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TIME SUBMITTED	30-MAR-2019 08:50AM (UTC+0700)	WORD COUNT	11687
SUBMISSION ID	1102441217	CHARACTER COUNT	60464

Volume 57 Issues 24–26 December 2010 ISSN 0967-0645

ELSEVIER

DEEP-SEA RESEARCH

PART II

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Species Diversity of Marine Zooplankton

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Deep-Sea Research II 57 (2010) 2076–2088

Contents lists available at ScienceDirect

Deep-Sea Research II

journal homepage: www.elsevier.com/locate/dsr2

Mesozooplankton distribution in the Spermonde Archipelago (Indonesia, Sulawesi) with special reference to the Calanoida (Copepoda)

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ARTICLE INFO

Article history:
Received 18 September 2010
Accepted 18 September 2010
Available online 21 September 2010

Keywords:
Calanoida
Sulawesi
Spermonde Archipelago
Mesozooplankton
Multivariate Analysis

ABSTRACT

In September 2005 the mesozooplankton distribution, taxonomic composition and community structure were studied on four cross-shelf and one coastal transects in the Spermonde Archipelago off Makassar (SW Sulawesi). A total of 47 higher taxonomic groups and 89 calanoid copepod species were identified. Copepods outnumbered the other mesozooplankton taxa with 29 to 69%, increasing in importance towards the offshore stations. Appendicularians ranked second (16–24%) followed at the offshore stations by chaetognaths (4.5%) and, at shelf and coastal stations by echinoderm pluteus larvae (11–15%). Within the calanoids, species of the family Paracalanidae, especially *Paracalanus* cf. *parvus*, were dominant at all stations. Other abundant families were Temoridae (6.5–17%), Acartiidae (7.2%) and Pontellidae (6.2%) at shelf and coastal stations while Clausocalanidae (8.7%) and Calanidae (6.7) were more abundant at offshore stations.

To investigate the mesozooplankton distribution the 25 stations were grouped into 3 geographical zones based on their topographical and hydrographical differences (coastal, shelf and offshore zone). Some higher zooplankton taxa and about half of the calanoid species occurred only in one or two categories. In general the abundant taxa were spread throughout the Archipelago. To investigate their distribution the abundance data were subjected to a multivariate discriminant function analysis (MDFA). The results revealed that the composition of the mesozooplankton community changed from the coastal zone with a high abundance of meroplankton and neritic copepod species to an offshore community with a higher abundance of holoplanktonic organisms and oceanic copepod species.

1. Introduction

The Spermonde Archipelago is a tropical shelf system off southwestern Sulawesi. Shelf seas mark the transition between the terrestrial (i.e. riverine) and oceanic realm. Their living communities are, hence, influenced by distance from shore, shelf depth and exposure to oceanic currents (Cleary et al., 2005), offering the opportunity to study the gradual changes in the distribution of pelagic and benthic organisms from estuaries to the open sea. In contrast to temperate latitudes, only little is known from tropical shelf seas.

The Spermonde Archipelago represents a barrier reef system of about 4000 km^2 coverage and a maximum extension of 60 km (Pet-Soede et al., 1999). The shelf gradually declines towards offshore, reaching a maximum depth of 60 m. A discontinuous barrier reef with several islands and shoals divides the shelf from the deep Makassar Strait, a major throughflow of subtropical Pacific Ocean water. Aside from the barrier reef along the outer rim, the archipelago accommodates cay- crowned and submerged patch reefs (Hoeksema, 1990). The main freshwater input derives from the river Jene Berang south of Makassar. The Jene Berang also contains terrigenous sediments originating from a volcanic drainage area as well as nutrient loads and sewage water from Makassar, a city with more than one million inhabitants. During the dry season fluvial discharge has been reported to be restricted to an area of 4 km parallel to the coastline (Cleary et al., 2005). Other major rivers such as Tallo and Sangkarak are of less influence concerning input of sediments, nutrients and pollution products (Cleary et al., 2005). In spite of a number of benthic studies in the Spermonde Archipelago (e.g. Hoeksema, 1990; Renema and Troelstra, 2001; Cleary et al., 2005; Becking et al., 2006), information on the pelagic community is lacking.

