang zijn voor de verticale verspreiding van plankton.

In de noordwestelijke Indische Oceaan is opwelling geen barrière voor de verspreiding van euphausiidensoorten. Bovendien, de regelmatige afwisseling van de zeestromen zorgt voor een uitgestrekte min of meer eenvormige leefomgeving voor talloze organismen zonder grote ruimtelijke verscheidenheid. Het systeem van de omkerende moessonstromen in de Indische Oceaan (en ook in de Bandazee) maken het ontstaan van aparte fauna's mogelijk, maar op de schaal van het onderzoek zijn de verschillen klein. Het betreft daarbij vooral de aantalsdichtheid en veel minder de soortsamenstelling. In deze zin blijken euphausiidensoorten gebrekkige ecologische indicatoren te zijn. Niettemin springen drie soorten er uit omdat zij adequaat reageren op plaatselijk gunstige omstandigheden: *S. affine* in de Rode Zee, *E. diomedeae* in de Somali-opwelling en *T. tricuspidata* in de Bandazee.

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APPENDIX A

Rectangular Midwater Trawl 1+8, haul data during *Tyro* cruises B0, B1, and B2 of the *Netherlands Indian Ocean Programme* 1992-1993

(Estimated values for speed, distance run, filtered volume, concentration, and stock in italics due to unknow number of flow blips)

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Netherlands Indian Ocean Programme 1992-1993 - Haul data RMT 1+8, *Tyro* cruise B0

Station	Haul	JGOFS nr.	Start position		Date dd/m 1992	Period D=day N=night	Time		Depth		Temperature		Flow-blips	Duration mins
			lat. N dd.mm.dec	long. E dd.mm.dec			start local time	end	min. m	max. m	max. °C	min. °C		
RS 4	1	002	21.05.45	38.08.91	24/5	D/N	17.20	18.06	230	500	21.1	20.8	21.5	46
RS 4	2	002	21.07.58	38.08.09	24/5	N	18.38	19.26	0	200	25.6	21.2	20.5	48
RS 2	1	004	15.58.62	41.36.87	26/5	D	08.46	09.36	0	105	26.8	21.1	25.5	50
RS 2	2	004	15.58.76	41.34.50	26/5	D	10.01	10.51	106	200	21.2	20.9	26.5	50
RS 2	5	004	15.56.00	41.34.72	26/5	D	16.00	16.50	202	302	20.8	20.8	20.5	50
RS 2	4	004	15.55.03	41.33.80	26/5	D	14.41	15.28	310	402	20.8	20.8	16.5	47
RS 2	3	004	15.58.80	41.36.55	26/5	D	13.02	13.51	380	597	20.9	20.8	35	49
RS 2	6	004	15.47.75	41.25.37	26/5	N	23.18	00.08	0	99	27.9	21.5	17	50
RS 2	7	004	15.47.93	41.27.00	27/5	N	00.36	01.26	105	200	21.6	20.9	23.5	50
RS 2	9	004	15.50.11	41.28.65	27/5	N	03.46	04.35	205	400	20.9	20.8	30	49
RS 2	8	004	15.49.23	41.27.98	27/5	N	02.04	02.52	420	610	20.8	20.8	18	48
RS1	3	005	14.49.41	42.15.55	28/5	N	02.24	03.16	0	102	28.0	21.5	25	52
RS1	4	005	14.50.92	42.15.74	28/5	N	03.40	04.20	98	202	21.8	20.8	16	40
RS1	2	005	14.47.51	42.15.67	28/5	N	01.18	02.03	210	400	20.8	20.8	17	45
RS1	1	005	14.45.45	42.16.54	27/5	N	23.57	00.42	418	600	20.8	20.8	17.5	45
RS1	5	005	14.47.00	42.16.90	28/5	D	08.48	09.28	0	97	27.5	21.5	20	40
RS1	6	005	14.48.45	42.16.30	28/5	D	09.53	10.32	105	210	22.0	20.8	19	39
RS1	7	005	14.49.90	42.15.50	28/5	D	11.00	11.36	208	402	20.8	20.8	12.5	36
RS1	8	005	14.51.00	42.14.80	28/5	D	12.18	13.08	415	605	20.8	20.8	24.5	50
BEM	1	006	12.45.84	43.14.32	29/5	D	07.48	08.28	0	104	28.0	22.4	15.5	40
BEM	2	006	12.45.26	43.14.48	29/5	D	08.46	09.13	105	163	23.1	21.7	4.8	27
US2	1	024	10.47.06	51.58.20	4/6	D	13.45	14.35	0	200	27.0	14.7	27	50
US2	2	024	10.46.83	51.01.09	4/6	D	15.10	15.50	215	490	14.5	11.4	16	40

Station	Haul	Speed	Distance run	Filtered volume		Displacement		Concentration		Stock		Stock		Depth range
				RMT1	RMT8	RMT1	RMT8	RMT1	RMT8	RMT1	RMT8	RMT1	RMT8	
		kn	m	m^3	m^3	ml	ml	ml/m^3	ml/m^3	ml/m^2	ml/m^2	ml/m^2	ml/m^2	m
RS 4	1	1.3	1903	2161	20526	32	197	0.015	0.010	4.0	2.6			
RS 4	2	1.2	1793	2168	19645	34	182	0.016	0.009	3.1	1.9	7.1	4.4	0-500
RS 2	1	1.4	2222	2388	23617	158	1271	0.066	0.054	6.9	5.7			
RS 2	2	1.5	2315	2400	24346	81	104	0.034	0.004	3.2	0.4			
RS 2	5	1.2	1821	2230	20016	95	291	0.043	0.015	4.3	1.5	14.4	7.5	0-300
RS 2	4	1.0	1465	1906	16323	84	152	0.044	0.009	4.1	0.9			
RS 2	3	2.0	3085	2201	28121	30	537	0.014	0.019	3.0	4.1	21.4	12.5	0-600
RS 2	6	1.0	1543	2014	17203	125	398	0.062	0.023	6.1	2.3			
RS 2	7	1.4	2084	2354	22446	75	665	0.032	0.030	3.0	2.8			
RS 2	9	1.7	2632	2329	26258	50	382	0.021	0.015	4.2	2.8	13.4	7.9	0-400
RS 2	8	1.1	1600	2036	17739	80	198	0.039	0.011	7.5	2.1	20.8	10.1	0-600
RS1	3	1.4	2199	2458	23622	180	466	0.073	0.020	7.5	2.0			
RS1	4	1.2	1420	1760	15650	51	624	0.029	0.040	3.0	4.1			
RS1	2	1.1	1528	1930	16912	42	157	0.022	0.009	4.1	1.8	14.6	7.9	0-400
RS1	1	1.1	1556	1951	17192	40	51	0.021	0.003	3.7	0.5	18.3	8.5	0-600
RS1	5	1.4	1753	1906	18692	180	134	0.094	0.007	9.2	0.7			
RS1	6	1.4	1685	1853	18024	55	19	0.030	0.001	3.1	0.1			
RS1	7	1.0	1111	1450	12386	45	63	0.031	0.005	6.0	1.0	18.3	1.8	0-400
RS1	8	1.4	2161	2375	23108	154	935	0.065	0.040	12.3	7.7	30.6	9.5	0-600
BEM	1	1.1	1370	1725	15158	192	338	0.111	0.022	11.6	2.3			
BEM	2	0.5	417	584	4712	52	425	0.089	0.090	5.2	5.2	16.7	7.5	0-160
US2	1	1.5	2269	2395	23987	334	213	0.139	0.009	27.9	1.8			
US2	2	1.1	1389	1735	15337	70	386	0.040	0.025	11.1	6.9	39.0	8.7	0-500

