Andaman Sea copepods: spatio-temporal variations in biomass and production, and role in the pelagic food web

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ABSTRACT: Copepod community structure and productivity was investigated off the west coast of Phuket, Thailand, along transects from the shallow coastal water across the shelf break to the deep oceanic stations in the Andaman Sea. Cruises were conducted during the 2 monsoons, the calm and dry NE monsoon (November to March), and the stormy and wet SW monsoon (May to September). The copepod community was sampled with a 50 µm net to include the smallest species characteristic of oligotrophic waters. The copepod community was characterized by high species diversity; high-resolution analysis of species composition at the coast, the shelf break and the deep off shore stations, however, revealed no differences in species composition between areas. Small copepods, mainly cyclopoids and poecilostomatoids (dominated by *Oithona* spp. and *Oncaea* spp.), made up half of the number and ca. 25 % of the copepod biomass. Despite the presence of highly dynamic internal waves at the shelf break, no response in either copepod biomass or potential prey biomass (phytoplankton and protozooplankton) was observed at the shelf break. Egg production rates of 5 calanoid species (*Acrocalanus gibber*, *Acartia australis*, *Centropages furcatus*, *Temora discaudata*, *Euchaeta marinella*), 1 cyclopoid (*Oithona plumifera*) and 1 poecilostomatoid (*Oncaea venusta*) were measured and compared along transects and between seasons. No spatial or seasonal patterns in biomass or egg production rates of the investigated copepods were observed. Carbon flow budgets for the 3 areas investigated suggest that the production of the copepod community in this picoplankton-dominated environment is strongly dependent on protozooplankton as prey to fuel the measured egg production rates.

KEY WORDS: Tropical copepod community · Calanoids · Cyclopoids · Egg production · Secondary production · Andaman Sea

INTRODUCTION

Copepods dominate the mesozooplankton in the oceans and play a key role in transferring primary production to higher trophic levels in all pelagic ecosystems (Verity & Smetacek 1996). Knowledge about rates (production and grazing) is essential in the framework of understanding the flux of carbon and nutrients through the food chain. Unfortunately, most of our information on carbon fluxes in the pela-

gial is based on investigations conducted in polar and temperate ecosystems. Despite the fact that tropical seas cover 42 % of the world's oceans (Longhurst & Pauly 1987), comparatively little is known about pelagic carbon and nutrient fluxes in tropical marine ecosystems.

Polar and temperate seas are characterised by pronounced seasonal fluctuations in irradiance, temperature, phytoplankton biomass and species composition, all factors which directly or indirectly influence

growth rate and production of copepods (Kiørboe & Nielsen 1994, Madsen et al. 2001). In comparison, tropical seas have minor seasonal fluctuations in irradiance and temperature. Studies so far carried out in tropical areas covering a gradient from eutrophic coastal waters (e.g. Chisholm & Roff 1990a,b, Webber & Roff 1995a, Lugomela et al. 2001) to oligotrophic deep waters (e.g. Madhupratap et al. 1996, Landry et al. 2001) suggest that tropical oceans are characterised by relatively constant phytoplankton biomass and composition. The seasonal fluctuations observed in the tropics, although relatively weak compared with higher lattitudes, are usually related to the rather variable pattern of rainfall (Chisholm & Roff 1990b), or increased storm frequency during monsoon periods and associated upwelling events (Smith 1982, Schalk 1987, Baars et al. 1990).

In the oligotrophic tropical seas, the primary producers are often dominated by picoplankton (Li et al. 1983, Lebouteiller et al. 1992, Garrison et al. 2000) and thus not directly available to the copepods. Field studies on rates of egg production by copepods have documented that female fecundity is often limited by food availability, particularly in the tropics (Kimmerer & McKinnon 1987, Kiørboe & Nielsen 1994, McKinnon 1996, Hopcroft & Roff 1998a,b, Calbet & Augustí 1999). Thus, copepod production may potentially be strongly food limited in tropical oligotrophic seas. Consequently, the microbial food web may play a significant role by making the primary producers available to higher trophic levels, thereby compensating for the very low concentrations of phytoplankton prey. Recently large multidisciplinary research programmes have been directed to investigations of the dynamics of the tropical Arabian Sea (Burkill et al. 1993, Krishnaswami & Nair 1996, Smith et al. 1998). These studies have significantly improved our knowledge and understanding of the seasonal and spatial variability of the oceanography and biogeochemical cycling of tropical oceans driven by monsonal forcing, like the Andaman Sea.

The Andaman Sea off the western coast of Thailand is a very important fishing ground providing ca. $\frac{1}{3}$ of the annual marine fish catch in Thailand (Fisheries Statistics of Thailand, Anon 1997). Knowledge about the food web that supports this fish stock is, however, very limited. Most of the research in plankton ecology in Thai waters has been focused on the coastal ecosystem (Boonruang 1985, Sündstrøm et al. 1987, Janekarn & Hylleberg 1989). Studies on copepods from Thai coastal waters have been restricted to (1) species composition and abundance (Boonruang 1985, Satapoomin 1999, Satapoomin & Pornchai 2002), and (2) seasonal and temporal variability in the community structure of copepods. Studies of copepod production are completely lacking.

The oceanography and pelagic community structure at the shelf break front in the Andaman Sea has previously only been considered by Kiørboe et al. (1991). During a transect study across the shelf break, they measured a 3-fold increase in primary production and much higher abundance of tunas, marine mammals and sea birds at the shelf break compared to the coastal and shelf areas. These observations led to the hypothesis that the shelf break was a very important site of primary and secondary production, and thus an area in which pelagic fisheries could be developed (Kiørboe et al. 1991). This hypothesis was a central part of the scientific background for the project 'Pelagic Andaman Sea structure, function and productivity with particular emphasis on an access of potential fisheries resources' under a Thai–Danish scientific co-operation program. The present investigation on community structure, biomass and productivity of the Andaman Sea copepods was part of this program, which was initiated in 1996 at Phuket Marine Biological Center.

We investigated spatial and temporal variability in biomass, community structure, production and the trophic role of the Andaman Sea copepods along transects from the coastal shallow water across the shelf to the deep oceanic areas. The emphasis was on the role of the shelf break area in the secondary production of the Andaman Sea.

MATERIALS AND METHODS

Study area. The investigation was conducted in the Andaman Sea on the western coast of Thailand during 4 cruises in 1996 and 1997. Two cruises were conducted each year representing the 2 monsoon seasons, northeast (NE) and southwest (SW). Cruises in 1996 were carried out during the periods of March 11 to 27 (NE monsoon), and August 15 to 29 (SW monsoon). Cruises in 1997 were carried out from February 11 to 27 (NE monsoon), and August 26 to 28 and September 1 to 11 (SW monsoon). These cruises will be referred to as cruises NE-96, SW-96, NE-97 and SW-97, respectively.

Sampling was carried out along transects perpendicular to the shoreline from the coast, across the shelf, to the offshore area, with approximately 12 stations on each transect (Fig. 1). The distance between stations was 5 n miles, except on the shelf break and the deeper outermost stations where the resolution was 2.5 and 10 n miles, respectively. The total number of stations visited per cruise varied due to the interference of bad weather. At all stations visited, profiles of salinity and temperature were taken and samples for phyto- and zooplankton biomass were collected, while rate
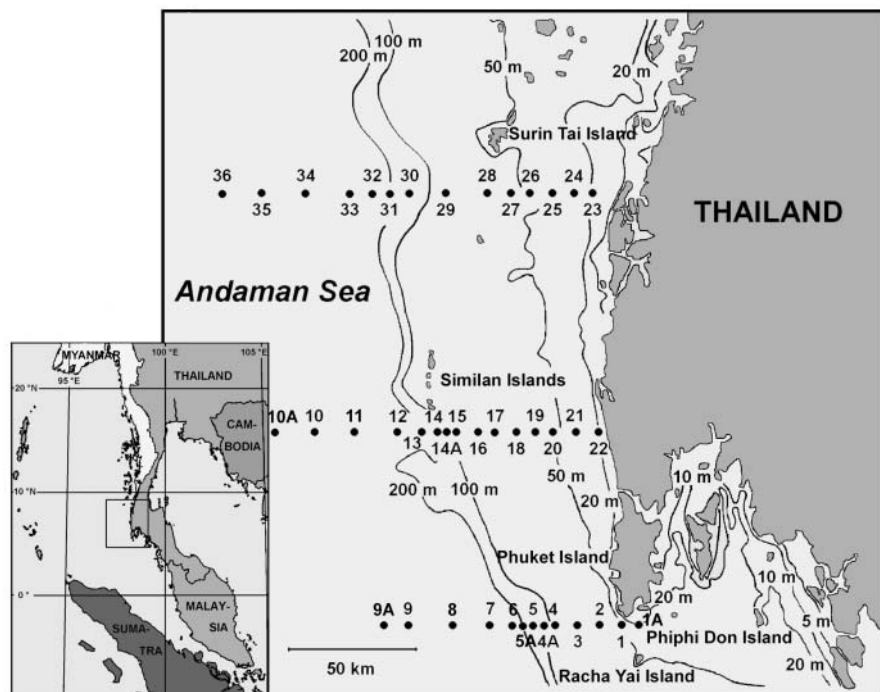
Fig. 1. Positions of stations and transects investigated during the 3 cruises in the Andaman Sea off the western coast of Thailand. The southern transect is #1, the northern is # 3

measurements were conducted with lower spatial resolution, approximately at every second station.

Detailed information on the oceanography and plankton community structure from the 2 cruises in 1996 is presented in Nielsen et al. (2004 this issue) and Munk et al. (2004 this issue). Since no experiments on copepods egg production were performed during Cruise NE-96, this paper only presents data collected on the last 3 cruises.

Hydrography. At each station, the vertical structure of the water column was characterized using a Sea-Bird SBE 25-01 Sealogger CTD equipped with a Chelsea fluorometer. At all stations, the CTD casts were repeated 5 times in a connected series from the surface to a depth of ca. 150 m at deep stations, and 5 m above sea bottom at shallow stations, in order to describe the dynamic pycnocline (for further details see Nielsen et al. 2004). The downcast sequence was averaged every 0.3 m for presentation of profiles.

Copepod food. *Total chl a:* At each station, 4 l of water were taken for the measurement of total chl *a* concentration at 5 depths covering the upper 100 m of the water column. The phytoplankton were collected on a GF/C filter by filtration. Filters were then homogenized and extracted in 90 % acetone for 6 h in darkness. Extractions were analyzed on a spectrophotometer and the total chl *a* concentration was calculated using the equation of Jeffrey & Humphrey (1975). The

relative profiles of chlorophyll fluorescence values were converted to chl *a* from a linear regression between the fluorescence (fluo) and spectrophotometric measurements of chl *a* covering all transects (chl *a* = fluo/0.6506 − 0.012, r^2 = 0.83, n = 113). Chl *a* was converted to carbon applying a general conversion factor of 54.5, or 74 or 35 for the surface and pycnocline respectively (Nielsen et al. 2004).

Fractionated chl a: On Cruise NE-97, the size distribution of phytoplankton was investigated at the surface (5 m depth) and at the depth of maximum fluorescence (FM). Fluorescence was measured in the 0.7−1, 1−5 , 5−10, 10−50 and >50 µm size fractions at all stations where copepod production was measured. Triplicate samples (280 ml) were filtered using 0.7 µm GF/F filters, 1 and 5 µm Poretics filters and 10 and 50 µm Nitex-filters. The filters were extracted in 5 ml of 95 % ethanol for 6 h and measured on a 10-AU Turner Fluorometer. The fluorescence was calibrated against a purified chl *a* standard.

Protozooplankton (ciliates and heterotrophic dinoflagellates): The focus in the present study was on ciliates and heterotrophic dinoflagellates (>10 µm); i.e. heterotrophic flagellates <10 µm were not quantified. Samples were taken from 3 depths (5 m, FM, and 100 m). Water samples were gently poured into a 300 ml bottle and fixed with 2 % Lugols (final concentration). Identification and enumeration of the organisms were done after overnight sedimentation using an Olympus CK-2 inverted microscope. Cell volumes were estimated from linear dimensions using simple volumetric formulae, and carbon biomass was calculated using a conversion factor of 12 pg C µm^{-3} (Hansen et al. 1997).

Copepod community. Samples for mesozooplankton abundance and biomass were taken by vertical net hauls with a 200 µm WP-2 and a net with 50 µm mesh. On Cruise SW-97, a submersible plankton pump (Grundfos SP16-2) equipped with a 50 µm net was used. A General Oceanic flow meter was mounted across the net mouth to measure the volume filtered. Samples were taken from bottom to surface at the shallow coastal stations or from 100 m to surface at the deeper stations. Nets were retrieved at ca. 12 m min^{-1}. To compensate for the difference in sampling gear, a net-pump inter-calibration was performed. At Stn 12, 5 replicated samples were taken from 50 m to the sur-

Table 1. Length to carbon-weight (L–W) equations applied for biomass calculation of different copepod species. Sources: (1) Satapoomin (1999a); (2) Kiørboe & Sabatini (1994); (3) Hygum et al. (2000)

Taxon	L–W regression	Source
Acartia australis	Eqn of *C. furcatus*	(1)
Acrocalanus gibber	9.66×10^{-7} L$^{2.26}$	(1)
Centropages furcatus	2.11×10^{-11} L$^{3.82}$	(1)
Euchaeta marinella	1.15×10^{-11} L$^{3.82}$	(1)
Temora discaudata	2.6×10^{-10} L$^{3.55}$	(1)
Calanoids	As *A. gibber*	(1)
Corycaeus spp.	4.98×10^{-6} L$^{1.99}$	(1)
Oithona similes	As *Oithona* spp.	(2)
Oithona spp.	9.47×10^{-7} L$^{2.16}$	(2)
Oncaea venusta	As *Oncaea* spp.	(1)
Oncaea spp.	2.51×10^{-8} L$^{2.9}$	(1)
Other cyclopoid copepods (*Sappharina* and *Copelia*)	As *Corycaeus* spp.	(1)
Harpacticoids	8.5×110^{-4} L$^{1.03}$	(1)
Nauplii	4.17×10^{-6} L$^{2.03}$	(3)

face by each set of gears and the size distribution of copepods compared.