The zooplankton composition of tropical shelf regions is characterized by a persistent gradient from in- to offshore (Sammarco and Crenshaw, 1984; Williams et al., 1988; McKinnon and Thorrold, 1993). Generally, the inshore plankton is characterized

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doi:10.1016/j.dsr2.2010.09.011

by small copepods, many of which are either rare or absent offshore (McKinnon et al., 2005; McKinnon et al., 2008). In the Indonesian Archipelago quantitative zooplankton studies have been carried out in offshore waters (e.g. Wickstead, 1961; van Couwelaar, 1994; Schalk, 1987, 1990; Baars et al., 1990; Arinardi, 1991; Nishikawa et al., 2007). Often only the biomass was calculated. The present study will provide a first comprehensive overview of the plankton community in shelf systems of Indonesia.

The present study is part of a joint German-Indonesian multidisciplinary project SPICE (Science for the Protection of Indonesian Coastal Ecosystems) on the coral and plankton interactions of the Spermonde Archipelago and will describe the plankton community on the shelf along four cross-shelf transects. The focus is on the species diversity and distribution of calanoid copepods.

2. Material and methods

Data were collected from the vessel "Ciska" between September 6 and 14 in 2005 in the Spermonde Archipelago. The study was carried out at 25 stations on one coastal and four cross shore transects (Fig. 1). Three geographical zones were established according to previous investigations (see below) with 5 stations situated in the offshore zone, and 10 each in the shelf and coastal zone, respectively (Table 1).

2.1. Geographical zones

Based on the geomorphology, location of islands and offshore distance, van Vuuren (1920) distinguishes four ecological zones in the Spermonde archipelago. These zones are orientated parallel to the coast and roughly concur with the course of the isobaths on the shelf. Various benthic taxa have been studied and confirmed the ecological differences between the zones (e.g. Hoeksema, 1990; Renema and Troelstra, 2001).

To investigate the distribution pattern of mesozooplankton we distinguished three geographical zones representing the different ecological zones on the Spermonde Archipelago established by van Vuuren (1920). These geographical zones show distinct topo- and hydrographic differences and represent areas within which one would expect homogeneous zooplankton assemblages:

(1) The 'coastal zone' is close to the coastline and influenced by city sewage and river discharge. The effect of the inshore environmental conditions persists across the shelf and declines with increasing distance from the shore line (Hoeksema, 1990; Edinger et al., 1998; Renema and Troelstra, 2001). Water depth is generally less than 20 m.

(2) The 'shelf zone' includes the midshelf and outer shelf zone described by van Vuuren (1920). It covers the area between the near shore zone and the outer barrier reef. Water depth is between 20 and 60 m and has a higher transparency than the coastal zone.

(3) The 'offshore zone' includes the area outside the barrier reef which is influenced by the currents of the Makassar Strait (see Gordon, 2005). This zone is characterized by a steep slope at the border of Makassar Strait.

2.2. Environmental variables

Profiles of temperature and salinity were obtained at each station for the entire water column using a CTD probe (Seabird SBE19plus). For chlorophyll *a* analysis, water was collected using a Niskin water sampler at 3, 20, 45 and 180 m depending on the depth of the stations. At stations shallower than 20 m the deepest water samples were taken near the bottom. The chlorophyll *a* content was analysed by reverse-phase HPLC, using a modified method from Barlow et al. (1997) and quantified based on peak areas of external standards, which were spectrophotometrically calibrated using extinction coefficients published by Bidigare (1991). For correction of experimental losses and volume changes, the concentrations of the pigments were normalised to the internal standard canthaxanthin.