Netherlands Indian Ocean Programme 1992-1993 - Haul data RMT 1+8, Tyro cruise B1

Sta-tion	Haul	JGOFS nr.	Start position lat. dd.mm.	long. E dd.mm.	Date dd/m 1992	Period D=day N=night	Time start local	end time	Depth min. m	max. m	Temperature max. °C	min. °C	Flow-blips	Dura-tion mins
SB0	test	206	02° 15' S	44°56'	14/7	D	11.32	12.32	0	300	25.0	12.0	40	60
SB 1	1	209	00° 04' S	45°39'	15/7	D	13.30	14.00	0	98	27.4	21.9	x	30
SB 1	2	209	00° 04' S	45°59'	15/7	D	14.57	15.59	105	300	27.4	21.9	x	62
SB 1	3	209	00° 08' S	46°05'	15/7	N	21.25	22.17	0	102	25.3	23.2	42	52
SB 1	4	209	00° 05' S	46°04'	15/7	N	22.46	23.32	102	202	23.2	12.0	32	46
SB 1	5	209	00° 03' S	46°03'	16/7	N	0.04	0.49	198	305	12.1	10.7	28.5	45
SB 1	6	209	00° 02' S	46°01'	16/7	N	1.39	2.31	300	600	10.8	8.9	27.5	52
US 0	1	214	03° 08' N	48°17'	17/7	D	8.49	9.27	0	102	25.0	23.6	25	38
US 0	2	214	03° 08' N	48°17'	17/7	D	9.51	10.39	102	300	24.2	11.2	31	48
US 0	5	214	03° 16' N	48°27'	17/7	D	16.20	16.47	305	405	11.3	10.7	19	27
US 0	4	214	03° 16' N	48°26'	17/7	D	14.52	15.53	400	595	10.7	9.0	32	61
US 0	3	214	03° 17' N	48°25'	17/7	D	12.55	13.35	600	1010	8.9	7.2	37	58
US 0	6	214	03° 29' N	48°34'	17/7	N	23.36	0.16	0	102	25.0	22.6	23	40
US 0	7	214	03° 29' N	48°34'	18/7	N	0.43	1.20	102	203	22.6	12.0	28	37
US 0	8	214	03° 29' N	48°34'	18/7	N	1.54	2.44	205	302	12.6	10.8	32	50
US 0	9	214	03° 28' N	48°33'	18/7	N	3.16	4.05	310	600	11.2	8.8	27	49
US 1	1	221	07° 02' N	49°59'	19/7	D	8.08	8.53	0	100	21.0	14.8	17	45
US 1	3	221	07° 08' N	50°18'	19/7	D	13.18	13.50	130	300	14 *	12 *	x	32
US 1	2	221	07° 03' N	49°59'	19/7	D	9.25	10.18	400	600	10.0	9.6	25	53
US 1	4	221	07° 39' N	50°32'	19/7	N	22.38	23.31	0	110	17.8	14.5	40	53
US 1	5	221	07° 39' N	50°32'	19/7	N	23.54	0.44	120	210	14.7	13.0	31	50
US 1	6	221	07° 36' N	50°32'	20/7	N	1.28	2.18	203	310	12.9	12.2	38	50
US 1	7	221	07° 34' N	50°31'	20/7	N	3.03	3.53	310	800	12.2	9.2	30	50
US 2	1	230	10° 45' N	51°53'	21/7	D	8.30	9.21	0	103	18.8	15.6	32	51
US 2	5	230	10° 40' N	51°55'	21/7	D	15.54	16.32	110	295	15.8	12.3	20	38
US 2	4	230	10° 41' N	51°55'	21/7	D	14.36	15.18	315	405	12.1	11.2	21	42
US 2	2	230	10° 44' N	51°52'	21/7	D	9.54	10.40	400	605	11.5	10.4	34	46
US 2	3	230	10° 43' N	51°53'	21/7	D	12.36	13.32	600	970	10.5	8.4	32	56
US 2	6	230	10° 52' N	52°03'	21/7	N	22.34	23.24	0	125	20.6	14.8	32	50
US 2	7	230	10° 54' N	52°19'	22/7	N	20.48	21.30	103	298	18.2	12.3	27	42
O F Z	1	236	07° 33' N	55°59'	26/7	D	11.00	12.24	0	98	26 *	25 *	x	84
SB 2	1	240	06° 45' N	54°30'	27/7	D	8.24	8.34	0	10	25 *	25 *	x	13
SB 2	2	240	06° 43' N	54°30'	27/7	D	10.24	11.34	0	105	25.0	24.5	46	70
SB 2	3	240	06° 07' N	54°25'	27/7	N	20.48	21.28	0	100	23.8	23.7	25	40
SB 2	4	240	06° 02' N	54°23'	27/7	N	21.58	22.44	104	200	24.0	16.5	32	46
SB 2	5	240	05° 55' N	54°20'	28/7	N	23.28	0.18	200	340	18.5	11.0	60	50

Station	Haul	Speed	Distance run	Filtered volume		Displacement		Concentration		Stock		Stock		Depth range
				RMT1	RMT8	RMT1	RMT8	RMT1	RMT8	RMT1	RMT8	RMT1	RMT8	
		kn	m	m^3	m^3	ml	ml	ml/m^3	ml/m^3	ml/m^2	ml/m^2	ml/m^2	ml/m^2	m
SB0	test	1.9	3531	2776	33612	148	126	0.053	0.004	15.9	1.1	15.9	1.1	0-300
SB 1	1	*1.9*	*1759*	*1390*	*16783*	100	78	*0.072*	*0.005*	*7.1*	*0.5*			
SB 1	2	*2.0*	*3827*	*2812*	*35361*	84	196	*0.030*	*0.006*	*5.8*	*1.1*	*12.9*	*1.5*	0-300
SB 1	3	2.3	3756	2157	30531	360	1082	0.167	0.035	17.0	3.6			
SB 1	4	2.0	2836	2088	26225	46	614	0.022	0.023	2.2	2.3			
SB 1	5	1.8	2504	2121	24569	2	356	0.001	0.014	0.1	1.6	19.3	7.5	0-300
SB 1	6	1.5	2391	2495	25192	50	500	0.020	0.020	6.0	6.0	25.3	13.5	0-600
US 0	1	1.9	2204	1767	21155	315	154	0.178	0.007	18.2	0.7			
US 0	2	1.8	2729	2248	26485	102	170	0.045	0.006	9.0	1.3			
US 0	5	2.0	1685	1218	15451	35	156	0.029	0.010	2.9	1.0	30.0	3.0	0-300
US 0	4	1.5	2782	2924	29375	158	230	0.054	0.008	10.5	1.5	40.6	4.5	0-600
US 0	3	1.8	3253	2727	31791	18	168	0.006	0.005					
US 0	6	1.6	2006	1921	20574	150	405	0.078	0.020	8.0	2.0			
US 0	7	2.2	2497	1602	21580	100	383	0.062	0.018	6.3	1.8			
US 0	8	1.8	2814	2348	27451	60	444	0.026	0.016	2.5	1.6	16.7	5.4	0-300
US 0	9	1.6	2350	2357	24463	20	190	0.008	0.008	2.5	2.3	19.2	7.6	0-600
US 1	1	1.1	1514	1920	16772	52	136	0.027	0.008	2.7	0.8			
US 1	3	*2.0*	*1975*	*1451*	*18251*	34	61	*0.023*	*0.003*	*4.0*	*0.6*	*6.7*	*1.4*	0-300
US 1	2	1.3	2184	2488	23578	38	160	0.015	0.007	3.1	1.4	9.7	2.7	0-600
US 1	4	2.2	3566	2298	30891	480	634	0.209	0.021	23.0	2.3			
US 1	5	1.8	2719	2371	26977	80	455	0.034	0.017	3.0	1.5			
US 1	6	2.2	3389	2159	29178	50	384	0.023	0.013	2.5	1.4	28.5	5.2	0-300
US 1	7	1.7	2624	2388	26443	45	288	0.019	0.011	9.2	5.3	37.7	10.5	0-800
US 2	1	1.8	2809	2410	27699	1300	6000	0.539	0.217	55.6	22.3			
US 2	5	1.5	1739	1823	18346	60	139	0.033	0.008	6.1	1.4	61.7	23.7	0-300
US 2	4	1.4	1827	1998	19510	32	176	0.016	0.009	1.4	0.8			
US 2	2	2.1	3027	2020	26697	-	224	0.000	0.008	0.0	1.7	63.1	26.2	0-600
US 2	3	1.6	2790	2691	28682	80	265	0.030	0.009	11.0	3.4			
US 2	6	1.8	2814	2348	27451	700	910	0.298	0.033	37.3	4.1			
US 2	7	1.8	2376	1970	23120	8	378	0.004	0.016	0.7	3.2	38.0	7.3	0-300
O F Z	1	-	-	*2360*	*30000*	400	754	*0.169*	*0.025*	*16.6*	*2.5*	*16.6*	*2.5*	0-100
SB 2	1	-	-	-	-	400	-	-	-	-	-			
SB 2	2	1.9	4056	3258	38959	240	151	0.074	0.004	7.7	0.4	7.7	0.4	0-105
SB 2	3	1.8	2194	1892	21679	240	540	0.127	0.025	12.7	2.5			
SB 2	4	2.0	2836	2088	26225	106	712	0.051	0.027	4.9	2.6			
SB 2	5	3.3	5154	1554	26364	38	371	0.024	0.014	3.4	2.0	21.0	7.1	0-340

Netherlands Indian Ocean Programme 1992-1993 - Haul data RMT 1+8, Tyro cruise B1

Sta- tion	Haul	JGOFS nr.	Start position		Date	Period	Time		Depth		Temperature		Flow- blips	Dura- tion
			lat. dd.mm.	long. E dd.mm.	dd/m 1992	D=day N=night	start local time	end	min. m	max. m	max. °C	min. °C		mins
SB 2	6	240	05° 48' N	54°17'	28/7	N	0.17	1.00	255	318	13.5 *	12 *	60	43
US1.5	1	253	09° 27' N	51°19'	29/7	N	21.24	22.14	0	100	17.3	14.6	35	50
S I	1	264	12° 01' N	56°13'	31/7	N	22.08	22.56	0	100	22.4	20.5	28	48
S I	2	264	12° 00' N	56°14'	1/8	N	23.59	0.50	100	212	20.5	14.5	30	51
S I	3	264	12° 03' N	56°16'	1/8	N	2.19	3.04	165	335	17.5	12.4	38	45
S I	4	264	12° 07' N	56°17'	1/8	N	4.42	5.14	300	570	13.1	11.2	20	32
S I	5	264	12° 03' N	56°21'	1/8	D	8.22	9.12	0	125	22.5	20.7	36	50
GA 1	1	271	12° 26' N	49°48'	4/8	N	19.24	20.15	0	100	27.5	20.1	36	51
GA 1	2		12° 27' N	49°46'	4/8	N	20.37	21.28	100	375	20.4	13.0	33	51
GA 2	1	276	12° 12' N	47°01'	5/8	N	20.10	21.00	0	105	28.0	17.7	38	50
GA 2	2	276	12° 08' N	46°56'	5/8	N	21.22	22.10	105	260	18.1	14.3	35.5	48
GA 2	3	276	12° 07' N	46°54'	5/8	N	23.04	23.53	202	300	14.7	14.1	42	49
GA 2	4	276	12° 03' N	46°50'	6/8	N	0.37	1.38	305	578	14.8	13.5	48.5	61
GA 2	5	276	12° 09' N	46°38'	6/8	D	10.08	10.58	0	98	27.6	17.7	31.5	50
GA 2	6	276	12° 09' N	46°35'	6/8	D	11.16	12.03	105	300	18.0	13.9	36.5	47
GA 2	7	276	12° 05' N	46°31'	6/8	D	14.12	14.59	296	410	14.0	13.4	29	47
GA 2	8	276	12° 03' N	46°34'	6/8	D	15.40	16.28	405	578	14.2	13.4	28	48