Copepod biomass: Samples were fixed in borax buffered formalin (2% final concentration). Dependent on density, subsamples ($\frac{1}{32}$ of total) were counted until approximately 400 copepods were sorted and identified to order, genera or species level. Each category of copepods was measured (cephalothorax length), except for total length of nauplii and harpacticoids. The lengths were later converted to carbon from relevant length-weight regressions (Table 1).

Species composition: The focus of the present investigation was to compare different functional groups of copepods. Therefore, we generally separated the copepods into 4 major groups: calanoids, cyclopoids, harpacticoids and nauplii. Although *Oncaea* spp. have recently been transferred from the Cyclopidea to the order Poecilostomatoida (Ho 1991), we have presented them together. Species composition was studied, how-

ever, at higher taxonomic resolution at Stns 18, 14 and 10 on the middle transect of each cruise representing coastal, shelf front and offshore areas, respectively. Cluster analysis was applied to determine the community structure in the 3 different areas.

Patchiness test: To investigate the plankton patchiness between stations, a grid of 12 stations was laid in the vicinity of Stns 14 and 14a. Two new stations were selected between those 2 stations and 2 parallel transects were sampled on each side of the main transect, making the resolution in space only 500 m. Samples were taken from 100 m depth to surface by a Grundfos-pump equipped with a 50 µm mesh cod-end. Specimens were processed to the same level as for the routine copepod biomass samples.

Copepod production. *Egg production by free spawning species:* Copepods for the egg production experiments were collected from vertical tows starting from just below the pycnocline using the 50 and 200 µm plankton nets. On deck, the contents of the cod ends were diluted in a 25 l bucket containing surface seawater and brought directly to the laboratory. Within the next few hours, females were sorted, and 2 to 6 females were placed in each of 3 to 6 glass jars of 500 ml for each species. The females were incubated at 25°C for 6 to 10 h, after which the spawned eggs were counted and female lengths and egg diameters were measured (Table 2).

Egg production by egg carrying species: Egg production rates were measured for representatives of 3 dominant groups of egg carrying copepods: Oncaeidae, *Oncaea vensuta*; Oithonidae, *Oithona plumifera*; and Euchaetidae, *Euchaeta marinella*. Females with egg sacs were placed individually in tissue culture plates (NUNC™ Multi wells) containing 2 ml of 50 µm filtered surface water and incubated at 25 ± 1°C. The wells were inspected and temperature recorded at 3 to 6 h intervals. Hatching percentage was calculated from number of clutches hatched divided by the number of females incubated. Hatching rate was calculated from

Table 2. Size (µm), size range (µm), number of specimens (n) and carbon content (µg C ind.$^{-1}$) of female copepods and their eggs from egg production experiments

	Female				Egg			
	Length		n	Carbon content	Diameter		n	Carbon content
	Mean ± SE	Range			Mean ± SE	Range		
Acartia australis	1132 ± 2.0	900–1240	489	9.77	81 ± 0.6	75–85	19	0.039
Acrocalanus gibber	898 ± 2.1	700–1100	801	4.56	99 ± 0.6	90–110	55	0.071
Centropages furcatus	1125 ± 1.9	1000–1260	465	9.54	79 ± 0.4	75–90	55	0.036
Euchaeta marinella	1697 ± 13.0	1520–1880	240	25.01	245 ± 1.7	225–260	29	1.081
Oncaea venusta	724 ± 1.4	600–820	712	4.93	51 ± 0.8	35–60	44	0.010
Oithona similis	559 ± 1.7	460–680	220	0.81	62 ± 0.7	55–75	54	0.017
Temora discaudata	1104 ± 2.5	880–1260	630	16.50	71 ± 0.5	63–75	42	0.027

the slope of a linear regression between the incubation time and the cumulative hatching percentage. Hatching time (HT) is defined as the time required to reach 100% hatching, as predicted from these regressions.

Egg production rates of the egg carrying species were then calculated from the egg-hatching rate and the *in situ* egg:female ratio of the population (i.e. including loose sacs and females nor carrying egg sacs) from the 50 µm net samples. For *Oncaea venusta*, which carry 2 very dense egg sacs with >50 eggs sac^{-1}, it was impossible to count the eggs in the samples. We therefore determined egg number from the number of hatched nauplii. For this purpose, 24 to 48 females with

2 egg sacs were transferred individually into 2 ml of seawater in NUNC^{TM} multiwell at each station.

The egg production rates (EP; egg fem^{-1} d^{-1}) of the egg carrying species were calculated from the *in situ* ratio of egg:female ratio and hatching rate (HR):

$$EP = (egg:female) \times HR$$

Carbon-specific egg production rates (SEP) were calculated according to the equation:

$$SEP = EP \times (C_e/C_f)$$

where: C_e = egg carbon calculated from egg volume and a volume to carbon ratio of 0.14 pg C µm^{-3}

Table 3. Position, depth (m) and averaged water column temperature from surface to bottom or 100 m (mean ± SE, n) of the stations of 3 cruises in the Andaman Sea

Stn	Longitude	Depth	SW-96	NE-97	SW-97
1a	98.20	32		28.95 ± 0.01, 83	27.98 ± 0.06, 28
1	98.15	60	28.72 ± 001, 187	28.46 ± 0.06, 185	26.82 ± 0.19, 59
2	98.10	72	28.26 ± 0.06, 235	27.63 ± 0.13, 235	
3	98.05	69	28.32 ± 0.06, 218		27.33 ± 0.06, 471
4	98.00	69	28.54 ± 0.03, 118	28.03 ± 0.10, 205	
4a	97.58	133		26.23 ± 0.15, 328	26.85 ± 0.15, 101
5	97.55	172	27.00 ± 0.13, 331	25.60 ± 0.18, 330	28.38 ± 0.05, 101
5a	97.53	188			25.3 ± 0.4, 100
6	97.50	253	26.73 ± 0.16, 331	26.65 ± 0.13, 327	26.66 ± 0.27
7	97.44	300	27.56 ± 0.10, 332		
8	97.35	424	27.56 ± 0.10, 329	24.87 ± 0.16, 333	26.41 ± 0.31, 101
9	97.41	437	26.42 ± 0.14, 330		
9a	97.20	491			25.94 ± 0.28, 101
22	98.13	18	29.22 ± 0.01, 62	28.84 ± 0.03, 53	29.08 ± 0.11, 18
21	98.08	38	29.28 ± 0.02, 126	28.68 ± 0.04, 117	
20	98.03	58	29.09 ± 0.02, 186	28.06 ± 0.08, 154	28.53 ± 0.08, 52
18	97.53	68	28.35 ± 0.14, 225	26.76 ± 0.14, 225	
19	97.58	77	28.09 ± 0.14, 253	27.28 ± 1.35, 237	
17	97.48	80	27.59 ± 0.15, 256	27.50 ± 0.10, 235	27.24 ± 0.23, 77
15	97.38	87	27.21 ± 0.15, 287	25.24 ± 0.15, 287	26.66 ± 0.27, 82
16	97.43	87	27.31 ± 0.15, 279	25.31 ± 0.16, 268	26.96 ± 0.26, 78
14a	97.34	110		28.08 ± 0.07, 165	25.87 ± 0.33, 101
14	97.33	194	26.73 ± 0.14, 333	26.45 ± 0.13, 332	27.72 ± 0.12, 101
13	97.28	279	26.42 ± 0.16, 332	24.74 ± 0.15, 332	26.72 ± 0.26, 101
12	97.23	355	28.10 ± 0.06, 331	25.57 ± 0.15, 332	
11	97.13	413	28.40 ± 0.03, 251	26.43 ± 0.13, 332	26.12 ± 0.30, 101
10	97.03	460	27.37 ± 0.10, 333	25.31 ± 0.15, 323	
10a	96.52	483		26.42 ± 0.12, 323	27.10 ± 0.21, 101
23	98.10	23		28.57 ± 0.01, 67	
24	98.06	35	28.89 ± 0.001, 128	28.06 ± 0.05, 104	
25	98.01	46		27.65 ± 0.07, 138	
26	97.56	56	28.98 ± 0.003, 52	26.62 ± 0.13, 181	
27	97.51	68		26.96 ± 0.12, 208	
28	97.46	79		25.42 ± 0.15, 248	
29	97.36	85		25.55 ± 0.16, 266	
30	97.25	163		25.10 ± 0.13, 330	
31	97.20	203		22.75 ± 0.24, 330	
32	97.16	250		23.81 ± 0.20, 329	
33	97.10	280		25.34 ± 0.15, 330	
34	97.01	380		27.15 ± 0.06, 326	
35	96.51	380		25.57 ± 0.15, 326	
36	96.41	400		27.28 ± 0.07, 300	

(Huntley & Lopez 1992) and C_f = female carbon biomass estimated from length-carbon regressions (Table 1).

Copepod production was then calculated by multiplying biomass with SEP, assuming that SEP of adult females equals the growth rates of the juvenile stages (Berggreen et al. 1988). For those species in which egg production was not measured, the average SEP for the relevant taxonomical group was applied. In the case of nauplii, the average SEP of all groups was used. The egg production rates of all species investigated were recalculated to *in situ* temperature conditions using the mean temperature from surface to bottom or 100 m at each station (Table 3), and a Q_{10} value of 2.8 (Hansen et al. 1997).

Depth integration. All biological data are presented per m^2. The biomass of the discrete samples of micro-protozooplankton (3 to 5 depths per station) and chl *a* fluorescence (50 to 200 measurements) were transformed by trapezoidal integration to 100 m, or the bottom at the shallower stations. The copepod communities were integrated during sampling from the bottom at the shallower and the upper 100 m at the off-shelf station. The grazing and production rates were corrected according to average temperature in the water column sampled using a Q_{10} of 2.8 (Hansen et al. 1997).

Data analysis. Correlations were calculated based on the raw data set, while 1-way ANOVA and cluster analysis were based on log $(x+1)$ transformed data. In general, a significance level of 5% was used.
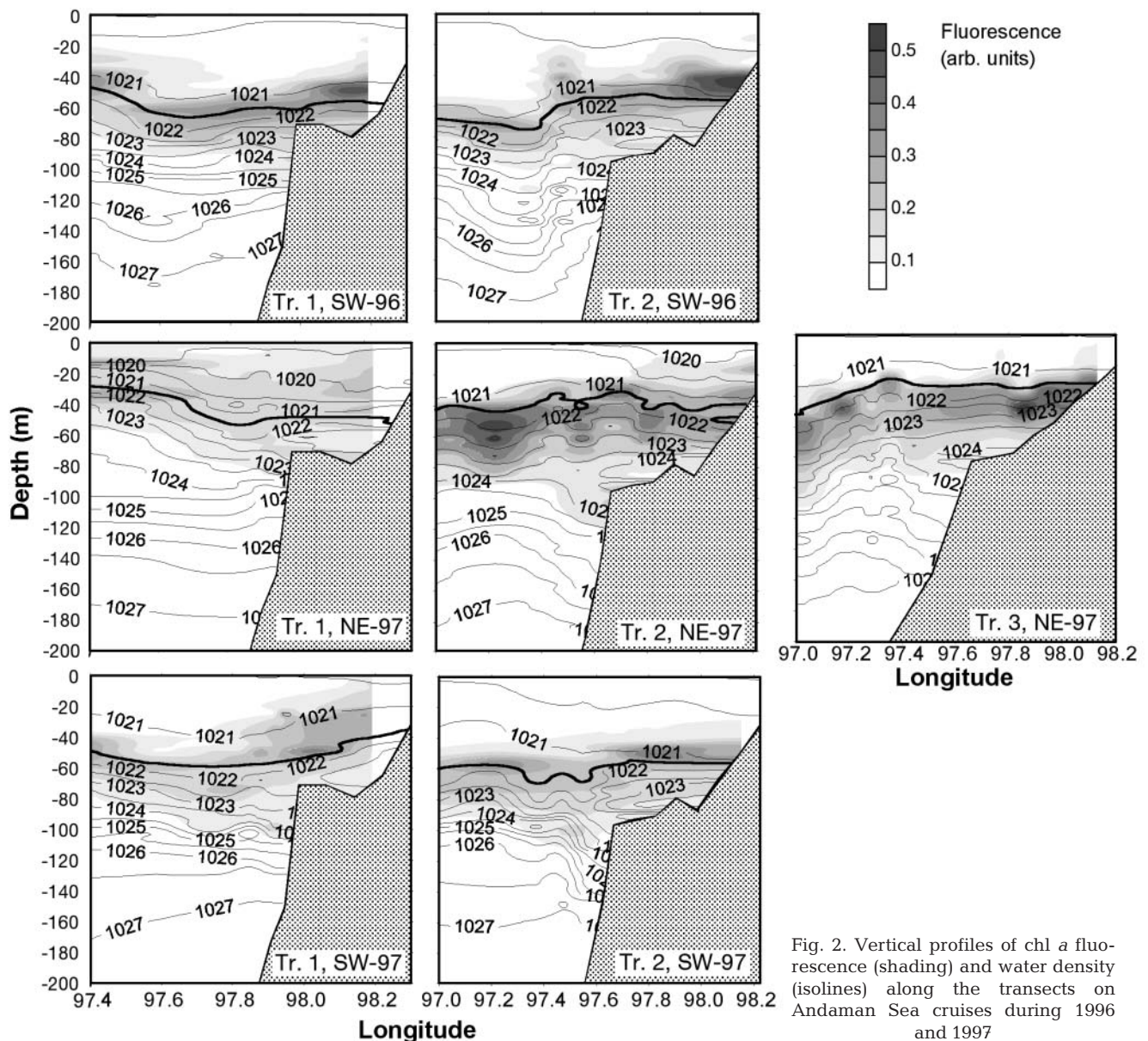