2.3. Zooplankton sampling

For mesozooplankton, stratified vertical hauls were carried out using an opening-closing Apstein net (0.02 m^2 aperture, 200 μm

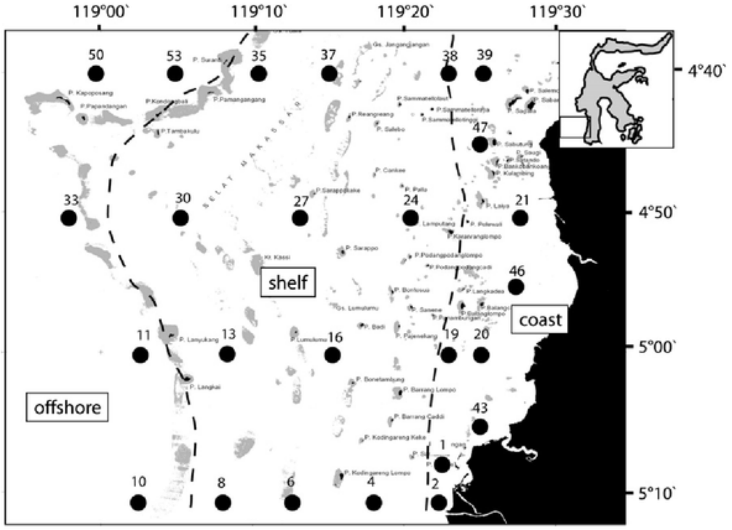

Fig. 1. The Spermonde Archipelago off Makassar (SW Sulawesi) with the sampled stations and the geographical zones.

Table 1
Zooplankton station profiles in September 2005; C coastal, S shelf, O offshore, grey fields mark stations sampled at night.

Station	Depth interval (m)							Date (dd.mm.yy)	Total depth (m)	Zone	Start (local time)
1	5-0	10-5	20-10					06.09.05	28	C	16:45
2	5-0	10-5	15-10					06.09.05	19	C	18:40
4	5-0	10-5	20-10	30-20				07.09.05	34	S	9:45
6	5-0	10-5	20-10	30-20				07.09.05	36	S	15:20
8	5-0	10-5	20-10	30-20	50-30			07.09.05	51	S	18:35
10	5-0	10-5	20-10	30-20	50-30	100-50		08.09.05	250	O	10:00
11	5-0	10-5	20-10	30-20	50-30	100-50		08.09.05	416	O	13:20
13	5-0	10-5	20-10	30-20				08.09.05	49	S	16:40
16	5-0	10-5	20-10	30-20				09.09.05	45	S	8:15
19	5-0	10-5	20-10					09.09.05	24	C	14:25
20	5-0	10-5	15-10					09.09.05	17	C	15:45
21	5-0	no data	14-10					10.09.05	16	C	7:10
24	5-0	10-5	20-10					10.09.05	24	S	9:50
27	5-0	10-5	20-10	30-20				10.09.05	31	S	13:10
30	5-0	10-5	20-10	30-20	45-30			10.09.05	49	S	16:05
33	5-0	10-5	20-10	30-20	50-30	100-50	150-100	11.09.05	ca. 300	O	8:35
35	5-0	10-5	20-10	30-20				12.09.05	42	S	17:45
37	5-0	10-5	20-10	30-20	40-30			13.09.05	42	S	7:55
38	5-0	10-5	20-10					13.09.05	28	C	11:30
39	5-0	10-5	20-10					13.09.05	26	C	12:15
43	5-0	10-5						14.09.05	10.5	C	11:20
46	5-0	10-5						09.09.05	14.5	C	17:40
47	5-0	10-5						13.09.05	13	C	13:45
53	5-0	10-5	20-10	30-20	50-30	100-50		12.09.05	ca. 500	O	13:35
50	5-0	10-5	20-10	30-20	50-30	100-50	200-100	11.09.05	ca. 400	O	12:55

mesh size). Sampling was conducted during daytime with four exceptions (Table 1). The net was hand-towed as a winch was not available. For each net the estimated filtered water volume was calculated from the depth of the sampling interval and the mouth area of the net, assuming a 100% filtration efficiency. When strong currents biased the general scheme of the depth intervals, the actual sampled depth was calculated from the angle of the rope. Samples were immediately preserved in a borax-buffered 4% formaldehyde seawater solution.