Sta-tion	Haul	Speed kn	Distance run m	Filtered volume RMT1 m^3	Filtered volume RMT8 m^3	Displacement RMT1 ml	Displacement RMT8 ml	Concentration RMT1 ml/m^3	Concentration RMT8 ml/m^3	Stock RMT1 ml/m^2	Stock RMT8 ml/m^2	Stock RMT1 ml/m^2	Stock RMT8 ml/m^2	Depth range m
SB 2	6	3.7	4933	1211	21138	-	240	-	0.011	-	0.7			
US1.5	1	2.0	3103	2262	28564	400	1687	0.177	0.059	17.7	5.9	17.7	5.9	0-100
S I	1	1.6	2444	2302	24925	320	998	0.139	0.040	13.9	4.0			
S I	2	1.7	2620	2443	26629	300	542	0.123	0.020	13.8	2.3			
S I	3	2.4	3400	1809	26400	88	190	0.049	0.007	8.3	1.2	35.9	7.5	0-300
S I	4	1.8	1744	1504	17232	30	157	0.020	0.009	5.4	2.5	41.3	10.0	0-600
S I	5	2.1	3199	2229	28823	250	377	0.112	0.013	14.0	1.6	14.0	1.6	0-100
GA 1	1	2.0	3194	2297	29220	210	687	0.091	0.024	9.1	2.4			
GA 1	2	1.8	2905	2387	28162	82	463	0.034	0.016	9.4	4.5	18.6	6.9	0-300
GA 2	1	2.2	3389	2159	29178	146	577	0.068	0.020	7.1	2.1			
GA 2	2	2.1	3161	2107	27864	82	684	0.039	0.025	6.0	3.8			
GA 2	3	2.5	3758	1949	28716	62	354	0.032	0.012	3.1	1.2	16.3	7.1	0-300
GA 2	4	2.3	4335	2558	35786	42	347	0.016	0.010	4.5	2.6	20.7	9.7	0-600
GA 2	5	1.8	2767	2361	27226	146	342	0.062	0.013	6.1	1.2			
GA 2	6	2.2	3259	2001	27512	100	258	0.050	0.009	9.7	1.8			
GA 2	7	1.8	2542	2231	25281	100	256	0.045	0.010	5.1	1.2	20.9	4.2	0-300
GA 2	8	1.6	2444	2302	24925	100	385	0.043	0.015	7.5	2.7	28.4	6.9	0-600

Netherlands Indian Ocean Programme 1992-1993 - Haul data RMT 1+8, Tyro cruise B2

Station	Haul	JGOFS nr.	Start position		Date	Period	Time		Depth		Temperature		Flow-blips	Duration
			lat. N dd.mm.dec	long. E dd.mm.dec	dd/m 1993	D=day N=night	start local time	end	min. m	max. m	max. °C	min. °C		mins
SB2	1	809	06.13.1	52.27.0	15/1	D	08.18	09.06	0	97	25.3	18.0	36	48
SB2	2	809	06.15.5	52.26.2	15/1	D	09.36	10.30	104	320	17.1	11.2	37	54
SB2	4	809	06.21.5	52.27.8	15/1	D	14.08	15.02	311	505	11.6	10.1	32	54
SB2	3	809	06.17.9	52.17.0	15/1	D	12.02	13.00	540	860	10.0	8.8	33	58
SB2	5	809	06.18.3	52.21.4	15/1	N	20.22	20.56	0	102	-	17.4	30	34
SB2	6	809	06.19.9	52.22.7	15/1	N	21.19	22.00	95	200	16.8	12.9	26	41
SB2	7	809	06.22.2	52.24.1	15/1	N	22.38	23.18	188	298	13.2	11.5	33	40
SB2	8	809	06.24.8	52.25.9	16/1	N	00.17	01.07	300	498	11.7	10.0	45	50
SB2	9	809	06.19.3	52.22.0	16/1	N	02.14	03.02	502	990	10.1	7.8	36	48
SB2	10	809	06.12.0	52.26.0	16/1	D	12.38	14.15	940	1560	8.2	-	49	97
US1	1	813	07.34.6	50.30.8	18/1	D	08.20	09.09	0	100	25.2	21.9	33	49
US1	2	813	07.35.6	50.31.0	18/1	D	09.31	10.25	105	300	22.7	12.5	36	54
US1	3	813	07.37.2	50.31.5	18/1	D	11.32	12.37	303	500	13.1	11.5	41	65
US1	4	813	07.40.9	50.32.6	18/1	D	13.28	14.44	505	1010	11.8	7.7	45	76
US1	5	813	07.51.4	50.34.9	18/1	N	20.25	21.09	0	105	25.3	21.5	35	44
US1	6	813	07.52.3	50.35.9	18/1	N	21.30	22.21	105	202	21.7	15.1	43	51
US1	7	813	07.53.6	50.37.4	18/1	N	22.53	23.43	203	295	15.0	12.9	33	50
US1	8	813	07.55.0	50.38.7	19/1	N	00.14	01.14	302	520	13.4	11.1	33	60
US1	9	813	07.56.3	50.39.7	19/1	N	01.53	03.00	505	1010	11.5	8.0	31	67
US2	1	818	10.51.5	51.59.6	20/1	N	19.10	19.50	0	102	24.9	23.2	30	40
US2	2	818	10.53.9	52.00.2	20/1	N	20.08	20.48	90	200	23.7	16.2	37	40
US2	3	818	10.57.4	52.01.7	20/1	N	21.21	22.04	205	300	16.1	12.7	42	43
US2	4	818	11.02.3	52.03.3	20/1	N	23.22	00.06	300	500	13.0	11.8	40	34
US2	5	818	11.07.9	52.03.4	21/1	N	01.04	02.12	505	1000	11.5	8.3	34	68
US2	6	818	11.10.1	52.02.3	21/1	D	08.47	09.35	0	101	24.7	22.5	44	48
US2	7	818	11.07.8	52.02.1	21/1	D	09.58	10.42	102	302	22.6	12.5	36	44
US2	8	818	11.06.5	52.02.7	21/1	D	12.29	13.30	302	540	13.3	10.9	46	61
US2	9	818	11.09.8	52.03.5	21/1	D	14.14	15.14	502	1005	11.4	8.2	33	60
US2	10	818	11.18.9	52.01.7	21/1	N	22.53	23.53	1000	1492	9.5	3.9	28	60
US2	11	818	11.23.2	52.03.8	22/1	D	09.23	10.30	70	80	24.5	23.0	76	67
SI	1	820	12.03.2	54.58.1	24/1	D	08.02	08.42	0	105	24.8	21.4	30	40
SI	2	820	12.06.0	55.00.5	24/1	D	09.17	10.30	105	286	23.2	14.6	63	73
SI	3	820	12.06.3	55.01.9	24/1	D	11.58	12.51	305	495	14.8	11.5	35	53
SI	4	820	12.06.0	55.01.5	24/1	D	13.39	14.45	505	910	11.5	9.2	36	66
SI	5	820	12.04.9	54.53.9	24/1	N	20.44	21.29	0	100	24.8	20.5	30	45
SI	6	820	12.07.0	54.55.6	24/1	N	21.52	22.42	102	206	20.3	16.2	41	50
SI	7	820	12.09.4	54.57.9	24/1	N	23.10	24.00	200	303	17.1	14.3	31	50
SI	8	820	12.10.5	54.59.6	25/1	N	00.45	01.38	302	500	14.4	12.3	37	53
SI	9	820	12.06.8	54.56.5	25/1	N	02.37	03.37	502	1010	12.0	8.7	36	60