Fig. 2. Vertical profiles of chl *a* fluorescence (shading) and water density (isolines) along the transects on Andaman Sea cruises during 1996 and 1997
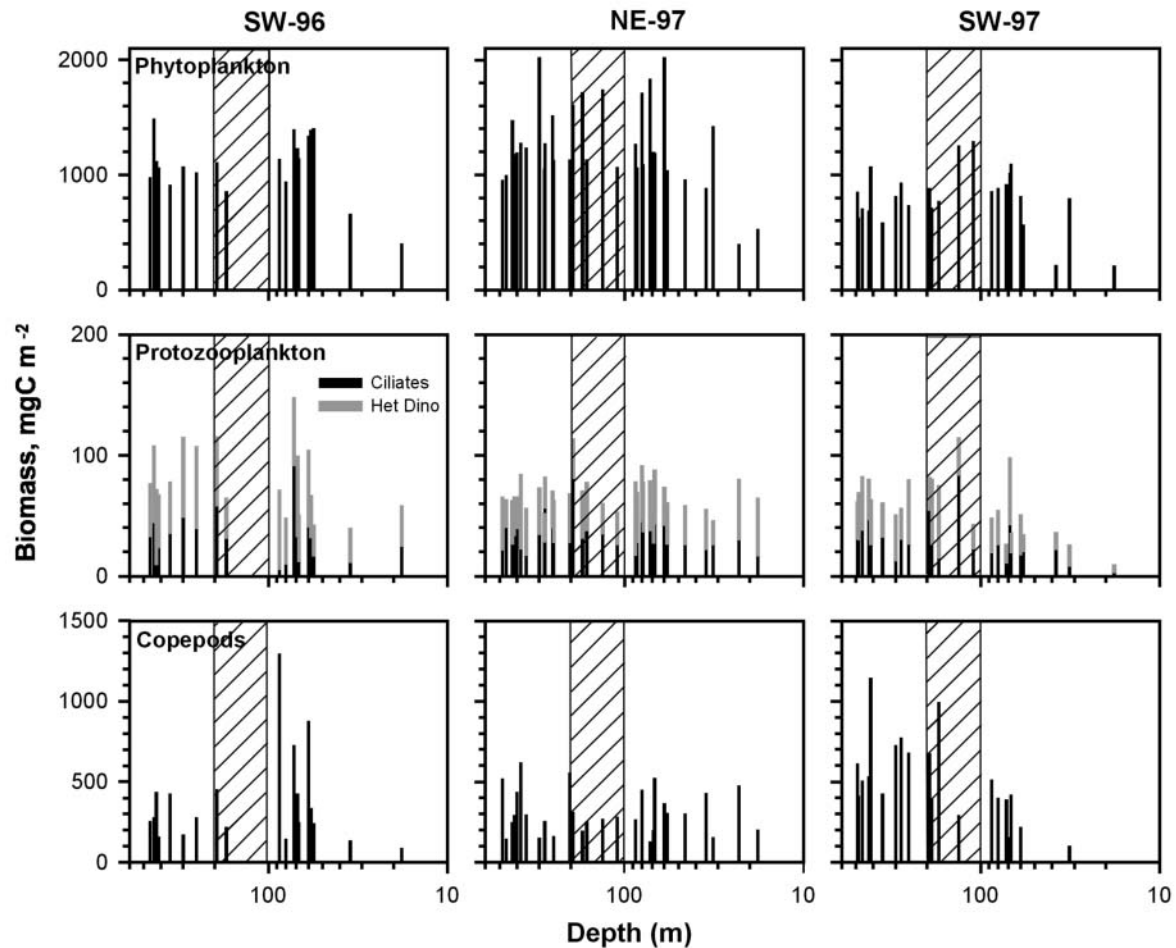
Fig. 3. Integrated biomass (mg C m^{-2}) of phytoplankton, microprotozooplankton (ciliates and heterotrophic dinoflagellate) and total copepods in the upper 100 m during Andaman Sea cruises during 1996 and 1997. Hatched area indicates the upper shelf break at 100 to 200 m

RESULTS

Summary of hydrography

The water column at the coastal stations on the shore side of the mid-shelf front was vertically mixed, while the deeper stations were strongly stratified (Fig. 2). The surface temperature ranged from 28 to 30°C, and the salinity ranged from 31.3 and 33.6 psu. The pycnocline (here defined as the isopycnal of 1021.5 kg m^{-3}) was located between 30 and 80 m. The depth of the upper mixed layer changed seasonally. During the NE monsoon the pycnocline was located at 40 m, while the increased wind stress during the SW monsoon eroded the pycnocline down to 60 m. Below the pycnocline, water temperature decreased to 14°C and salinity increased to 34.8 psu. Since no differences between transects were observed, we will focus on seasonal and inter-annual variations.

Phytoplankton

A subsurface fluorescence maximum occurred whenever a pycnocline was present. The fluorescence maximum covered the depth strata 40 to 100 m, with peak values located in the pycnocline. The surface layer was depleted in nitrogen (Nielsen et al. 2004). During the NE monsoon, the highest fluorescence values were observed at ca. 40 m in all transects, while the highest fluorescence during SW monsoon was located deeper, according to the mixing of the surface layer down to 60–70 m (Fig. 2). Chl a concentrations in the surface water (5 m) averaged 0.19 ± 0.02 µg l^{-1} (or 9.8 ± 0.9 µg C l^{-1}) (n = 82) for all cruises, and averaged 0.40 ± 0.02 µg l^{-1} (or 20.1 ± 0.9 µg C l^{-1}) (n = 82) in the FM. Depth-integrated phytoplankton biomass (calculated from the integrated chlorophyll value) ranged from 203 to 2011 mg C m^{-2}, averaging 1052 ± 39 mg C m^{-2} (n = 82) (Fig. 3). There was no statistical difference

in phytoplankton biomass between season (Cruise SW-96 vs NE-97, p > 0.1) or year (SW-96 vs SW-97, p > 0.1).

Fractionated chl *a* was only measured on Cruise NE-97. Small cells (<10 µm) dominated the phytoplankton community, contributing 68.0 ± 3.4% at 5 m and 89.4 ± 1.5% at FM. The lower contribution of small phytoplankton in the 5 m samples was caused by the occurrence of the large (>50 µm) colonial cyanobacteria *Trichodesmium* spp., in the surface water (Fig. 4).

Protozooplankton

The protozooplankton was dominated by heterotrophic dinoflagellates and ciliates. The 2 groups contributed equally to biomass, which averaged 1.1 ± 0.08 µg C l^{-1} in surface water (n = 82 range 0.2 to 5.6 µg C l^{-1}) and 1.1 ± 0.08 µg C l^{-1} at the FM (n = 81 range 0.2 to 5.6 µg C l^{-1}). Depth-integrated values for total ciliates and dinoflagellates ranged from 8.4 to 146.9 mg C m^{-2}, with a mean of 66.9 ± 2.6 mg C m^{-2}, n = 82 (Fig 3). Comparison of the integrated protozooplankton biomass showed no inter-annual difference (p > 0.2). There was also no difference between Cruises SW-96 and NE-97, but biomass for Cruise NE-97 was significantly higher than for Cruise SW-97 in the same year (p < 0.05)
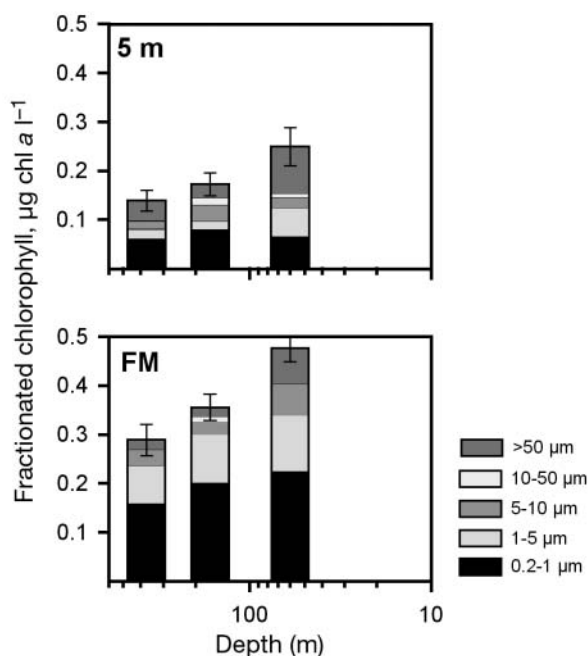

Fig. 4. Fractionated chl *a* (µg chl *a* l^{-1}) at 2 depths in the coastal, upper shelf break and the offshore stations investigated during Cruise NE-97
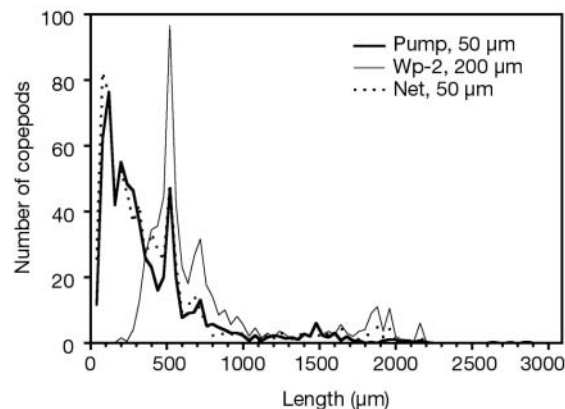

Fig. 5. Copepod size-spectra from different sampling gear (plankton net and submersible pump) and mesh sizes (50 and 200 µm) at Stn 12 on Cruise SW-97

Gear calibration

The 50 µm plankton net and the pump gave the same size distribution of the copepod community (Fig. 5). However, the 200 µm net severely undersampled specimens smaller than 400 µm total length. The copepod biomass (mg C m^{-3}) estimated from 50 µm tows was correlated with copepod biomass estimated using the pump with a 50 µm cod-end; r^2 = 0.69. However, the net tows caught 3.6 times more biomass than the pump. From the calibration, the pump samples were corrected according to the factor obtained from the regression between the pump and the 50 µm net collections. The size spectra of copepods collected by the 50 µm net covered a range from small nauplii (40 µm) to the adult stages of most copepod species, while the 200 µm net missed most of the naupliar stages (Fig. 5). Because of our interest in small taxa, only samples taken with the 50 µm screen, plankton net and pump are considered in the following sections.

Spatial variation

Patchiness test

The variability of sampling between stations was evaluated for copepod biomass data from 12 samples at the sub-stations. The results showed no difference among the 3 replicates or among the sub-stations (p > 0.5). Because the test was performed in the most hydrodynamically variable area (at the shelf break), the results suggest that a higher spatial resolution would not provide a different pattern than the observed one.

Abundance

The zooplankton community was dominated by copepods. Other important groups were appendicularians, thaliacean salps and chaetognaths. Among the copepods, no statistical differences were found between coastal and offshore areas during Cruises SW-96 and NE-97 (p > 0.1). However, the total copepod abundance during Cruise SW-97 was higher in the coastal area compared to the shelf and offshore areas (p < 0.05) due to the higher abundance of cyclopoid copepods.

On the middle transect of each cruise, where the copepod species composition was analyzed to a higher taxonomic level (Table 4) and subjected to cluster analysis, no distinct assemblages were found in the 3 defined areas on any of the cruises (Fig. 6). However, the dendrogram showed a clear separation of Cruise SW-97 from the SW-96 and NE-97 cruises.

Due to the general similarity in species composition throughout the study area during this investigation, the copepods were split into 4 major groups (calanoids, cyclopoids, here including the poecilostomatoids, har-
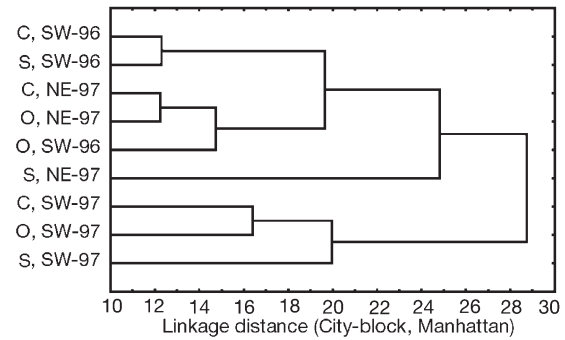

Fig. 6. Dendrogram from dissimilarity matrix (city-block [Manhattan] distance) of copepod abundance data (log [x+1] transformed) with unweighted pair-group average linkage. (C = coastal, S = shelf, O = offshore)

pacticoids and nauplii) for further analysis (Fig. 7, Table 5). Nauplii were the most abundant group on all cruises and transects (47.3 ± 1.8%, mean ± SE, n = 74) followed by calanoids and cyclopoids (22.6 ± 0.9 and 25.5 ± 1.0%, respectively). Harpacticoids made up the smallest fraction (4.6 ± 0.4%).