Prior to the numeration of higher mesozooplankton taxa the samples were divided using a Folsom splitter. Then, aliquots of 1/2 to 1/32 were counted. Copepods were sorted and identified from the entire sample. Only adult calanoid individuals were identified as species or genera, while juveniles were grouped in families. For identification many guides and manuscripts were consulted (e.g. Cleve, 1901; Bedot, 1909; Scott, 1909; Sewell, 1929; Früchtl, 1924; Vervoort, 1946; Mori, 1964; Tanaka (1956-1965); Bradford et al., 1983; Bradford-Grieve, 1994; 1999; Bradford-Grieve et al., 1999; Mulyadi, 2002, 2004; Razouls et al., 2005-2009).

2.4. Multivariate Discriminant Function Analysis

To analyse spatial distribution patterns of zooplankton species a Multivariate Discriminant Function Analysis (MDFA) was used. MDFA is a statistical method to discriminate samples among sets of naturally occurring categories (Fisher, 1936). MDFA requires samples to be a-priori assigned to exactly one category. In this set-up the $\log_{10}(1+x)$ transformed species abundances were used as variables and the previously defined geographical zones as categories. A subsequent Canonical Analysis (CA) was performed to identify how species discriminate between the geographical zones and describe relationships between them (Manley, 1994).

To identify whether geographic zones can be discriminated by zooplankton species showing a not obvious distribution pattern two different MDFA models were set up for non-copepod invertebrates (INV-MDFA, Table 2) and copepods (COP-MDFA, Table 3). Species absent from a geographical zone were discarded from the analysis as they have an already known distribution and would not contribute in gaining more information (Tables 2, 3). Zooplankton not determined to species level was also discarded to exclude effects of spatial differences among sites that could not be distinguished by the overlapping characteristics of such variables. Species included in the MDFA analysis are given in Tables 2 and 3. For each MDFA a linear computerised model was set up:

$$DS_c = k_c + \sum_{s=0}^{n-1} w_{cs} x_s$$

where DS is the discriminant classification score, k the geographical zone constant and w the automatically calculated weighing factor (Jennrich, 1977a, b) for species variables x. The subscript c denotes the respective geographical zone and s the index of the species. For each c the DS_c is calculated and probability determined to belong to one of the given geographical zones. Probabilities were weighed by the size class of the a priori defined geographical zones and results summarised in a classification matrix (Table 4). Wilk's λ was computed as a standard statistic to denote the significance of the model's discriminatory power (Rao, 1951) that can be converted to a probability value via F-test. For the hypothesis tests via F-test normality is required, but not for the method itself (Hair et al., 1998). As multivariate normality cannot be guaranteed in zooplankton data sets, we use both the standard Wilk's λ and F-test to interpret the discriminatory power of the models (Table 5).

The subsequent CA was used to identify how species contribute to discrimination among the three geographical zones. The CA extracts canonical functions, so called roots that distinguish best among zones. Significance of the root was calculated to identify whether the roots need to be interpreted (Table 6). The discriminative nature of each root was derived from the algebraic sign of the canonical means (Table 7).

The canonical factor structure coefficients (CFSC) give the unique partial loading of the respective species variables. While roots define the separating canonical planes for the geographical zones the CFSC values give the contribution of a variable to the

Table 2
Mesozooplankton: frequency of occurrence (freq.) as No. stations, and dominance (dom.) as mean abundance in each zone: x < 10 Ind. m^{-3}; xx 10–100; xxx 100–1,000; xxxx > 1,000, taxa included in the MDFA (incl.) and significant indicator taxa in MDFA (sign.). Original abundance data of the cruise are available at the database PANGAEA (Schnack-Schiel and Cornils, 2009).