Sta-	Haul	Speed	Distan-	Filtered volume		Displacement		Concentration		Stock		Stock		Depth
tion			ce run	RMT1	RMT8	RMT1	RMT8	RMT1	RMT8	RMT1	RMT8	RMT1	RMT8	range
		kn	m	m^3	m^3	ml	ml	ml/m^3	ml/m^3	ml/m^2	ml/m^2	ml/m^2	ml/m^2	m
SB2	1	2.2	3208	2089	27946	290	200	0.139	0.007	13.5	0.7			
SB2	2	2.0	3275	2469	30607	105	144	0.043	0.005	9.2	1.0	22.6	1.7	0-300
SB2	4	1.7	2796	2584	28333	103	323	0.040	0.011	7.7	2.2	30.4	3.9	0-500
SB2	3	1.6	2830	2789	29299	70	369	0.025	0.013	8.0	4.0	38.4	8.0	0-860
SB2	5	2.6	2683	1324	19861	380	516	0.287	0.026	29.3	2.7			
SB2	6	1.8	2285	1932	22403	50	208	0.026	0.009	2.7	1.0			
SB2	7	2.4	2907	1652	23488	50	170	0.030	0.007	3.3	0.8	35.3	4.4	0-300
SB2	8	2.6	4022	1919	29115	45	301	0.023	0.010	4.6	2.0	40.0	6.5	0-500
SB2	9	2.1	3161	2107	27863	55	419	0.026	0.015	12.7	7.3	52.7	13.8	0-1000
SB2	10	1.4	4221	4616	45071	52	155	0.011	0.003	7.0	2.1	7.0	2.1	1000- -1500
US1	1	1.9	2916	2258	27575	100	71	0.044	0.003	4.4	0.3			
US1	2	1.9	3178	2499	30253	95	243	0.038	0.008	7.4	1.6	11.8	1.8	0-300
US1	3	1.8	3601	3067	35412	140	274	0.046	0.008	9.0	1.5	20.8	3.3	0-500
US1	4	1.7	3932	3637	39854	64	500	0.018	0.013	8.9	6.3	29.7	9.7	0-1000
US1	5	2.3	3082	1862	25784	270	625	0.145	0.024	15.2	2.5			
US1	6	2.4	3803	2070	29942	50	814	0.024	0.027	2.3	2.6			
US1	7	1.9	2911	2323	27883	80	441	0.034	0.016	3.2	1.5	20.7	6.6	0-300
US1	8	1.6	2872	2885	29911	75	421	0.026	0.014	5.7	3.1	26.4	9.7	0-500
US1	9	1.3	2673	3111	29019	45	198	0.014	0.007	7.3	3.4	33.7	13.1	0-1000
US2	1	2.2	2674	1741	23288	190	372	0.109	0.016	11.1	1.6			
US2	2	2.6	3261	1519	23232	120	736	0.079	0.032	8.7	3.5			
US2	3	2.8	3734	1552	24557	160	529	0.103	0.022	9.8	2.0	29.6	7.2	0-300
US2	4	3.3	3452	1072	18087	60	518	0.056	0.029	11.2	5.7	40.8	12.9	0-500
US2	5	1.4	2959	3236	31596	50	283	0.015	0.009	7.6	4.4	48.5	17.3	0-1000
US2	6	2.6	3887	1833	27916	160	81	0.087	0.003	8.8	0.3			
US2	7	2.4	3220	1809	25839	70	65	0.039	0.003	7.7	0.5	16.6	0.8	0-300
US2	8	2.2	4101	2647	35551	130	553	0.049	0.016	11.7	3.7	28.2	4.5	0-500
US2	9	1.5	2827	2884	29583	45	405	0.016	0.014	7.8	6.9	36.1	36.1	0-1000
US2	10	1.3	2448	2807	26474	24	317	0.009	0.012	4.2	5.9	4.2	5.9	1000-
US2	11	3.2	6610	2167	36211	70	168	0.032	0.005	0.3	0.0	0.3	0.0	-1500
SI	1	2.2	2674	1741	23288	100	38	0.057	0.002	6.0	0.2			
SI	2	2.5	5637	2889	42757	55	189	0.019	0.004	3.4	0.8	9.5	1.0	0-300
SI	3	1.9	3039	2475	29358	126	319	0.051	0.011	9.7	2.1	19.1	3.0	0-500
SI	4	1.5	3132	3173	32706	56	460	0.018	0.014	7.1	5.7	26.3	8.7	0-1000
SI	5	1.9	2600	2096	25013	170	393	0.081	0.016	8.1	1.6			
SI	6	2.4	3668	2052	29362	45	612	0.022	0.021	2.3	2.2			
SI	7	1.7	2671	2380	26715	80	280	0.034	0.010	3.5	1.1	13.9	4.8	0-300
SI	8	2.0	3280	2401	30252	80	321	0.033	0.011	6.6	2.1	20.5	6.9	0-500
SI	9	1.7	3149	2865	31731	70	351	0.024	0.011	12.4	5.6	32.9	4.8	0-1000

Netherlands Indian Ocean Programme 1992-1993 - Haul data RMT 1+8, Tyro cruise B2

Sta-	Haul	JGOFS	Start position		Date	Period	Time		Depth		Temperature		Flow-	Dura-
tion		nr.	lat. N dd.mm.dec	long. E dd.mm.dec	dd/m 1993	D=day N=night	start local	end time	min. m	max. m	max. °C	min. °C	blips	tion mins
GA1	1	826	12.50.4	50.05.9	27/1	D	08.16	09.09	0	98	24.6	24.6	37	53
GA1	2	826	12.53.3	50.07.4	27/1	D	09.30	10.18	105	295	21.6	13.9	42	48
GA1	3	826	12.57.9	50.09.1	27/1	D	11.27	12.27	305	504	14.5	12.7	43	60
GA1	4	826	13.02.7	50.11.2	27/1	D	13.22	14.39	530	992	13.4	9.5	44	77
GA1	5	826	13.16.1	50.13.1	27/1	N	20.54	21.34	0	105	24.6	22.5	30	40
GA1	6	826	13.18.1	50.14.3	27/1	N	21.56	22.44	105	200	24.3	16.4	31	48
GA1	7	826	13.20.8	50.15.7	27/1	N	23.13	00.05	205	300	15.7	14.1	41	52
GA1	8	826	13.24.4	50.18.5	28/1	N	00.42	01.39	300	505	14.1	13.4	33	57
GA1	9	826	13.27.4	50.19.8	28/1	N	02.19	03.29	500	1004	13.2	10.2	36	70
GA2	1	832	12.24.4	46.58.5	29/1	D	07.28	08.23	0	100	24.3	20.5	49	55
GA2	2	832	12.27.6	47.00.6	29/1	D	08.44	09.47	100	297	19.6	14.0	39	63
GA2	3	832	12.33.0	47.01.9	29/1	D	11.27	12.38	300	515	14.8	13.2	64	71
GA2	4	832	12.33.6	46.56.1	29/1	D	13.19	14.34	505	995	14.4	11.8	45	75
GA2	5	832	12.44.4	46.45.0	29/1	N	19.21	20.12	0	98	24.4	21.7	41	51
GA2	6	832	12.45.2	46.41.2	29/1	N	20.36	21.21	105	200	20.4	16.0	44	45
GA2	7	832	12.46.0	46.36.6	29/1	N	21.54	22.44	200	300	16.3	14.5	52	50
GA2	8	832	12.52.2	46.31.9	29/1	N	23.31	00.30	300	495	15.6	14.9	40	59
GA2	9	832	12.52.4	46.31.9	30/1	N	01.11	02.14	505	999	15.4	11.3	28	63
GA2	10	832	12.52.8	46.37.0	30/1	D	14.43	16.00	960	1140	11.1	9.0	x	77
GA2	11	832	12.54.5	46.30.0	30/1	N	21.43	23.12	1000	1540	13.1	5.1	35	89
BEM	1	838	12.44.5	43.13.7	1//2	D	14.37	15.15	0	79	24.7	24.6	20	38
BEM	2	838	12.44.7	43.13.9	1//2	D	15.47	16.22	90	170	24.0	21.8	20	35
RS1	1	840	14.36.1	42.20.1	2//2	D	09.33	10.19	0	97	24.5	21.9	36	46
RS1	2	840	14.35.6	42.20.7	2//2	D	10.39	11.27	100	202	21.1	20.9	30	48
RS1	3	840	14.36.4	42.19.1	2//2	D	13.20	14.28	194	305	21.0	20.9	43	68
RS1	6	840	14.31.6	42.18.5	3//2	N	23.34	00.29	0	105	24.4	21.5	33	55
RS1	4	840	14.37.5	42.16.6	2//2	N	21.14	22.04	95	198	21.7	20.9	40	50
RS1	5	840	14.34.1	42.17.3	2//2	N	22.31	23.16	193	300	20.9	20.9	32	45
RS2	1	842	15.55.2	41.37.2	3//2	N	20.38	21.19	0	100	24.6	21.6	31	41
RS2	2	842	15.53.0	41.37.6	3//2	N	21.40	22.30	105	200	21.5	21.0	29	50
RS2	3	842	15.50.7	41.38.5	3//2	N	23.01	23.51	192	300	20.9	20.9	30	50
RS2	4	842	15.53.5	41.38.3	4//2	N	00.22	01.25	300	493	20.9	20.9	32	63
RS2	5	842	15.56.5	41.37.0	4//2	N	02.06	03.22	505	999	20.9	20.9	38	76
RS2	6	842	16.01.7	41.30.9	4//2	D	08.06	08.54	0	100	24.7	21.7	37	48
RS2	7	842	16.04.2	41.30.0	4//2	D	09.16	10.16	100	300	21.4	20.9	42	60
RS2	8	842	15.58.7	41.32.4	4//2	D	13.13	14.07	300	500	21.0	20.9	42	54
RS2	9	842	15.58.8	41.32.2	4//2	D	14.59	15.57	505	1005	20.9	20.9	36	58