Table 4. Abundance (ind. m^{-2}; mean ± SE) of copepods at 3 different localities along the middle transect from 3 cruises on the Andaman Sea

| Taxa	Coastal (Stn 18)	Shelf (Stn 14)	Offshore (Stn 10)
Acartia spp.	308 ± 142	7322 ± 458	245 ± 143
Acrocalanus spp.	952 ± 487	2486 ± 1125	755 ± 285
Calanopia elliptica	109 ± 33	221 ± 148	60 ± 4
Calocalanus pavo	66 ± 66	107 ± 107	164 ± 42
Calocalanus spp.	185 ± 95	693 ± 376	76 ± 47
Candacia spp.	233 ± 150	289 ± 180	230 ± 81
Canthocalanus pauper	275 ± 71	414 ± 36	205 ± 90
Centropages sp.	0	107 ± 107	9 ± 9
Centropges furcatus	277 ± 144	245 ± 125	104 ± 104
Copilia spp.	39 ± 39	182 ± 151	120 ± 28
Corycaeus spp.	5356 ± 3421	8512 ± 2445	7085 ± 3584
Cyclopoid (juvenile)	0	4971 ± 4971	0
Diaixis spp.	5 ± 5	3581 ± 3306	53 ± 40
Eucalanus spp.	392.4 ± 131.6	1582 ± 1582	499 ± 100
Euchaeta spp.	433 ± 104	1762 ± 295	380 ± 157
Farranula gibbula	267 ± 16	826 ± 241	1109 ± 344
Harpacticoid sp. (juvenile)	8225 ± 8225	0	1803 ± 1803
Harpacticoid sp.	113 ± 106	14 ± 14	686 ± 647
Labidocera laevidentata	5 ± 5	0	0
Macrosetella sp.	413 ± 200	7224 ± 7034	1502 ± 1295
Metacalanus aurivilli	207 ± 103	227 ± 227	56 ± 30
Microsetella sp.	6028 ± 4310	34455 ± 31208	4400 ± 2277
Oithona spp.	19908 ± 11983	23653 ± 15029	22787 ± 16133
Oncaea spp.	7167 ± 1448	33081 ± 21818	21131 ± 10741
Other calanoid	15580 ± 7861	92640 ± 44574	19323 ± 7351
Pontellina spp.	10 ± 10	83 ± 43	66 ± 36
Pontellopsis yamadae	0	7 ± 7	0
Sapphirina	98 ± 98	13 ± 12	200 ± 73
Scolecthricella longispinosa	42 ± 21	537 ± 457	171 ± 57
Temora spp.	113 ± 76	331 ± 174	47 ± 25
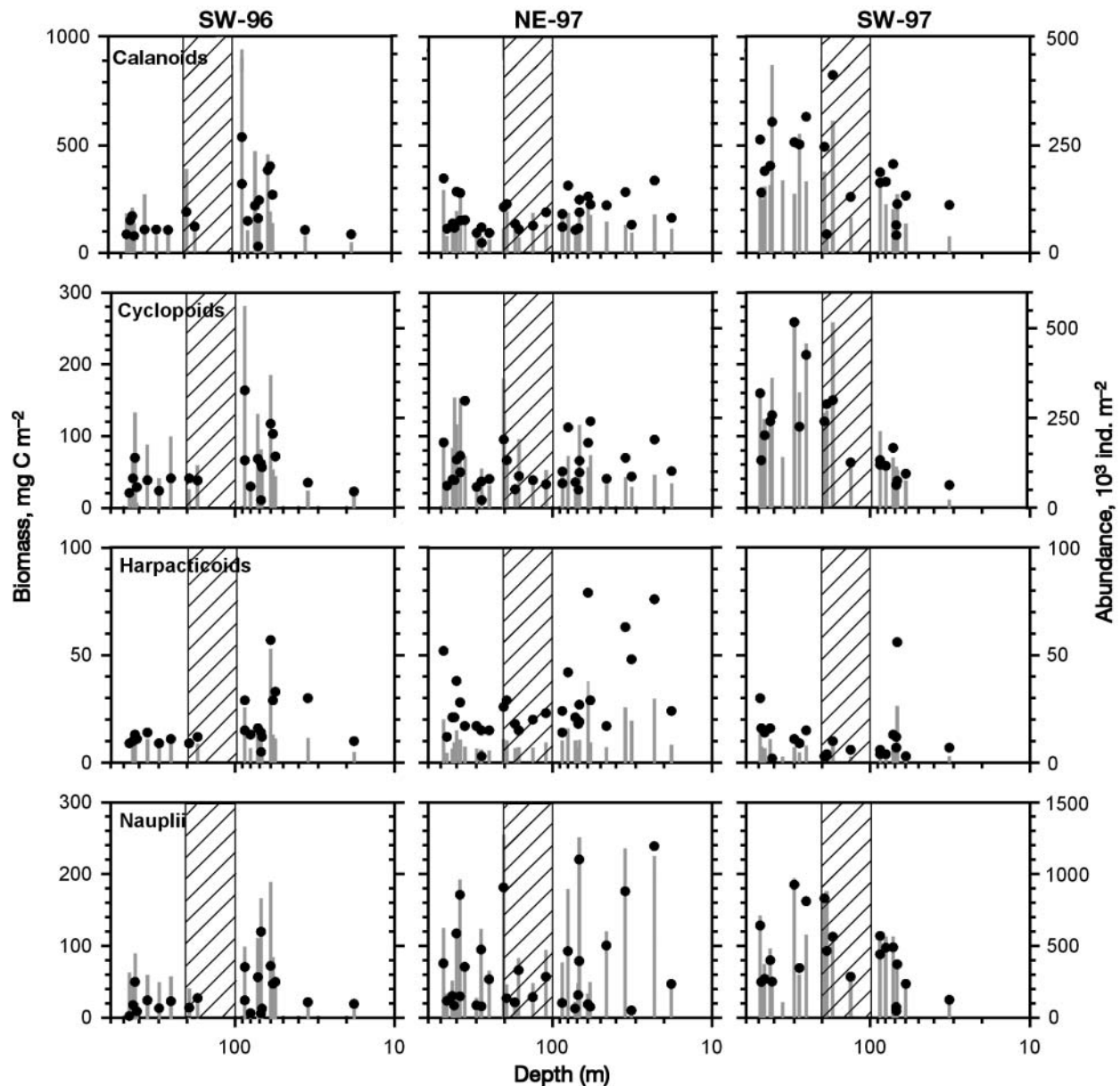
Fig. 7. Biomass (bars, left axis; mg C m^{-2}) and abundance (dots, right axis; # m^{-2}) for 4 major copepod groups on Andaman Sea cruises during 1996 and 1997. Hatched area indicates the upper shelf break at 100 to 200 m

Table 5. Abundance (10^3 ind. m^{-2}; mean ± SE) of major copepod groups from all cruises and transects in the Andaman Sea

	SW-96				NE-97				SW-97		
	1 (n = 9)	2 (n = 10)	3 (n = 2)	All (n = 21)	1 (n = 8)	2 (n = 13)	3 (n = 11)	All (n = 32)	1 (n = 12)	2 (n = 9)	All (n = 21)
Nauplii	213 ± 60	114 ± 33	178 ± 71	162 ± 32	105 ± 14	214 ± 39	658 ± 105	339 ± 57	421 ± 82	424 ± 63	422 ± 53
Calanoids	80 ± 16	110 ± 25	94 ± 41	96 ± 14	69 ± 9	91 ± 11	106 ± 13	91 ± 7	182 ± 33	196 ± 20	188 ± 21
Cyclopoids	104 ± 21	114 ± 28	106 ± 36	109 ± 16	82 ± 15	128 ± 23	123 ± 13	115 ± 11	223 ± 44	167 ± 22	199 ± 27
Harpacticoids	16 ± 5	15 ± 2	31 ± 1	17 ± 3	30 ± 8	24 ± 3	31 ± 6	28 ± 3	11 ± 2	13 ± 6	12 ± 3
Total	414 ± 92	353 ± 86	410 ± 150	385 ± 56	286 ± 32	458 ± 65	917 ± 130	573 ± 69	837 ± 152	799 ± 74	820 ± 91

Biomass

Copepod biomass ranged from 80 to 1300 mg C m^{-2}, with an average of 381 ± 28 mg C m^{-2}. The average biomasses from Cruises SW-96, NE-97 and SW-97 were 366 ± 65, 310 ± 25, and 493 ± 56 mg C m^{-2}, respectively. No distinct peaks or patterns could be observed in any specific areas on the transects (Fig. 3).

The calanoids made up to half of the total copepod biomass, 54.1 ± 1.6% (mean ± SE, n = 75), while the cyclopoid and poecilostomatoids contributed less, 21.4 ± 1.1%. The nauplii (of all copepod species) contributed 21.6 ± 1.4% of the total biomass, and harpacticoid copepods accounted for only 2.9 ± 0.3%. The diversity of the calanoid copepods was very high, with more than 100 species. The Cyclopoids primarily belonged to *Oithona*, poecilostomatoids were dominated by *Oncaea* and *Corycaeus*, and the harpacticoids belonged to 2 genera, *Microsetella* and *Macrosetella*.

EP and SEP

Despite the very high diversity of copepods it was possible to find 7 species that were present at all stations visited (Table 6). Four were broadcast spawners (*Acartia australis*, *Acrocalanus gibber*, *Centropages furcatus* and *Temora discaudata*) and 3 were egg-carriers (the cyclopoid *Oithona plumifera*, the poecilostomatoid *Oncaea venusta*, and the calanoid *Euchaeta marinella*).

Free-spawning species

The egg production of the selected species varied along transects and between cruises (Fig. 8, Table 6). *Temora discaudata* had the highest EP rate (35.9 ± 2.0 egg fem^{-1} d^{-1}), followed by *Acrocalanus gibber*

(8.8 ± 0.6 egg fem^{-1} d^{-1}), *Centropages furcatus* (7.7 ± 0.8 egg fem^{-1} d^{-1}), and *Acartia australis* (1.8 ± 0.2 egg fem^{-1} d^{-1}, Table 6). *A. gibber* had the highest SEP (0.14 ± 0.02, n = 61), followed by *T. discaudata* (0.08 ± 0.02, n = 58), *C. furcatus* (0.03 ± 0.01, n = 61) and *A. australis* (0.01 ± 0.002, n = 60) (Fig. 9. In general, no patterns in egg production were observed along a transect (p > 0.1). However, *A. australis* was an exception during Cruise NE-97 (coastal > shelf > offshore, p < 0.01). Since the egg production experiments were conducted along the transects, the incubations were started at different times of the day, i.e. from 09:00 to 18:00 h. The potential influence of diel cycles on EP rates was tested by comparing EP in relation to the mid-time of the experiment. The experiments were divided into the following 3 time groups: 12:00 to 14:00, 15:00 to 18:00 and 18:00 to 21:00 h. In general, no significant difference was observed in the EP rate in relation to time of the day, except for *Acrocalanus*, where production was significantly higher around dusk 18:00 to 21:00 (p < 0.001). Another potential source of variability in egg production could be egg cannibalism; However, the number of females in the incubation bottles (1 to 6) and the measured egg production rate were uncorrelated, indicating that egg predation was insignificant.

Egg carrying species

Hatching rate was determined routinely for *Oncaea venusta* at all stations. For *Oithona plumifera* and the *Euchaeta marinella*, most females lost their egg sacs in the net, and only a few experiments were conducted (Table 7). Because of the limited numbers of hatching experiments for *O. plumifera* and *E. marinella*, their mean values were used in the SEP calculations for all stations. The daily egg production rate of the egg-carrying species ranged from 2.4 ± 0.2 for *Oithona* to 3.2 ± 0.3 for *Euchaeta*, to 11.5 ± 0.9 for *Oncaea*