Taxa				Offshore (5)		Shelf (10)		Coast (10)		MDFA	
				Freq.	Dom.	Freq.	Dom.	Freq.	Dom.	Incl.	Sign.
Cnidaria	Anthozoa		Actinula larvae	2	x	5	x	10	x		
	Medusae			5	xx	10	xxx	10	xxx	x	
	Siphonophora			5	xx	10	xx	10	xxx	x	
Ctenophora	Tentaculifera			4	x	10	xx	9	xx	x	
Plathelminthes	Turbellaria		Müller's larvae	5	x	9	x	8	xx	x	
Nemathelminthes	Nemertini		Pilidium larvae	5	x	10	xx	10	xxx	x	
Mollusca	Bivalvia		Larvae	5	x	10	xx	10	xxx	x	
	Cephalopoda		Larvae	2	x	1	x				
	Gastropoda		Veliger larvae	5	xx	10	xxx	10	xxx	x	
			Pteropoda	5	xx	10	xx	10	xx	x	x
			Heteropoda	3	x						
	Nudibranchia		*Phyllirhöe*	1	x						
Annelida	Polychaeta		Trochophora larvae	5	xx	10	xxx	10	xxx	x	
			Holoplankton	5	x	3	x				
			Meroplankton	5	xx	10	xxx	10	xxx	x	
Arthropoda	Crustacea	Amphipoda			5	x		x			
		Cladocera	*Pseudevadne tergestina*	5	xx	10	xxx	10	xxx	x	x
			Penilia avirostris	3	x	4	x	5	x		
		Cirripedia	Nauplii	5	x	10	xx	10	xx		
			Cypris larvae	4	x	10	x	9	xx		
		Copepoda	Calanoida	5	xxxx	10	xxxx	10	xxxx		
			Cyclopoida	5	xxx	10	xxxx	10	xxxx		
			Harpacticoida	5	xx	10	xxx	10	xxx		
		Decapoda	Holoplankton	5	xx	10	xx	10	xxx	x	
			Meroplankton	5	xx	10	xx	10	xx	x	
		Euphausiacea	Metanauplii	5	x	2	x			x*	
			Calyptopis	5	x	6	x	1	x		
			Furcilia	5	x						
			Juveniles	4	x						
		Isopoda		4	x	6	x				
		Mysidacea		3	x	1	x	1	x		
		Ostracoda		5	xx	8	x	5	x	x	
		Stomatopoda		1	x	1	x	1	x		
Tentaculata	Brachiopoda		Larvae	1	x			3	x		
	Phoronidea		Actinotrocha larvae	3	x	6	x	10	xx	x	
Chaetognatha				5	xxx	10	xxx	10	xxx	x	
Tunicata	Appendicularia			5	xxxx	10	xxxx	10	xxxx	x	x
	Ascidiacea		Tadpole larvae	2	x	6	x	1	x		
	Thaliacea		Doliolida	5	xx	10	x	8	x	x	x
			Salpidae	4	xx	3	x				
Echinodermata	Asteroidea		Bipinnaria larvae	5	x	9	x	7	x	x	
	Echinoidea/Ophiuroidea		Pluteus larvae	5	xx	10	xxxx	10	xxxx	x	
	Holothuroidea		Doliolaria larvae					1	x		
			Auricularia larvae	1	x	4	x	8	xxx		
	Ophiuroidea		Juvenile	4	x	7	x	5	x		
Hemichordata	Enteropneusta		Tornaria larvae	4	x	10	xx	8	x	x	
Vertebrata	Pisces		Eggs and Larvae	5	x	10	xx	9	xx		

* All euphausids were chosen.

roots and represent relative species dominance in the samples of a zone. The higher the absolute CFSC value is for a respective root the larger is its proportional share within the assigned zone. This does not imply exclusive appearance, but gradual distribution and allows comparing variables regardless from absolute abundances.

3. Results

3.1. Environment

In September 2005 the water column of the Spermonde Archipelago was well mixed on the shelf. At the offshore stations a thermocline was visible between 70 and 150 m depth. Warmer regions with less saline water were found in the shallower areas along the coast. The sea surface temperature varied from 25 °C (offshore) to 29 °C (coastal). The salinity ranged from 34.42 to 34.48 with lower values along the coast compared to the outer rim.