Station	Haul	Speed	Distance run	Filtered volume		Displacement		Concentration		Stock		Stock		Depth range
				RMT1	RMT8	RMT1	RMT8	RMT1	RMT8	RMT1	RMT8	RMT1	RMT8	
		kn	m	m^3	m^3	ml	ml	ml/m^3	ml/m^3	ml/m^2	ml/m^2	ml/m^2	ml/m^2	m
GA1	1	2.0	3280	2401	30252	490	146	0.204	0.005	20.0	0.5			
GA1	2	2.5	3713	1897	28109	235	192	0.124	0.007	23.5	1.3	43.5	1.8	0-300
GA1	3	2.0	3772	2698	34417	128	559	0.047	0.016	9.4	3.2	53.0	5.0	0-500
GA1	4	1.6	3836	3699	39431	57	574	0.015	0.015	7.1	6.7	60.1	11.7	0-1000
GA1	5	2.2	2674	1741	23288	450	1042	0.258	0.045	27.1	4.7			
GA1	6	1.8	2729	2248	26483	150	392	0.067	0.015	6.3	1.4			
GA1	7	2.3	3617	2210	30450	100	596	0.045	0.020	4.3	1.9	37.8	8.0	0-300
GA1	8	1.6	2879	2735	29450	100	728	0.037	0.025	7.5	5.1	45.3	13.0	0-500
GA1	9	1.4	3130	3347	33218	40	571	0.012	0.017	6.0	8.7	51.3	21.7	0-1000
GA2	1	2.6	4338	2143	32130	240	103	0.112	0.003	11.2	0.3			
GA2	2	1.8	3420	2988	33958	200	388	0.067	0.011	13.2	2.2	24.4	2.6	0-300
GA2	3	2.6	5720	2721	41333	126	838	0.046	0.020	10.0	4.4	34.3	6.9	0-500
GA2	4	1.7	3936	3581	39664	16	963	0.004	0.024	2.2	11.9	36.5	18.8	0-1000
GA2	5	2.3	3620	2140	29917	525	1193	0.245	0.040	24.0	3.9			
GA2	6	2.8	3911	1623	25691	220	797	0.136	0.031	12.9	2.9			
GA2	7	3.0	4590	1722	27969	100	954	0.058	0.034	5.8	3.4	42.7	10.3	0-300
GA2	8	1.9	3537	2710	33297	150	1121	0.055	0.034	10.8	6.6	53.5	16.8	0-500
GA2	9	1.3	2461	2902	26802	40	557	0.014	0.021	6.8	10.3	60.3	27.1	0-1000
GA2	10	*1.2*	*2852*	*3464*	*31285*	38	315	*0.011*	*0.010*	*2.0*	*1.8*	*2.0*	*1.8*	
GA2	11	1.1	3074	3857	33970	40	292	0.010	0.009	5.6	4.6	65.9	31.7	0-1500
BEM	1	1.5	1739	1822	18345	334	269	0.183	0.015	14.5	1.2			
BEM	2	1.6	1743	1681	17923	1000	2478	0.595	0.138	47.6	11.1	62.1	12.2	0-170
RS1	1	2.3	3216	1949	26951	255	209	0.131	0.008	12.7	0.8			
RS1	2	1.8	2633	2271	26016	124	139	0.055	0.005	5.6	0.5			
RS1	3	1.8	3730	3217	36856	100	100	0.031	0.003	3.5	0.3	21.7	1.6	0-300
RS1	6	1.7	2839	2633	28804	425	1688	0.161	0.059	16.9	6.2			
RS1	4	2.3	3576	2088	29343	60	94	0.029	0.003	3.0	0.3			
RS1	5	2.0	2841	2019	25845	65	120	0.032	0.005	3.4	0.5	23.4	7.0	0-300
RS2	1	2.1	2717	1794	23830	220	539	0.123	0.023	12.3	2.3			
RS2	2	1.6	2530	2399	25865	170	368	0.071	0.014	6.7	1.3			
RS2	3	1.7	2624	2388	26443	120	508	0.050	0.019	5.4	2.1	24.4	5.7	0-300
RS2	4	1.4	2741	2998`	29273	70	160	0.023	0.005	4.5	1.1	28.9	6.7	0-500
RS2	5	1.4	3307	3617	35313	40	160	0.011	0.005	5.5	2.2	34.4	9.0	0-1000
RS2	6	2.2	3256	2072	28015	200	396	0.097	0.014	9.7	1.4			
RS2	7	2.0	3676	2731	34131	110	207	0.040	0.006	8.1	1.2	17.7	2.6	0-300
RS2	8	2.3	3751	2297	31617	120	34	0.052	0.001	10.4	0.2	28.2	2.8	0-500
RS2	9	1.7	3110	2758	31053	50	313	0.018	0.010	9.1	5.0	37.2	7.9	0-1000

APPENDIX B

Euphausiacea, species and standard numbers (n 1000^{-1} m^{-3}) from stratified RMT8 samples during day and night in monsoons, from Banda Sea, Red Sea and NW Indian Ocean

- All samples are sequenced according to dendrogram obtained with cluster analysis (Chapter 3).
- Table continues over ten pages
- Top line: cluster code: A, B, C, C1, C2, C3.1, C3.2, D, E, F, G, H, I, O.
- Second line: *Tyro* cruises 312 (SE monsoon) and 322 (NW monsoon) at Banda Sea during *Indonesian-Dutch Snellius II Expedition* 1985-1985, and *Tyro* cruises B0 (onset SW monsoon), B1 (SW monsoon), and B2 (NE monsoon) during *Netherlands Indian Ocean Programme* 1992-1993 (*NIOP*)
- Third line: station codes A, B, C, D for cruises 312 and 322 during *Snellius II*, and RS4, RS2, RS1, BEM (Red Sea), GA1, GA2 (Gulf of Aden), US1, US1.5, US2 (Somali Current), US0, SB0, SB1 (equatorial Somali Basin), SB2, OFZ, SI (northern Somali Basin), during *NIOP*.
- Forth line: period of day (D) or night (N)
- Fifth and sixth line: minimum and maximum depth of sample
- Seventh line: number of taxa in sample
- Second column: presence of species in sample set (n=215) as percentage of occurrence in samples.

Cluster		C1	C1	C1	C1	C3.1	C3.1	C3.1	C3.1	C3.1	C3.1	C3.1	C3.1	C3.1	C3.1	C3.1	C3.1	C3.1	C3.1	C3.1	C3.1	C3.1	C3.1	C3.2	C3.2
Tyro cruise		312	B2	B1	B1	B0	B0	B0	B2	B0	B2	B0	B0	B0	B0	B2	B2	B2	B2	B0	B2	B2	B2	B0	B0
Station		A	US1	GA2	US0	RS4	RS2	RS2	RS2	RS1	RS1	RS2	RS1	BEM	RS2	RS2	RS1	RS2	RS2	RS1	RS1	RS1	RS1	RS2	RS2
Period (D=day, N=Night)		D	D	D	D	N	N	N	N	N	N	D	D	D	D	D	D	D	N	N	D	N	N	D	N
Minimum depth (m)		0	0	0	0	0	105	0	0	0	0	202	208	105	310	300	194	100	505	98	100	95	193	380	420
Maximum depth (m)		100	100	98	102	200	200	99	100	102	105	302	402	163	402	500	305	300	999	202	202	198	300	597	610
Number of taxa		1	1	2	3	5	5	5	5	5	4	3	4	4	4	4	4	4	5	2	4	5	4	2	3
Concentration - - (n/1000 m^3)	presence (%) (n=215)																								
E.diomedeae	68					2.34	0.36	33.25	2.35	0.13	0.42		0.08		0.55	0.16	0.03	0.23	0.06						
E.gibba	1																								
E.hemigibba	2																								
E.mutica	0.5																								
E.paragibba	7																								
E.pseudogibba	13													0.21											
E.sanzoi	16					0.81	2.32	7.61	2.52	0.34		0.10	0.08	0.21	1.35	0.32	0.03	0.06	0.03			0.03	0.04	1.67	0.51
E.sibogae/distinguenda	40					0.81	0.13	3.55	34.75	5.29	104.15	0.10	0.10	0.85	1.72	0.54	13.57	5.86	0.20	3.07	3.73	0.34	0.31		
E.similis	21																								
E.tenera	3																								
N.atlantica	1																								
N.gracilis	35			0.04																					
N.microps	24																								
N.tenella	40																								
Nb.boopis	27																								
Nb.flexipes	29																								
Nb.sexpinosus	2																								
P.latifrons	1																								
S.abbreviatum	36	0.84	1.20	1.84	0.76	0.56	3.12	2.56	6.71	0.68	0.69								0.03		0.04	0.41			0.11
S.affine	30					1.02	2.09	5.64	5.04	0.30	0.14	1.35	4.04	3.82	4.10	0.44	0.68	1.61	0.23	12.08	0.31	10.46	3.87	1.07	1.63
S.carinatum	4																								
S.elongatum	1																								
S.insulare	1																								
S.longicorne	31				0.09																0.04	0.07	0.12		
S.maximum	33																								
S.robustum	6																								
T.aequalis	5																								
T.astylata	13																								
T.cristata	2																								
T.monacantha	44																								
T.obtusifrons	2																								
T.orientalis	43				0.05																				
T.pectinata	2																								
T.tricuspidata	27																								