Table 6. Mean egg production rates ± SE (egg fem^{-1} d^{-1}) of selected copepod species during 3 cruises in 1996–1997. Rate range and number of experiments (n) are given in parentheses

|	SW-96			NE-97			SW-97			All cruises		
	Mean ± SE	Range	n	Mean ± SE	Range	n	Mean ± SE	Range	n	Mean ± SE	Range	n
Acartia australis	2.1 ± 0.3	0–10.7	85	1.8 ± 0.3	0–19.3	145	1.3 ± 0.7	0–36.9	63	1.8 ± 0.2	0–36.9	293
Acrocalanus gibber	8.9 ± 1.0	0–28.3	66	10.9 ± 1.0	0–61.9	142	5.4 ± 0.9	0–50.8	93	8.8 ± 0.6	0–61.9	301
Centropages furcatus	10.4 ± 2.3	0–54.7	46	8.3 ± 1.1	0–80.3	131	5.4 ± 1.2	0–47.8	85	7.7 ± 0.8	0–80.3	262
Euchaeta marinella	4.2 ± 1.0	0.9–11.1	10	2.3 ± 0.3	0.5–4.9	22	3.7 ± 0.6	0.1–10.5	22	3.2 ± 0.3	0.1–11.1	54
Oncaea venusta	9.0 ± 1.0	4.0–17.7	18	15.8 ± 1.5	4.5–38.1	32	7.1 ± 0.9	0.6–14.3	22	11.5 ± 0.9	0.6–38.1	72
Oithona plumifera	3.1 ± 0.4	0.9–9.0	21	2.7 ± 0.4	0.3–11.2	32	1.4 ± 0.2	0.2–3.6	22	2.4 ± 0.2	0.2–11.2	76
Temora discaudata	32.6 ± 4.1	0–137.3	62	42.5 ± 2.8	0–195.3	139	23.2 ± 3.1	0–174.4	78	34.9 ± 2.0	0–195.3	279
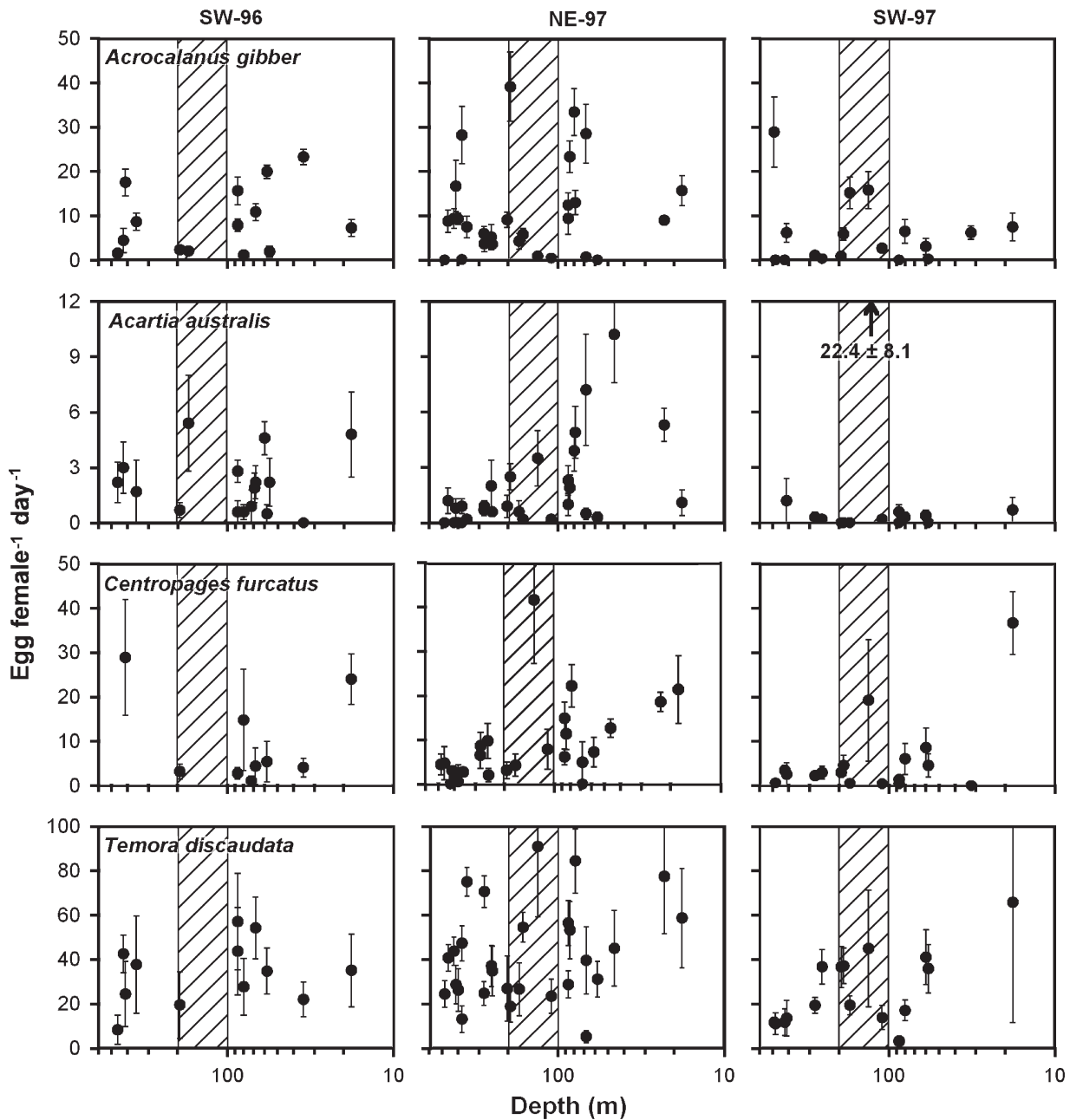
Fig. 8. Egg production rates of 4 broadcasting calanoid copepods (egg fem^{-1} d^{-1}) on Andaman Sea cruises in 1996 and 1997. Hatched area indicates the upper shelf break at 100 to 200 m

Table 7. Hatching rates (HR) of the 3 egg carrying species at 25°C. n: number of experiments

	HR (% d^{-1})		
	Mean ± SE	Range	n
Euchaeta marinella	49.1 ± 2.6	34.7–57.7	8
Oncaea venusta	23.4 ± 0.8	17.5–39.9	45
Oithona plumifera	49.2 ± 1.7	46.4–54.2	4

(Table 6, Fig. 10). *Euchaeta* had the highest SEP (0.15 ± 0.02, n = 54), followed by *Oithona* (0.05 ± 0.01, n = 75), and *Oncaea* (0.02 ± 0.002, n = 72) (Fig. 11). In general, there was no difference in EP for the 3 egg carrying species among localities (p > 0.05, Fig. 9, Table 6), except for *O. venusta* during Cruise NE-97. On this cruise, *O. venusta* at the coastal stations had a higher EP than the females from the shelf and offshore areas (p < 0.05).

Productivity

Copepod productivity ranged from 2 to 70 mg C m^{-2} d^{-1} (Fig. 12, Table 8). Highest production was found at the shelf break front region on Cruises SW-96 and NE-97, while Cruise SW-97 had highest productivity towards the outermost stations. There were, however, no significant differences between localities ($p > 0.1$) for any cruise. Locality differences could only be seen when data from all cruises were pooled, showing higher production for harpacticoids at the coastal stations, compared to shelf and offshore areas ($p < 0.05$).

Inter-annual variation

Data on copepod abundance, biomass and production between the 2 cruises during the SW-monsoon period (Cruises SW-96 and SW-97) were compared using the *F*-test in 1-way ANOVA. Data from all transects of each cruise were pooled in order to achieve a larger data set.

Abundance and biomass

The 2 cruises showed inter-annual differences for abundance in all major groups of copepods. Total
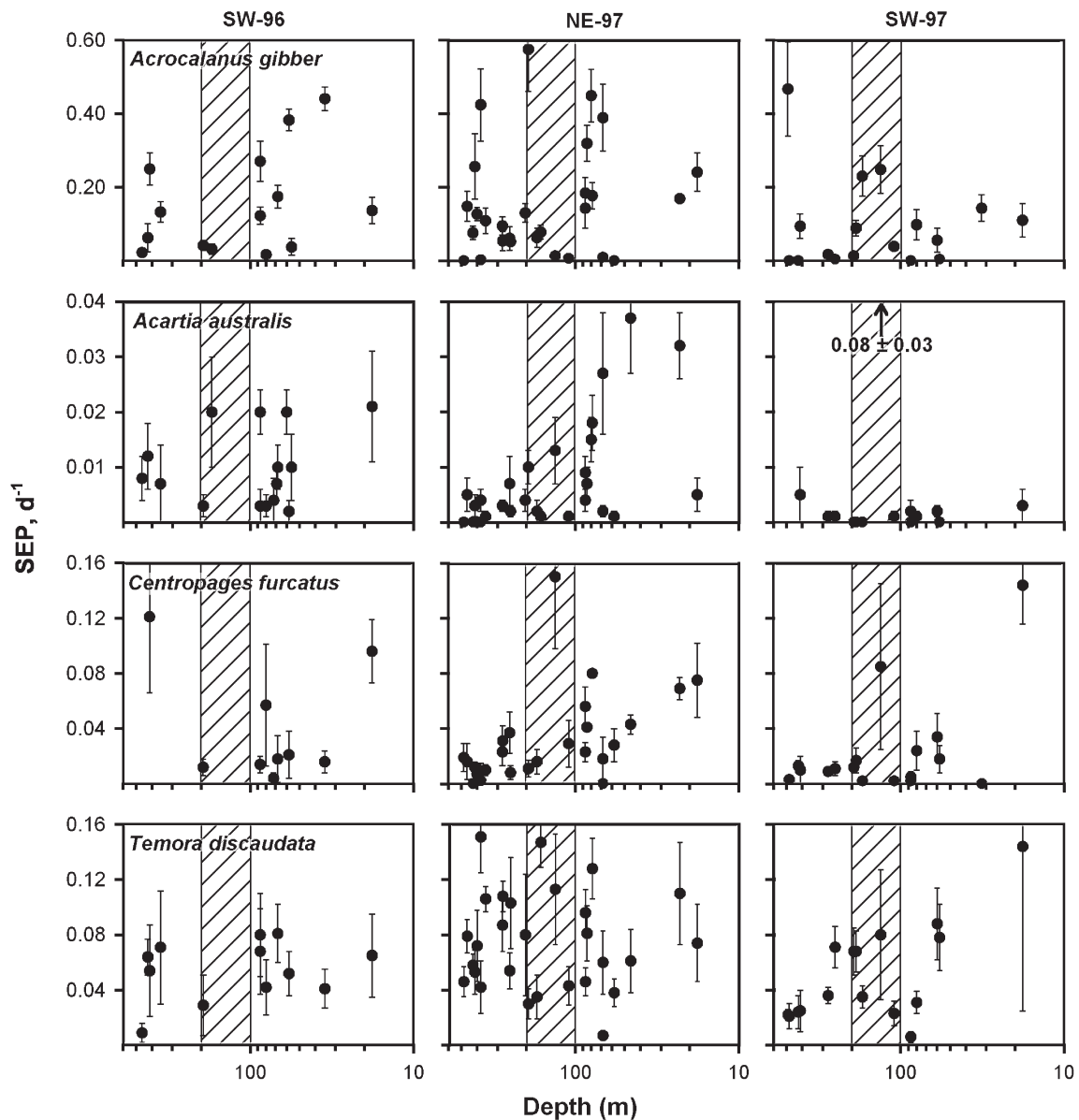

Fig. 9. Carbon-specific egg production rate (SEP, d^{-1}) of the 4 broadcasting calanoid copepods on Andaman Sea cruises during 1996 and 1997. Hatched area indicates the upper shelf break at 100 to 200 m
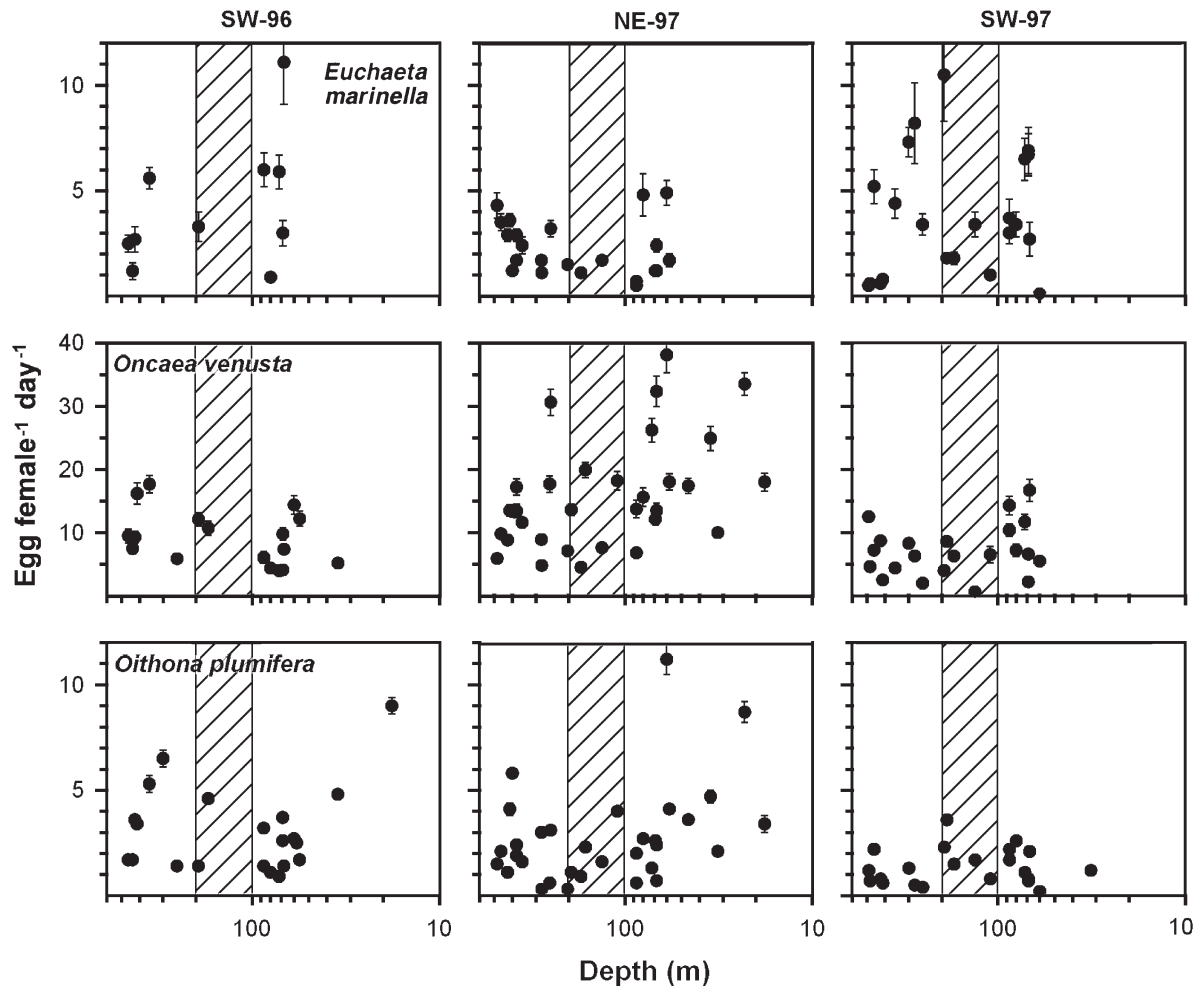
Fig. 10. Egg production rates of 3 egg carrying copepods (egg fem^{-1} d^{-1}) on Andaman Sea cruises in 1996 and 1997. Hatched area indicates the upper shelf break at 100 to 200 m

copepods abundance was significantly higher on Cruise SW-97 (p < 0.001). At the major group level, only harpacticoids had a higher abundance in 1996 (p < 0.05), while the other groups had a higher abundance in 1997 (nauplii, p < 0.001; cyclopoids, p < 0.01; calanoids, p < 0.001). Total copepod biomass displayed no inter-annual differences (p > 0.7), but the cyclopoids had significantly higher biomass in 1997 compared to 1996 (p < 0.05).

Egg production and productivity

Generally, no EP differences were found for copepod species between the SW monsoon cruises of 1996 and 1997 (Table 6). The exceptions were higher EP for *Acartia australis* (p < 0.05) *and Oithona plumifera* (p < 0.001) in 1996 and higher SEP for *Centropages furca-*

tus (p < 0.05) and *O. plumifera* (p < 0.001) in 1996. There were no differences between years for total copepod production or production of individual groups, except higher production of harpacticoids (p < 0.001) in 1996 compared to 1997.

Seasonal variation

Data from Cruise SW-96 were selected to represent the SW monsoon, based on the same type of sampling gear employed during Cruises SW-96 and NE-97. Only minor differences were observed between the 2 seasons. The only significant differences were: (1) higher abundances of nauplii (p < 0.05); harpacticoids (p < 0.0001) and total copepods (p < 0.05) during the NE monsoon and (2) higher EP and SEP for *Oncaea venusta* during the NE monsoon (p < 0.001).

Table 8. Copepod productivity calculated from the carbon-specific egg production rates (SEP; mg C m^{-2} d^{-1}), contribution to total production (percentage of total) and productivity:biomass (P:B) ratio averaged for 3 cruises in the Andaman Sea

|		SW-96	NE-97	SW-97	All cruises
Calanoid	Productivity	17.3 ± 3.6	10.5 ± 1.2	19.4 ± 3.2	15.1 ± 1.5
	Percentage of total	70.4 ± 14.6	52.0 ± 5.9	72.0 ± 12.0	64.3 ± 6.5
	P:B	0.08 ± 0.01	0.08 ± 0.01	0.08 ± 0.01	0.08 ± 0.004
Cyclopoid	Productivity	2.7 ± 0.5	2.7 ± 0.4	2.0 ± 0.3	2.5 ± 0.2
	Percentage of total	10.8 ± 2.0	13.4 ± 1.9	7.4 ± 1.1	10.6 ± 1.0
	P:B	0.05 ± 0.01	0.04 ± 0.004	0.02 ± 0.01	0.03 ± 0.003
Harpacticoid	Productivity	0.6 ± 0.1	0.9 ± 0.3	0.2 ± 0.05	0.6 ± 0.1
	Percentage of total	2.6 ± 0.6	4.3 ± 1.4	0.6 ± 0.2	2.5 ± 0.5
	P:B	0.06 ± 0.01	0.05 ± 0.01	0.03 ± 0.004	0.05 ± 0.01
Nauplii	Productivity	4.0 ± 0.7	6.1 ± 1.1	5.4 ± 1.3	5.3 ± 0.7
	Percentage of total	16.2 ± 3.0	30.3 ± 5.7	20.0 ± 5.0	22.6 ± 2.8
	P:B	0.07 ± 0.01	0.07 ± 0.004	0.06 ± 0.01	0.06 ± 0.003
Total	Productivity	24.6 ± 4.4	20.1 ± 2.3	26.9 ± 4.5	23.4 ± 2.1
	Percentage of total	100	100	100	100
	P:B	0.07 ± 0.01	0.06 ± 0.004	0.06 ± 0.01	0.064 ± 0.003
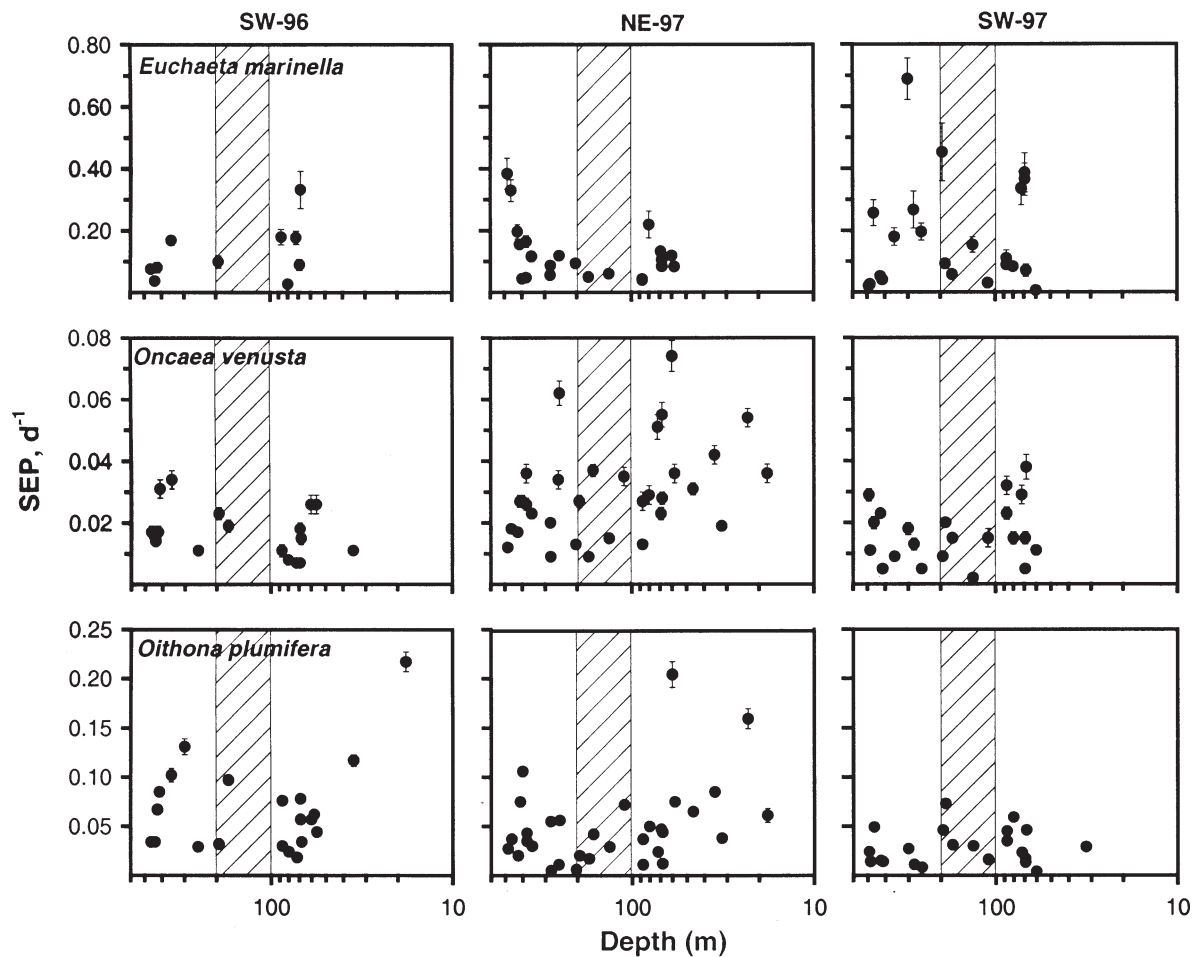
Fig. 11. Carbon-specific egg production rate (SEP, d^{-1}) of the 3 egg carrying copepods on Andaman Sea cruises during 1996 and 1997. Hatched area indicates the upper shelf break at 100 to 200 m
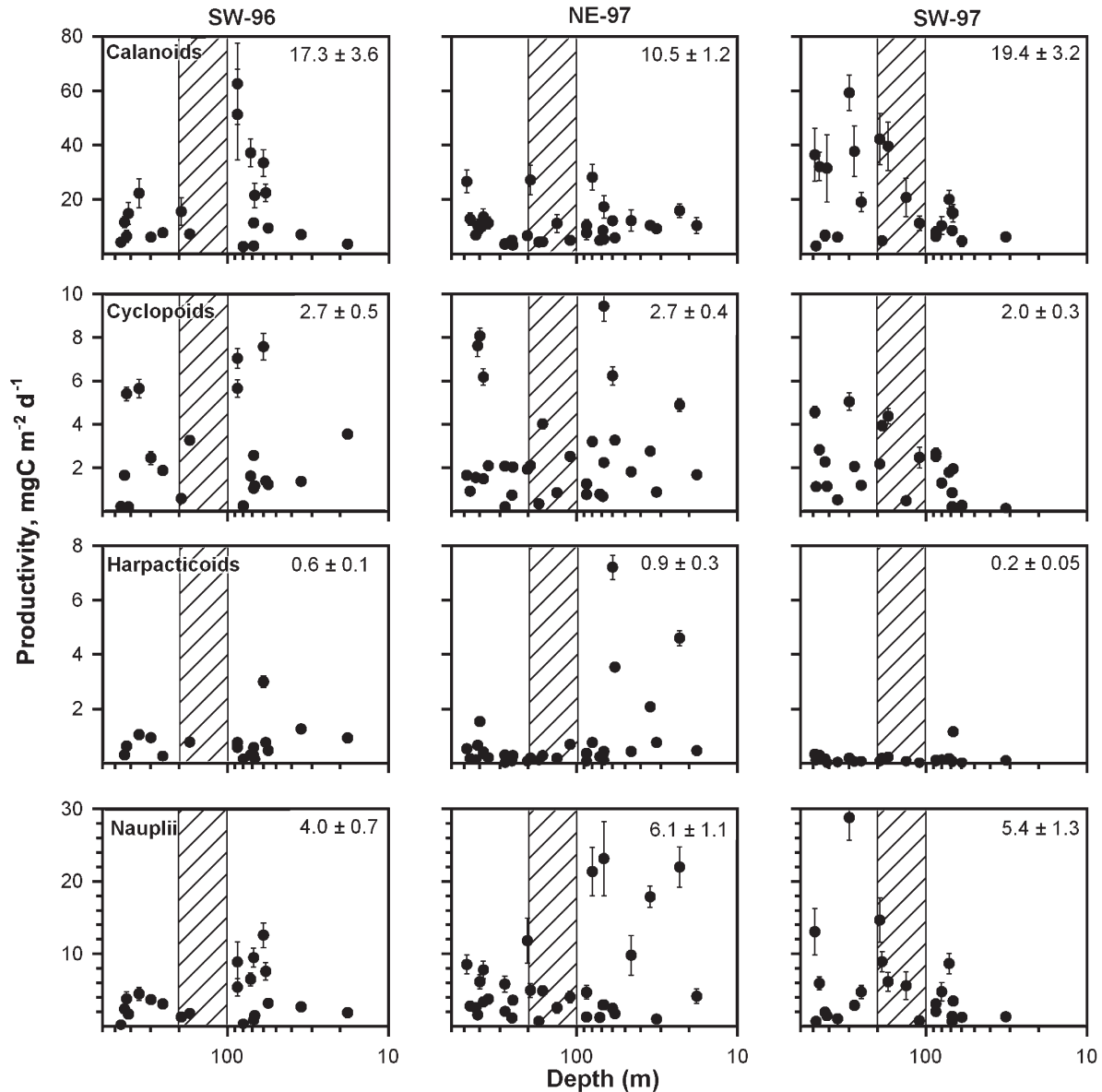
Fig. 12. Copepod productivity (mg C m^{-2} d^{-1}) on Andaman Sea cruises during 1996 and 1997. Hatched area indicates the upper shelf break at 100 to 200

Correlation between SEP and food availability

Correlations of SEP among different copepod species were low (Table 9). *Oithona plumifera* and *Oncaea venusta* were the most correlated (p < 0.001, n = 71), followed by *Centropages furcatus* and *Acartia australis* (p < 0.01, n = 57), and *C. furcatus* and *O. plumifera* (p < 0.05, n = 57). Specific egg production of *A. australis* was also significantly correlated to SEP of *Acrocalanus gibber* (p < 0.05, n = 57).

Correlations between SEPs of these 7 copepod species and food availability were calculated at 2 depths, 5 m and FM (Table 10). SEPs of the free-spawners were significantly correlated to phytoplankton and ciliate biomass but not to the abundance of heterotrophic dinoflagellates. For *Euchaeta marinella*, SEP had the poorest correlations to all food types at both depths, and many of them were even negative, illustrating its well-known predatory feeding biology. SEP of *Oithona plumifera* was significantly correlated to most of the food types (p < 0.001, see Table 10). SEP of *Oncaea venusta* correlated well with phytoplankton and biomass of all prey items combined (p < 0.01), but not to heterotrophic dinoflagellates alone. Copepod production was not significantly correlated to any of the potential prey items.