Cluster	C3.2	C3.2	C3.2	C3.2	C3.2	C3.2	C3.2	C3.2	C3.2	C3.2	C3.2	C3.2	C3.2	C2	F	F	F	F	F	F	F	F	F	F
Tyro cruise	B0	B2	B0	B0	B2	B2	B0	B0	B2	B0	B0	B0	B0	B2	312	B1	312	312	322	322	312	312	322	B2
Station	RS2	RS2	RS2	RS1	RS2	RS2	RS2	RS1	RS2	RS1	RS1	RS1	BEM	SI	C	SB1	C	C	C	C	A	A	A	SB2
Period (D=day, N=Night)	N	N	D	D	N	N	D	D	D	D	N	N	D	D	N	N	D	D	D	D	N	N	N	D
Minimum depth (m)	205	105	0	415	192	300	106	0	0	105	210	418	0	0	300	0	400	300	200	100	100	0	0	0
Maximum depth (m)	400	200	105	605	300	493	200	97	100	210	400	600	104	100	400	102	500	400	300	200	200	100	100	97
Number of taxa	4	5	1	1	1	1	2	2	2	2	3	3	2	2	5	7	4	5	6	5	7	9	3	5
Concentration - - (n/1000 m^3)																								
E.diomedeae	0.11														0.07	1.05	0.12	1.71	0.37	1.79	0.41	1.53	15.10	5.87
E.gibba																								
E.hemigibba																							0.10	
E.mutica																								
E.paragibba															0.11	0.36				0.04				
E.pseudogibba																								
E.sanzoi	0.11	0.39																			0.03	0.23		
E.sibogae/distinguenda		0.04									0.06	0.70												0.82
E.similis																					0.96	0.19		
E.tenera																								
N.atlantica																								
N.gracilis																								
N.microps														0.13					0.78	1.37	3.61			
N.tenella																								0.14
Nb.boopis																			0.09					
Nb.flexipes																								
Nb.sexpinosus																								
P.latifrons																								
S.abbreviatum	0.11	0.58					0.41	0.05	0.04	0.22	0.06	0.06			0.18	0.39			0.09	0.19	3.09	0.57	2.62	1.86
S.affine	3.62	3.87	0.25	0.35	1.02	1.71	0.74	4.98	1.43	15.81	1.54	4.25	3.30	0.13						0.49		0.23		
S.carinatum													0.73									0.08		
S.elongatum																								
S.insulare																						0.11		
S.longicorne																			0.37					
S.maximum																								
S.robustum																								
T.aequalis																0.20								
T.astylata																		0.11						
T.cristata																								
T.monacantha		0.04														0.92	2.94	0.07			0.10	0.08		0.29
T.obtusifrons																								
T.orientalis															0.14	0.07	0.36	0.19						
T.pectinata																								
T.tricuspidata															0.04	4.98	0.08	0.15	0.32		0.03	0.11		

Cluster	F	F	F	F	F	F	F	F	F	F	F	F	F	F	F	F	F	F	F	F	F
Tyro cruise	B2	B2	B1	B2	B2	312	B1	B1	B2	B1	B1	B2	B2	B1	B1	B1	312	B2	322	B1	312
Station	SI	GA1	SB2	US2	GA2	B	GA2	SI	SB3	US1	US1.5	US1	SB2	US0	SI	GA1	B	US2	D	SB2	C
Period (D=day, N=Night)	N	N	N	N	N	D	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N
Minimum depth (m)	0	0	200	1000	0	0	0	165	0	0	0	0	0	0	0	0	0	0	0	0	0
Maximum depth (m)	100	105	340	1492	98	100	105	335	100	110	100	105	102	102	100	100	100	102	100	100	100
Number of taxa	4	3	3	3	7	4	7	4	11	9	13	8	6	10	8	7	4	5	7	7	6
Concentration - - (n/1000 m^3)																					
E.diomedeae	89.55	21.13	1.02	0.40	7.69	40.72	20.70	6.14	76.17	5.70	5.74	17.61	28.20	133.67	101.10	20.23	102.73	15.46	18.47	16.61	1.51
E.gibba																					
E.hemigibba												0.16									
E.mutica																					
E.paragibba											0.39			1.94							
E.pseudogibba																	0.22	0.05	11.97		0.56
E.sanzoi									0.91	24.54	0.46								0.32		
E.sibogae/distinguenda	12.79	2.32	0.11	0.04	0.20					33.67	0.60	1.86	0.13	3.50	3.37	5.55					
E.similis											0.07										
E.tenera							0.03		0.61												
N.atlantica																					
N.gracilis										2.59	1.23		1.21	0.63	0.48	2.19					
N.microps										0.78	1.05			0.05						0.18	0.52
N.tenella									1.37		0.74									0.09	
Nb.boopis																					
Nb.flexipes					0.03					1.04	1.30			1.56	1.93	0.27				0.55	
Nb.sexpinosus								0.14													
P.latifrons																					
S.abbreviatum	12.79	2.06		0.11	0.10		0.27		9.14	2.59	0.56	0.47	1.61		4.81						0.04
S.affine					0.03	0.38	0.14		2.59												
S.carinatum						0.30															
S.elongatum																					
S.insulare																			0.45		
S.longicorne											0.28										
S.maximum								0.08	0.91												
S.robustum									2.29			0.78									
T.aequalis									1.52												
T.astylata							1.37				0.25	0.31	0.40	2.13	0.48	0.31		0.09	0.09	0.18	
T.cristata																					
T.monacantha			0.04		0.03	0.04	3.22	0.34	2.29	0.78	0.77	1.09		0.83	2.73	0.68	3.76	0.60	0.54	0.65	1.47
T.obtusifrons							0.07														
T.orientalis	0.32													0.05							
T.pectinata																					
T.tricuspidata					0.10				1.07	0.78		0.47	2.01	3.26	0.16	0.03	124.60	1.37	0.54	0.83	5.04

Cluster	F	F	F	F	G	G	G	G	G	G	G	G	G	G	G	G	G	G	G	G	G	G	G	G	G	G
Tyro cruise	312	322	322	322	322	322	312	322	312	322	312	B2	B2	322	B1	B1	322	322	322	322	322	312	322	312	B2	312
Station	D	C	B	C	A	A	A	B	C	C	C	SB2	SB2	A	SB1	SB1	A	A	C	D	D	B	B	D	SB2	A
Period (D=day, N=Night)	N	N	N	N	N	N	D	N	N	N	N	N	N	D	N	N	N	N	N	N	N	N	N	N	N	N
Minimum depth (m)	0	100	0	0	100	200	200	200	200	200	100	95	188	100	102	198	400	300	400	200	300	200	300	400	300	300
Maximum depth (m)	100	200	100	100	200	300	300	300	300	300	200	200	298	300	202	305	500	400	500	300	500	300	500	500	498	400
Number of taxa	7	7	11	7	3	4	7	10	10	10	11	9	6	11	11	9	5	6	6	6	6	7	10	9	6	6
Concentration - - (n/1000 m^3)																										
E.diomedeae	3.81		14.53	3.88					0.16	0.07	0.09		0.55	1.22	0.31	0.16		0.04				0.07	0.08	0.54	0.41	0.19
E.gibba														0.07												
E.hemigibba														0.07												
E.mutica																										
E.paragibba																										
E.pseudogibba	0.87	0.28	0.94						0.12													0.67	0.08	0.69		
E.sanzoi		0.52		0.39																						
E.sibogae/distinguenda			0.17									0.09														
E.similis	0.25				0.83	3.32	5.99	1.19	0.04	0.55	0.09			0.31	0.31	0.24	6.22	1.23	0.13	0.21	0.03	0.77	1.48			0.53
E.tenera			0.30																							
N.atlantica																										
N.gracilis						0.16	0.70	1.54						0.49	0.76	0.16										
N.microps	1.78	3.36	4.96						0.62	3.31	0.17	0.13			0.23											
N.tenella								0.05				2.50			0.19	0.16	0.46	0.40	0.30	0.04	0.06	4.22	0.27	2.55	2.06	1.64
Nb.boopis							1.95	0.60	0.12	0.11				0.07			1.75	0.43	0.52	0.13	0.38	0.11	0.19	1.13	0.45	0.53
Nb.flexipes												0.80	0.72												0.03	
Nb.sexpinosus															0.08								0.04			
P.latifrons			0.13	3.19																						
S.abbreviatum	3.15	0.18		0.04	4.14		0.22		0.31	0.15	0.35	0.94	0.85	0.49	0.15	0.16										0.27
S.affine		0.15	0.94	0.26						0.18														0.05		
S.carinatum														0.35												
S.elongatum																										
S.insulare			0.34																							
S.longicorne								0.15																0.05		
S.maximum						0.24	0.36	0.84	0.43	0.40	0.22	1.47	1.11	0.10		0.16	0.10	0.04		0.68	0.50		0.34	0.10	0.31	
S.robustum																								0.10		
T.aequalis															0.15											
T.astylata			2.14	0.04				0.05			0.17															
T.cristata								0.05			0.04												0.04			
T.monacantha	1.04	0.40	2.22				0.22	1.69	0.78	0.11	0.35	0.40	1.28			0.57			0.09	0.04		0.42	0.15			0.04
T.obtusifrons															0.23	0.24										
T.orientalis					2.99	3.60	3.25	2.63	1.60	0.92	1.66	0.27	0.43	0.24	1.45	0.24	1.29	0.94	1.13	1.44	0.38	0.49	3.79	0.29	0.48	
T.pectinata											0.26	0.05														
T.tricuspidata	0.37	6.27	7.73	9.09					0.16	0.04	0.04			0.21	0.27				0.30		0.03					