Table 9. Correlations among carbon-specific egg production rates (SEPs) of different copepod species. Significant correlations are shown in **bold**. *p < 0.05; ***p < 0.001

	Acartia australis	Acrocalanus gibber	Centropages furcatus	Temora discaudata	Euchaeta marinella	Oncaea venusta
Acrocalanus gibber	**0.27***					
Centropages furcatus	**0.33***	−0.01				
Temora discaudata	0.13	0.00	0.01			
Euchaeta marinella	0.03	0.05	−0.05	0.11		
Oncaea venusta	0.03	0.17	0.01	0.21	−0.13	
Oithona plumifera	0.17	0.13	**0.33***	−0.02	−0.07	**0.52***

DISCUSSION

Spatial and temporal patterns in biomass and productivity: any pattern or trend?

The Andaman Sea is recognized as the site of the world's largest solitons (Osborne & Burch 1980). When the soliton packets encounter the shelf, nutrient rich water should intrude into the surface layer. Such hydrographic discontinuities or episodic disturbances of the water column are often sites of enhanced plankton production (Legendre 1981). The shelf-break front of the Andaman Sea has the potential of being a zooplankton hotspot (*sensu* Marine Zooplankton Colloquium 2001). Previous investigations in the Andaman Sea (Wium-Andersen 1977, Kiørboe et al. 1991) suggested that this front was highly productive and potentially important for the productivity of the area. However, we found no peak in primary production (Nielsen et al. 2004), copepod biomass (Figs. 3 & 7) or egg production (Figs. 8 & 10) in association with the shelf-break front. One possible explanation for our observations is that strong stratification of the water column prevented substantial breakage of the internal wave, and that only small pulses of nitrate are transported to the upper mixed layer at regular intervals. The only site of particular high production was at the persistent mid-shelf front where breaking of the shoaling waves introduced cold, salty and nutrient-rich water to the euphotic zone (Nielsen et al. 2004).

The seasonal patterns of tropical pelagic communities are fundamentally different from those at higher latitudes, since only weak seasonal variations in plankton communities are evident (Chisholm & Roff 1990b, Webber & Roff 1995a,b, Madhupratap et al. 1996, Roman et al. 2000). The relatively weak seasonal fluctuations in plankton biomass or productivity found in the tropics can be related to the rather variable pattern of rainfall (Chisholm & Roff 1990b) and increased storm frequency during monsoon periods and associated upwelling events (Smith 1982, Schalk 1987, Baars et al. 1990).

The Andaman Sea west of Thailand experiences 2 main seasons: the relatively calm dry NE monsoon (November to March) and the stormy wet SW (May to September) monsoon period. The NE monsoon is characterized by northeasterly dry winds off the Asian continent. Heavy rain and strong winds characterize the SW monsoon. Previous investigations in Thai coastal waters, which are more influenced by surface run-off from land, have shown that zooplankton usually peak in abundance during the NE monsoon (Suwanrumpha 1980a,b, Boonruang 1985, Poung-In 1992, Satapoomin 1999b, Satapoomin & Pornchai 2002).

During the present investigation, a significant deepening of the upper mixed layer through erosion of the pycnocline was observed during the 2 cruises in the SW monsoon compared to the NE monsoon (Fig. 2). However, this vertical mixing and introduction of nutrient rich waters to the upper part of the water column (Nielsen et al. 2004) was not reflected in the standing stock or production of the copepods during the SW monsoon. Also, despite the coverage from shallow coastal water across the shelf to oceanic deep stations, no spatial or seasonal variation in the species composition of the Andaman Sea copepod community was observed, i.e. no distinct coastal or deep-water communities were apparent (Table 4, Fig. 7). Moreover comparison between the 2 major seasons revealed no differences in the overall species composition of the copepod community either.

Such absence of detectable seasonality in the composition and biomass of zooplankton has been reported from other offshore tropical areas. In the Arabian Sea, although tropical and intensely seasonal (Burkill et al. 1993, Edwards et al. 1999, Roman et al. 2000), mesozooplankton standing stocks and abundance did not vary significantly between seasons and areas (Madhupratap et al. 1996), despite a clear seasonal pattern in phytoplankton biomass and primary production (Bhattathiri et al. 1996, Sawant & Madhupratap 1996). Madhupratap et al. (1996) suggested that herbivorous mesozooplankton in the Arabian Sea are able to survive during periods of low phytoplank-

Table 10. Correlations between copepod SEP and food availability at the sampling stations. Significant correlations are shown in **bold**. **$p < 0.01$; ***$p < 0.001$

	Acartia australis	*Acrocalanus gibber*	*Centropages furcatus*	*Euchaeta marinella*	*Oncaea venusta*	*Oithona plumifera*	*Temora discaudata*
Phyto, 5 m	0.15	0.08	**0.39**	−0.13	**0.33**	**0.37***	**0.24**
Ciliates, 5 m	0.14	0.22	0.10	−0.21	**0.24**	**0.38***	0.07
Het Dino, 5 m	0.15	0.08	0.18	−0.14	−0.05	**0.48***	0.10
Cili +Dino, 5 m	0.17	0.14	0.17	−0.21	0.10	**0.50***	0.10
Cili + Dino + Phyto, 5 m	0.15	0.09	**0.38**	−0.14	**0.33**	**0.39***	0.23
PP, 5 m	−0.02	0.02	**0.48***	−0.07	0.11	0.10	**0.49***
Phyto, FM	0.23	**0.43***	0.13	−0.16	**0.32**	**0.30**	0.13
Ciliates, FM	**0.44***	0.22	0.05	0.10	0.03	0.10	0.06
Het Dino, FM	0.18	0.14	0.24	−0.11	0.21	**0.50***	0.13
Cili + Dino, FM	**0.35**	0.20	0.20	0.03	0.14	**0.40***	0.12
Cili + Dino + Phyto, FM	0.24	**0.43***	0.23	−0.15	**0.32**	**0.32**	0.16
PP, FM	0.16	**0.49***	0.23	0.05	0.10	0.05	0.11

ton standing stock by feeding on organisms in the microbial loop, thereby keeping a constant biomass despite the seasonal variation in the primary producers. This is consistent with the fact that maximum biomass of microzooplankton occurred during an intermonsoon season, when primary production and chl *a* were low (Guans et al. 1996). In Jamaica, Hopcroft et al. (1998a) found no relationship between copepod biomass and chl *a*, and suggested that phytoplankton is generally not the factor modulating copepod community. Instead, they speculated that the copepod community might be predator regulated (Hopcroft et al. 1998a). Although significant fluctuations in most of the physical and chemical parameters occurred, detailed analysis of the annual structure of the copepod community off Discovery Bay, Jamaica, revealed no seasonality in overall copepod species composition or diversity (Webber & Roff 1995a).

The limited spatial and seasonal variation in planktonic communities in oligotrophic tropical ecosystems complicates determination of relationships between phytoplankton and zooplankton communities. In temperate and arctic ecosystems, where the range in biomass is wider, such relationships exist and phytoplankton and zooplankton do co-vary (Levinsen & Nielsen 2002). Analysis of longer time series may, however, reveal significant seasonal variation in zooplankton biomass. Although the pelagic food web in the central North Pacific Ocean has long been characterized by its general monotony, Landry et al. (2001) found significant seasonal differences, with highest biomass observed during the summer, using the analysis of a long time series of mesozooplankton off Hawaii. Surprisingly, the peak of mesozooplankton biomass did not match the winter peak in phytoplankton generated by the winter storms; the summer peak was rather a response to the summer blooms of the nitrogen-fixing cyanobacteria, *Trichodesmium*.

Due to the lack of any seasonal or spatial variation in copepod biomass, production and species composition in the Andaman Sea, the following discussion will focus on the structure, function and productivity of the copepod community at a more general level, taking an overall life strategy and functional approach.

Contribution of different groups of copepods to overall biomass and production

The use of 200 µm nets recommended by UNESCO (1968) for sampling of copepods unfortunately still biases our knowledge about copepods. The available literature primarily addresses the role of the larger calanoid copepods in the marine environment. Recently, studies in which appropriate sampling gear has been used (i.e. with mesh size ≤50 µm) have documented the importance of small copepods in temperate (Nielsen & Sabatini 1996, Nielsen & Andersen 2002), subtropical (Paffenhöfer 1993) and especially tropical seas (Webber & Roff 1995a,b, Böttger-Schnack 1996). Comparisons of the obtained size spectra of copepods sampled with different gear during the present investigation clearly illustrate the potential bias for interpreting the role of copepods if inappropriate sampling gear is used (Fig. 5). In the Andaman Sea, small copepods, mainly cyclopoids and poecilostomatoid (dominated by *Oithona* spp. and *Oncaea* spp.), made up half of the number and ca. 25% of the copepod biomass. Similar observations were made off Discovery Bay, Jamaica, where *Oithona* and *Oncaea* also were among the most important genera (Webber & Roff 1995a, Hopcroft et al. 1998a).

The importance of egg-carrying species in the Andaman Sea copepod community stresses the significance of this life strategy in tropical oligotrophic ecosystems (Hopcroft et al. 1988a, Chisholm & Roff

1990b, Calbet & Agustí 1999). The relatively high biomass of egg-carrying species, regardless of their significantly lower egg production rate compared to co-occurring broadcast species (*t*-test, p < 0.0001), indicates an adaptive advantage of this life strategy. The advantages of egg-carrying species vary from lower egg mortality (Kiørboe & Sabatini 1994) to lower metabolic demand (Lampit & Gamble 1982), and to behavioral adaptations that reduce predation (Paffenhöfer 1993). While little is known about egg mortality and metabolic demand of tropical copepods, some information on behavioral adaptations that can reduce predation is available for the 3 important genera of egg-carrying species, *Microsetella*, *Oncaea* and *Oithona.*

Such adaptations include colonization of surfaces and reduction of jump frequencies. Examples of surface-associated species include the genus *Microsetella*, which is often associated with the large colonial cyanobacterium *Trichodesmium* (Dagg & Green 1994, Roman et al. 2000, Landry et al. 2001, T.G.N. pers. obs.) and *Oncaea* spp., which are often found on and in aggregates and houses of appendicularians (Aldredge 1972). Both of these habitats may reduce the predation risk significantly. The swimming behavior of the cyclopoid *Oithona*, with much lower jump frequency than the continuously swimming calanoids, reduces its vulnerability to predators by only rarely producing signals to potential predators (Paffenhöfer 1993).

Rates of egg production by free spawning copepod species are routinely used to estimate copepod production in the field (e.g. McLaren & Corkett 1981, Saiz et al. 1997), assuming that adult females do not grow, but rather allocate the ingested carbon into the production of eggs (Berggreen et al. 1988). While the SEP of broadcast spawning copepods is generally estimated from 24 h incubation of females, this method cannot be directly applied to egg-carrying species that typically produce clutches of eggs which they carry for several days. In the present study, the egg production rates of egg-carrying copepods were measured in parallel with the free-spawning calanoid copepods from experimentally determined hatching rates (Table 7) and *in situ* egg:female ratios. No response in egg production rate was observed for any of the 2 life strategies in association with the shelf break or between the 2 monsoon seasons. In temperate and arctic ecosystems, egg production of the cyclopoid *Oithona* spp. was much less variable in time and space than the co-occurring calanoid copepods (Kiørboe & Nielsen 1994, Nielsen & Sabatini 1996). The free spawning calanoids are more opportunistic and ready to exploit small pulses in the prey field (Tester & Turner 1990), while the production of the egg carriers is integrated over a longer period of time, leading to a less opportunistic life strategy (Kiørboe & Sabatini 1994, Nielsen & Sabatini 1996). This difference in the variability of egg production rates was also observed in the Andaman Sea, where variability was higher for the free-spawners compared to the egg-carrying spp. (Table 6).

Can copepod egg production rate be used to estimate community growth and ingestion rates?

The central assumption behind the egg production method is that the weight-specific egg production rate (SEP) is equal to the growth rate of the younger stages (Berggreen et al. 1988). If so, total copepod production can be estimated from SEP and the standing stock. This assumption has been verified for calanoid copepods in eutrophic temperate waters (Sekiguchi et al. 1980, Berggreen et al. 1988, Fryd et al. 1991). In more oligotrophic waters, however, juvenile stages are less food-limited that the copepod adults (Webber & Roff 1995a,b, McKinnon 1996, Hopcroft & Roff 1998b). On the other hand, when resources are not limiting, growth rates may be approximately constant across all development stages and comparable to the weight-specific egg production rate (Fryd et al. 1991, Hopcroft & Roff 1998b), and egg production can be used as measure of production of the entire copepod community.

In the Andaman Sea, females of the various species considered contributed 46 to 61% of the biomass (Table 11), illustrating that our production and grazing calculations are representative for the majority of the copepod community standing stock. However, since the egg production rate of the Andaman Sea copepods was clearly food limited, an obvious question arises regarding the potential bias of our production estimate when SEP is assumed to be the growth rate of the entire community.

Off Jamaica, Hopcroft & Roff (1998a,b) compared copepod production estimates calculated from (1) direct measurement of naupliar and copepodite somatic growth and SEP, and (2) application of SEP to all stages. At the eutrophic Kingston Habour (1.75 µg chl *a* l^{-1}), SEP underestimated production by 40%, while at the oligotrophic Lime Cay (0.2 µg chl *a* l^{-1}), comparable to the Andaman Sea, the deviation was more pronounced. Here the SEP gave 260% less production that the estimate considering the growth rate of the specific stages.