Cluster	G	G	G	G	G	G	G	G	G	G	G	G	G	G	G	G	G	G	G	I	I	I	I
Tyro cruise	322	312	312	312	312	312	322	322	322	322	312	312	312	312	312	B1	312	322	322	B1	B1	B1	B1
Station	B	D	B	D	B	B	C	B	C	B	D	D	D	B	D	SB1	B	D	C	US0	US0	US0	US0
Period (D=day, N=Night)	D	D	D	D	N	N	D	D	D	N	N	N	N	N	D	D	D	N	N	D	D	N	D
Minimum depth (m)	400	400	300	300	400	300	300	300	400	100	300	200	100	100	200	105	200	100	300	400	305	102	102
Maximum depth (m)	500	500	400	400	500	400	400	400	500	200	400	300	200	200	300	300	300	200	400	595	405	203	300
Number of taxa	8	10	12	10	10	13	11	11	9	11	9	11	12	11	5	6	8	6	6	8	15	11	11
Concentration - - (n/1000 m^3)																							
E.diomedeae	0.05	0.81	0.32	0.04	0.50	0.40	1.32	0.48	0.37	0.14	0.10	4.38	0.35	60.90	2.04	3.87	2.67			0.10	0.13	0.42	2.04
E.gibba																							
E.hemigibba																					0.13	0.23	
E.mutica																					0.45		
E.paragibba																				0.24	0.45	0.05	
E.pseudogibba	0.05	1.06	1.60		0.42	0.36	0.09	3.12	0.33		0.30	2.19	0.39	0.61			0.04	0.13	0.04				
E.sanzoi						0.07												0.09	1.11				
E.sibogae/distinguenda																					0.65		3.02
E.similis	0.05	2.32	0.05	0.85	0.04	0.07	0.04	2.95	1.33	0.27	0.15	2.19	0.24	2.21	0.04					0.07	0.13	0.14	
E.tenera								0.74															1.70
N.atlantica														30.45			0.04						
N.gracilis								2.00												0.58	4.01	0.83	0.23
N.microps	0.84	3.23	1.60	0.21		0.15	0.85	1.60	2.59	5.91	0.15	3.06	12.97			0.06				0.17	0.32	1.39	0.23
N.tenella	0.42	1.46	3.58	1.41	2.13	1.28	3.19	2.95		2.52	2.12	4.82	1.88	12.79	0.58	0.62	0.04	0.30		0.14	0.26	0.74	
Nb.boopis	0.47	2.87	1.77	0.51	0.88	2.37	0.81	1.21	1.59		0.61	0.44			0.09	0.08			0.21	0.10			
Nb.flexipes																					0.06	0.74	0.04
Nb.sexpinosus													0.08										
P.latifrons																							
S.abbreviatum												1.75	1.18										0.04
S.affine										0.32		1.75	0.12	2.44									0.11
S.carinatum					0.17	0.15																	
S.elongatum																							0.11
S.insulare																							
S.longicorne			0.03			0.15	0.13			0.09	0.61	6.13	0.12	0.61							0.06		0.38
S.maximum			0.03	0.04	0.04	0.18	0.17	0.35			0.45	0.88	0.04	0.61	0.22	0.17	0.50		0.17		0.06	0.14	
S.robustum										0.05								0.04					
T.aequalis				0.04																	0.65	0.37	
T.astylata							0.38		0.70	0.41										0.61			
T.cristata			0.03																				
T.monacantha	1.40	1.56	3.16	1.19	0.04	0.04			0.07	2.38	0.10	2.19	1.41	1.67			0.04				0.06	0.97	
T.obtusifrons		0.10																					
T.orientalis	0.88	0.25	0.62	0.04	0.29	0.62	1.15	0.65	1.67	1.01			0.20	0.19			0.12	1.58	2.34				
T.pectinata																							
T.tricuspidata		0.05	2.51	0.90	0.54	0.18	0.81	3.38	0.04	0.09				2.13		4.27	4.88	0.89	0.09		0.06		0.26

Cluster	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I
Tyro cruise	322	B2	B2	B1	B2	B1	B2	B2	B2	B2	B2	B2	B1	B2	B1	B1	B1	B2	B1	B2	B2
Station	B	SB2	US2	US1	GA2	US1	US2	US1	US2	SB2	SI	US1	GA2	US1	US0	US0	SI	GA2	GA2	GA1	GA2
Period (D=day, N=Night)	D	D	D	N	N	N	N	N	D	D	D	N	N	D	N	N	N	N	D	N	D
Minimum depth (m)	100	104	102	203	1000	310	505	302	502	540	505	505	305	105	205	310	300	505	405	500	505
Maximum depth (m)	300	320	302	310	1500	800	1000	520	1005	860	910	1010	578	300	302	600	570	999	578	1004	995
Number of taxa	11	9	6	7	8	6	10	7	6	6	6	9	8	6	11	11	4	7	9	9	7
Concentration - - (n/1000 m^3)																					
E.diomedeae	1.99	6.86	0.12	0.38	0.47	0.11	0.22	0.17	0.27	0.17	0.58	0.14	0.31	1.59	0.11	0.25	0.46	0.63	0.64	0.18	0.23
E.gibba																					
E.hemigibba																					
E.mutica																					
E.paragibba												0.03			0.07	0.08					
E.pseudogibba																					
E.sanzoi																					
E.sibogae/distinguenda	0.05		0.27	0.86	0.03	0.08			0.03	0.14	0.12	0.03			0.25	0.20		0.11	0.20	0.06	
E.similis															0.29	0.04					
E.tenera	0.34																				
N.atlantica																					
N.gracilis						0.11	0.76	0.94	0.57	0.34	0.24	0.28	0.36	0.34	1.82	0.61	0.23	0.15	1.81	0.27	0.66
N.microps	0.15			0.07	0.09																
N.tenella	0.44	1.05	0.31	0.55		0.23	0.32	0.30	0.34	0.51	0.09	0.10	0.34	0.26	0.69	0.20					0.05
Nb.boopis							0.09	0.03		0.03					0.07	0.20		0.06	0.04	0.19	
Nb.flexipes		0.29	0.08	0.69	0.06	0.04	0.03	0.10	0.03				0.11	0.07	0.11	0.04	0.29	0.26	0.04	0.06	0.10
Nb.sexpinosus																					
P.latifrons																					
S.abbreviatum														0.13						0.03	
S.affine	0.39																				
S.carinatum																					
S.elongatum		0.03																			
S.insulare																					
S.longicorne	0.24	0.26	0.31	0.10	0.12		0.03			0.07	0.06	0.07	0.22	0.20	0.80	0.04		0.15	0.04		
S.maximum	0.05	0.16			0.03	0.04	0.03						0.14		1.82	0.08			0.04	0.06	
S.robustum		0.39	0.19					0.07				0.10									
T.aequalis																					0.03
T.astylata					0.03		0.03						0.03								
T.cristata																					
T.monacantha	0.05											0.03	0.08				0.23	0.11	0.28	0.12	0.15
T.obtusifrons																					
T.orientalis	0.19	0.13		0.21	0.21		0.06	0.23	0.07		0.03	0.03				0.08			0.48	0.75	0.63
T.pectinata															0.07						
T.tricuspidata	0.63	0.13					0.03														

Cluster	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I	I
Tyro cruise	B2	B2	B0	B2	B2	B2	B2	B2	B2	B2	B2	B2	B1	B2	B2	B2	B1	B1	B2	B1	B1
Station	SI	GA2	US2	US2	SI	GA1	GA2	US1	US2	GA2	US2	GA2	US1	GA1	SI	GA2	GA1	GA2	SI	US2	GA2
Period (D=day, N=Night)	N	D	D	D	D	D	D	N	N	N	N	N	N	N	N	N	N	N	N	N	N
Minimum depth (m)	502	960	215	302	305	305	300	203	205	105	300	300	120	300	200	200	100	202	302	103	105
Maximum depth (m)	1010	1140	490	540	495	504	515	295	300	200	500	495	210	505	303	300	375	300	500	298	260
Number of taxa	5	6	11	14	13	8	7	10	12	11	10	9	8	9	10	10	9	10	9	9	9
Concentration - - (n/1000 m^3)																					
E.diomedeae	0.69	0.35	0.26	1.29	10.90	4.65	6.77	1.47	0.77	1.21	0.66	1.17	0.22	0.71	0.30	1.64	0.21	0.14	0.20	0.99	0.29
E.gibba																					
E.hemigibba																					
E.mutica																					
E.paragibba																					0.04
E.pseudogibba																					
E.sanzoi																					
E.sibogae/distinguenda			0.13	2.90	4.77	0.41	5.81		0.12	0.04	1.66	0.75	3.45	2.70	1.50	0.86	0.07	0.07	0.03		0.18
E.similis																					
E.tenera																					
N.atlantica																					
N.gracilis	0.19		8.67	3.99	4.43	0.52	3.87	1.43	2.69	2.18	4.37	1.23	0.89	1.26	5.39	1.61	4.65	1.88	1.72	0.22	1.76
N.microps			0.52	0.23	0.07				0.20												
N.tenella			1.24	1.01	0.14	0.12		0.65	0.45	0.39	1.44	0.18	0.41	0.07	0.45	0.14	0.07	0.07	0.13	0.64	
Nb.boopis			0.07	0.23	0.07						0.28							0.03		0.04	
Nb.flexipes		0.10	0.52	0.65	2.45	0.46	1.06	0.82	0.65	1.95	0.22	1.83	0.78	0.85	2.62	4.50	0.82	1.18	0.13	2.08	0.97
Nb.sexpinosus																					
P.latifrons																					
S.abbreviatum				0.06						0.43				0.10	0.07					0.17	
S.affine		0.03						0.57	0.77			0.09			4.04	0.04			0.03		
S.carinatum																					
S.elongatum																					
S.insulare																					
S.longicorne	0.03	0.06	0.13	0.06	0.14	0.06		0.36	2.04	0.78	0.33	0.45	0.26	0.14	0.90	3.58	1.78	2.05	0.13	0.13	1.33
S.maximum			0.07	0.11	0.14		0.19	0.04	0.04	0.04			0.19	0.27	0.75	1.04	0.67	1.08	0.73	0.65	
S.robustum								0.04			0.39	0.51									
T.aequalis																					
T.astylata				0.34	0.07					0.08											0.43
T.cristata																					
T.monacantha	0.03	0.03	0.46	1.83	0.89	1.16	1.45	1.61	0.57	0.51	0.11					0.07	0.46	0.10			5.02
T.obtusifrons																					
T.orientalis	0.41	0.38	0.20	0.76	0.20	1.28	3.29	1.33	2.85	3.50	0.83	0.48	0.19	0.41	2.25	1.64	1.46	0.38	0.33	0.69	3.01
T.pectinata									0.04												
T.tricuspidata				0.08	0.07																

Cluster	I	I	I	I	I	I	I	I	I	I	I	I	I	I	H	H	H	H	H	H	H
Tyro cruise	B2	B2	B1	B2	B2	B2	B1	B2	B1	B1	B1	B1	B1	B1	312	312	B1	B2	B2	B0	B2
Station	GA1	GA1	SI	SI	SB2	US1	SB1	US1	US1	GA2	US2	US2	US2	US2	D	B	GA2	SI	GA1	US2	GA1
Period (D=day, N=Night)	N	N	N	N	D	N	N	D	D	D	D	N	D	D	D	D	D	D	D	D	D
Minimum depth (m)	105	205	100	102	311	105	300	303	0	296	110	0	400	600	100	100	105	105	105	0	0
Maximum depth (m)	200	300	212	206	505	202	600	500	100	410	295	125	605	970	200	200	300	286	295	200	98
Number of taxa	8	8	11	7	11	10	9	10	3	4	6	4	3	6	4	6	7	8	3	9	6
Concentration - - (n/1000 m^3)																					
E.diomedeae	0.38	0.43	6.57	0.07	0.85	1.04	0.08	4.18	0.30	6.68	0.93	2.08			0.54	0.86	0.80	0.02	0.68	0.38	0.26
E.gibba																					
E.hemigibba																					
E.mutica																					
E.paragibba																					
E.pseudogibba																					
E.sanzoi					0.04						0.38	0.51								0.04	
E.sibogae/distinguenda	0.64	0.16			2.62	0.03			0.83	1.03	7.63	58.29	0.34	0.80		2.72	0.25	0.05		0.08	
E.similis					0.04																
E.tenera																					
N.atlantica																					
N.gracilis	3.85	0.72	8.56	6.54	4.41	7.01	1.11	2.99	0.18	0.40	3.87	2.02	0.37	0.28						0.08	
N.microps			0.19	0.27	0.46	0.37												0.05			
N.tenella					0.35	1.34	0.44	1.24					0.07	0.07	0.03	0.41		0.02			
Nb.boopis					0.39		0.16	0.34			0.11			0.10							
Nb.flexipes	0.42	5.25	5.37	1.70		0.07		0.51									1.34	0.58		0.42	0.26
Nb.sexpinosus			0.07																		
P.latifrons																					
S.abbreviatum	3.06	2.23	3.15	5.11		0.13									0.54	0.48	1.13	0.12		0.04	
S.affine						0.20														0.63	1.23
S.carinatum														0.04						1.33	
S.elongatum																					
S.insulare																					
S.longicorne	0.23	0.99	2.40	0.48						0.04					0.34	1.75	1.42	0.98	0.64	0.13	0.07
S.maximum			0.04				0.16	0.28									0.55	0.05	0.36		0.60
S.robustum																					
T.aequalis							0.04	0.06													
T.astylata			0.30																		
T.cristata																0.07					
T.monacantha	6.42	0.03	0.38		0.04	0.33	0.24	4.29													
T.obtusifrons																					
T.orientalis	2.83	3.02	0.11	0.20	0.53	0.27	0.24	1.98			0.22			0.03							
T.pectinata																					
T.tricuspidata					0.04		0.12	0.62									0.04				0.06

Cluster	H	E	E	E	E	E	E	E	D	D	B	B	B	B	B	B	B	A	O	O	O	O	O
Tyro cruise	B2	312	322	312	312	312	312	B2	B1	B2	B2	B2	B2	B1	B1	B1	B1	B1	B2	B1	B2	B1	322
Station	GA2	A	A	A	A	B	C	US2	SB2	SB2	US1	GA1	RS2	US1	US2	US2	US0	US1	BEM	OKZ	RS1	SB1	A
Period (D=day, N=Night)	D	D	D	N	N	D	N	N	N	N	D	D	D	D	D	D	D	D	D	D	D	D	D
Minimum depth (m)	100	300	400	200	400	400	400	90	104	502	505	530	505	400	0	315	600	130	0	0	0	0	0
Maximum depth (m)	297	400	500	300	600	500	500	200	200	990	1010	992	1005	600	103	405	1010	300	79	98	97	98	100
Number of taxa	6	2	3	4	5	6	7	10	3	3	3	3	3	2	1	1	4	1	0	0	0	0	0
Concentration - - (n/1000 m^3)																							
E.diomedeae	8.25							0.04	0.23	0.04													
E.gibba							0.03																
E.hemigibba																							
E.mutica																							
E.paragibba											0.03						0.03						
E.pseudogibba																							
E.sanzoi																							
E.sibogae/distinguenda								0.17					0.03										
E.similis				0.15	0.09																		
E.tenera																							
N.atlantica																							
N.gracilis											0.05	0.10	0.36	0.11	0.55	0.21	0.03						
N.microps	0.47					0.06	0.30	0.39									0.03						
N.tenella				0.15	0.09	0.06				0.14				0.13									
Nb.boopis		0.10	0.39	0.04	0.04	0.06	0.12	0.04									0.03						
Nb.flexipes	4.95							0.04	0.04														
Nb.sexpinosus																							
P.latifrons																							
S.abbreviatum							0.03																
S.affine	0.47							0.04					0.36										
S.carinatum																							
S.elongatum																							
S.insulare																							
S.longicorne										0.07													
S.maximum	1.88				0.04	0.03	0.03																
S.robustum																							
T.aequalis									0.11														
T.astylata								0.04															
T.cristata																							
T.monacantha	0.24	0.07	0.12	0.11	0.04	0.46	0.03	0.39			0.10	0.08											
T.obtusifrons																							
T.orientalis			5.60			0.09	0.09	0.09				0.18											
T.pectinata																							
T.tricuspidata								0.04										0.05					

Cluster	O	O	O	O	O	O	O	O	O	O	O
Tyro cruise	322	312	322	312	B2	B2	B1	B1	B2	312	B0
Station	B	C	C	D	GA2	US2	SB2	SI	BEM	C	RS4
Period (D=day, N=Night)	D	D	D	D	D	D	D	D	D	D	D
Minimum depth (m)	0	0	0	0	0	0	0	0	90	100	230
Maximum depth (m)	100	100	100	100	100	101	105	125	170	200	500
Number of taxa	0	0	0	0	0	0	0	0	0	0	0
Concentration - - (n/1000 m^3)											
E.diomedeae											
E.gibba											
E.hemigibba											
E.mutica											
E.paragibba											
E.pseudogibba											
E.sanzoi											
E.sibogae/distinguenda											
E.similis											
E.tenera											
N.atlantica											
N.gracilis											
N.microps											
N.tenella											
Nb.boopis											
Nb.flexipes											
Nb.sexpinosus											
P.latifrons											
S.abbreviatum											
S.affine											
S.carinatum											
S.elongatum											
S.insulare											
S.longicorne											
S.maximum											
S.robustum											
T.aequalis											
T.astylata											
T.cristata											
T.monacantha											
T.obtusifrons											
T.orientalis											
T.pectinata											
T.tricuspidata											