To evaluate the potential bias of our application of SEP to the entire copepod population, we recalculated our production values using data from Lime Cay off Jamaica comparable to the Andaman Sea. Average calanoid and cyclopoid growth rates of nauplii and copepodites originate from Table 1 in Hopcroft & Roff (1998b) and Table 1 in Hopcroft et al. (1998b), respec-

Table 11. Female contribution to the total biomass (%; mean ± SE, n) of the copepod species along the middle transect during 3 cruises in the Andaman Sea

	SW-96	NE-97	SW-97	All cruises
Acrocalanus gibber	44.1 ± 5.2, 10	43.9 ± 3.7, 13	46.0 ± 7.2, 9	44.5 ± 2.9
Acartia australis	41.2 ± 12.5, 4	55.8 ± 6.0, 10		56.6 ± 5.6
Centropages furcatus	44.3 ± 3.5, 7	47.1± 5.7, 10	46.5 ± 6.2, 6	46.1 ± 3.0
Temora discaudata	33.7 ±5.4, 5	61.3 ± 5.2, 11	47.8 ± 9.7, 4	51.7 ± 4.4
Euchaeta marinella	45.1 ± 9.6, 8	50.9 ±6.5, 10	46.1 ± 5.7, 8	47.6 ± 4.1
Oncaea venusta	57.6 ± 4.1, 9	44.6 ± 3.1, 13	61.6 ± 2.8, 9	53.3 ± 2.3
Oithona plumifera	70.5 ±3.9, 10	54.7 ± 4.3, 13	58.9 ± 4.2, 9	60.8± 2.6

Table 12. Comparison of copepod biomass, productivity and turnover rates in tropical marine waters. EM: empirical model; *estimated from the measured SEP and growth rates of nauplii and copepodites from Jamaica from Hopcroft & Roff (1998b) and Hopcroft et al. (1998b), respectively

Areas	Integration depth (m)	Biomass $(mg\,C\,m^{-2})$	Productivity $(mg\,C\,m^{-2}\,d^{-1})$	Production measured from	P/B (d^{-1})	Source
Zanzibar, coastal	22	100±13	88 ± 10	EM by Huntley & Lopetz (1992)	0.88	Lugomela et al. (2001)
Jamaica neritic	20	50	~35	EM by Middlebrook & Roff (1986)	0.75	Chisholm & Roff (1990a,b)
Jamaica oceanic	60	55	~11	*	0.2	Webber & Roff (1995a,b)
	200	96	~20	*	0.2	–
Hawaii	150	286	25	EM by Hirst & Lampit (1998)	0.09	Roman et al. (2002)
Bermuda	150	137	10	EM by Hirst & Lampit (1998)	0.07	Roman et al. (2002)
Arabian Sea	200	1320	156	EM by Hirst & Sheader (1997)	0.12	Roman et al. (2000)
Andaman Sea	100	381 ± 28	23 ± 2	Calculated from SEP	0.06	This study
			115 ± 10*		0.30*	

tively. The application of the Jamaica growth rates for juvenile stages gave a 5-times higher production than the estimates based on SEP alone. However, although the 2 areas seem comparable, the SEP of females off Jamaica (Hopcroft & Roff 1998a) were also significantly higher for calanoids (0.15 ± 0.04 compared to our 0.06 ± 0.01) and for the cyclopoid *Oithona plumifera* (0.38 compared to our 0.05 ± 0.01), indicating that Lime Cay in general is more productive. On the other hand, there is no doubt that our copepod production rates for the oligotrophic Andaman Sea are underestimated by not considering the fast growing smaller stages separately.

In the present study, copepod secondary production based on SEP was estimated to vary from 3 to 93 mg C $m^{-2}\,d^{-1}$ during 3 cruises, with an average of 23 ±2 mg C $m^{-2}\,d^{-1}$ (Table 8). Calanoids contributed most (64.3 ± 6.5%), followed by cyclopoids and poecilostomatoid (10.6 ± 1.0%) and harpacticoids (2.5 ± 0.5%). In general, the integrated biomass was within the range measured in similar environments (Table 12). The copepod production, however, was substantially lower than reported for the other areas primarily due to the low P:B ratio when SEP is used, indicating that growth rates of the smaller stages should be considered. If the Jamaica estimates of nauplii and copepodite growth were applied to the Andaman Sea community, the estimated production would be comparable to that of other areas.

Is copepod production in the Andaman Sea food limited?

The average chl *a* concentration in the Andaman Sea during the present investigation (0.19 to 0.4 µg chl *a* l^{-1} corresponding to 10 to 20 µg C l^{-1}) was far below saturation level of copepod clearance, indicating that the growth rate of the copepod community was food limited (Hansen et al. 1997). Knowledge about egg production potential of tropical marine copepods is, however, very limited; the highest values measured in our investigation are lower than the few available rates from other more eutrophic warm water ecosystems (Mckinnon 1996, Hopcroft & Roff 1998a), illustrating that the egg production rate is limited by potential food. In a much-debated paper, Huntley & Lopez (1992) state that temperature alone can explain >90% of the growth rates of copepods, and that food may not be limiting to growth in nature. They suggested a temperature-dependent model for the estimation of copepod secondary production. The above hypothesis

can be tested by applying the equation of Huntley & Lopez (1992), $P = B \cdot 0.0445e^{0.111T}$, where P = production, B = biomass and T = temperature, to our biomass data and the average temperature of each station. This results in production which is 18 times higher than the actual production obtained from our study. Despite the previously mentioned potential underestimation of production by the use of SEP to calculate community production, this shows that the temperature-dependent method suggested by Huntley & Lopez (1992) cannot be applied to the tropical Andaman Sea. Consequently temperature alone cannot be used as the control function of copepod growth and production. The results corroborate that the copepod community in the Andaman Sea was strongly food limited. The data that support the Huntley & Lopez hypothesis come mainly from arctic and temperate areas, and relatively few are from areas where the temperature exceeds 20°C. The few data points for areas with higher temperatures are from studies of productive eutrophic ecosystems (e.g. estuaries and upwelling areas), and not warm oligotrophic ecosystems, which characterize most subtropical and tropical seas (Calbet & Agustí 1999).

Trophic role of copepods in the Andaman Sea food web

The fate of primary production in the pelagic food web strongly depends on the size composition of the phytoplankton. The primary producers in oligotrophic tropical oceans are typically dominated by picoplankton (Campbell et al. 1997), which are not directly available to copepods (Hansen et al. 1994, Calbet et al. 2000). In the Andaman Sea, phytoplankton size distribution is bimodal with cells >50 or <1 μm (Fig. 5). Consequently, the copepod community has, to a large extent, to rely on an amplification of the average prey size through the microbial food web. During the NE-97 cruise, phytoplankton > 10 μm only contributed ca. 33% to the potential prey population available to the copepods (phytoplankton > 10 μm + protozooplankton), stressing the potential importance of microprotozooplankton as food for the copepod community. The actual available phytoplankton biomass may indeed be much lower, especially in the surface water, because of the filamentous cyanobacterium *Trichodesmium*, which is often a major component of the phytoplankton >10 μm (contributing 11 ± 8% at the FM and 32 ± 18% at 5 m to total biomass). The low availability of the dominating phytoplankton for the copepods stresses the need of alternative food sources, the most obvious being the protozooplankton, i.e. ciliates and heterotrophic dinoflagellates.

Unfortunately, the few measurements of energy flow through the tropical pelagic food web is a considerable obstacle for understanding the function of these globally important areas. Nonetheless, as a first attempt to illustrate the fate of the pelagic production in the Andaman Sea, we have established carbon flux budgets for the 3 identified regions along the studied transects, taking into account the observed variability in rates and distributions (Fig. 13). Assuming that adult copepods are not able to ingest the dominating primary producers directly (Hansen et al. 1994, Calbet et al. 2000), the protozooplankton play a key role in the transfer of energy up the food chain. The grazing rates of the heterotrophic dinoflagellates and ciliates were estimated assuming maximum clearance and a Q_{10} of 2.8 from the equation in Hansen et al. (1997). From the calculated ingestion rates, protozooplankton production was estimated assuming a growth yield of 33% (Hansen et al. 1997). The carbon need of the copepod community was estimated as biomass multiplied by SEP, also assuming a growth yield of 33%. This crude calculation shows that copepods ingest, on average, less than 19% of their total biomass daily, ~71 mg C m^{-2} d^{-1}. We may well have underestimated the copepod production, using the egg production method as discussed above, by a factor of ca. 2 to 3. If so, the copepod community also have to exploit the small primary producers directly (Fig. 13). However, this simple calculation highlights the potential role of the microbial food web in an oligotrophic tropical marine ecosystem. Nevertheless, there is a strong need for more direct information about the trophic coupling between copepods and protozooplankton in picoplankton-dominated marine systems.

CONCLUSIONS

Regardless of the high spatial resolution of sampling across of the very dynamic shelf, no zone of particularly high primary (Nielsen et al. 2004) or secondary production could be identified (Fig. 13). Consequently, the hypothesis suggested by previous investigators, that the shelf break in the Andaman Sea was particularly productive and should fuel a new unexploited fisheries resource (Wium-Andersen 1977, Yesaki & Jantarapagdee 1981, Kiørboe et al. 1991), could not be confirmed. Indications of enhanced fish larval abundance was observed, however, at the mid-shelf front (50 to 65 m bottom depth), where the abundance of fish larvae peaked in a zone where the pycnocline meets the sea-bottom and cold nutrient-rich salt water is introduced to the surface layer (Munk et al. 2004). No response in copepod secondary production was observed there. In general, copepod production in the Andaman Sea is rather high (Table 12), despite the
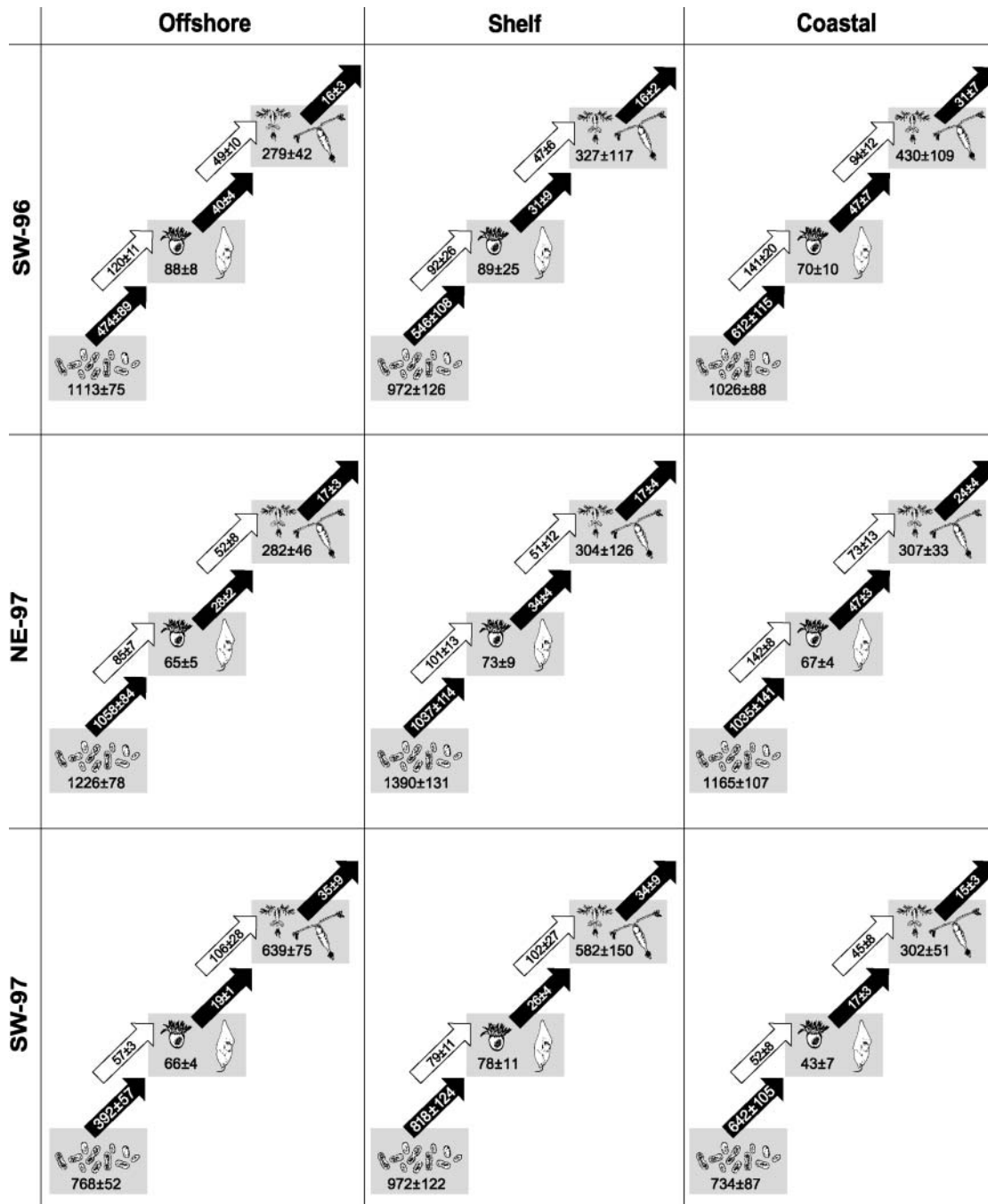
Fig. 13. Carbon-flow diagram of the coastal, shelf and offshore areas during the 3 cruises. Numbers in the boxes illustrate average biomass ± SE (mg C m^{-3}). Arrows represent daily production ± SE (black) and ingestion rate ± SE (white; mg C m^{-3} d^{-1}). Primary production originated from Nielsen et al. (2004) and Jarnekarn (unpubl.)

dominance of small primary producers. The relatively high biomass of protozooplankton available to copepods indicates a strong coupling between copepods and the microbial food web. Knowledge about this trophic pathway is very limited and needs to be further elucidated if the dynamics of oligotrophic tropical oceans such as the Andaman Sea are to be understood.

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