The chlorophyll *a* concentrations at 3 m depth varied between 0.20 and 0.59 μg L^{-1} (mean 0.37), at 20 m between 0.36 and 2.71 μg L^{-1} (mean 1.05) and at 45 m between 0.40 and 2.57 μg L^{-1} (mean 1.47). At 200 m depth at offshore stations the chlorophyll *a* concentrations were below 0.1 μg L^{-1}.

The chlorophyll *a* data indicate a subsurface maximum at all stations. At 20 m depth the chlorophyll *a* content was always higher than at 3 m depth. The phytoplankton composition changed between these depths. At 3 m depth *Synechococcus* (41%), prymnesiophytes (31%) and diatoms (20%) predominated while at 20 m diatoms made up for more than 50% of the total chlorophyll *a* (Schnack-Schiel, unpublished data). At 45 m depth the dominance of diatoms was even higher than at 20 m depth.

Table 3
Copepoda: Frequency of occurrence (freq.) as No. stations, and dominance (dom.) as mean abundance in each zone: x < 1 Ind. m^{-3}; xx 1–10; xxx 10–100; xxxx 100–1,000; xxxxx > 1,000, taxa included in the MDFA (incl.) and significant indicator taxa in MDFA (sign.). Original abundance data of the cruise are available at the database PANGAEA (Schnack-Schiel and Cornils, 2009).

Taxa		**Offshore (5)**		**Shelf (10)**		**Coastal (10)**		**MDFA**	
		Freq.	**Dom.**	**Freq.**	**Dom.**	**Freq.**	**Dom.**	**Incl.**	**Sign.**
Calanoida Sars, 1902									
Calanidae Dana, 1846	Juveniles	5	xxxx	10	xxxx	10	xxx		
	Canthocalanus pauper Giesbrecht, 1888	5	xx	6	xx	3	xx	x	
	Cosmocalanus darwini Lubbock, 1860	5	xx	1	x	1	x	x	
	Mesocalanus tenuicornis Dana, 1849	1	x						
	Nannocalanus minor Claus, 1863	3	x						
	Neocalanus gracilis Dana, 1849	3	x						
	Undinula vulgaris Dana, 1849	4	xx						
Paracalanidae Giesbrecht, 1893	Juveniles	5	xxxx	10	xxxx	10	xxxx		
	Acrocalanus Males	5	xx	4	xx	6	xx		
	Acrocalanus gibber Giesbrecht, 1888	5	xx	8	xx	7	xxx	x	
	Acrocalanus gracilis Giesbrecht, 1888	5	xx	4	xx	1	x		
	Acrocalanus longicornis Giesbrecht, 1888	5	xxx	7	xx	1	x	x	
	Acrocalanus monachus Giesbrecht, 1888			1	x				
	Bestiolina sp. (*zeylonica*)	5	xxx	10	xxxx	9	xxxx	x	
	Calocalanus spp.	5	xxx	10	xxx	9	xxx	x	
	Calocalanus pavo Dana, 1849	5	xx	2	x	1	x		
	Calocalanus plumulosus Claus, 1863	5	xx	4	xx	3	xx		
	Delibus nudus Sewell, 1929	5	xx	9	xxx	6	xxx	x	
	Paracalanus Males	5	xxx	10	xxx	10	xxx		
	Paracalanus aculeatus Giesbrecht, 1888	5	xxx	10	xxx	10	xxx	x	
	Paracalanus denudatus Sewell, 1929	5	xxx	10	xxx	7	xx	x	
	Paracalanus cf. *parvus* Claus, 1863	5	xxx	10	xxxx	9	xxxx	x	x
	Paracalanus cf. *nanus* Sars, 1907	5	xxx	10	xxx	7	xxx	x	
	Parvocalanus Males	2	x	9	xx	6	xxx		
	Parvocalanus crassirostris F. Dahl, 1894	4	xx	9	xxx	9	xxxx	x	
	Parvocalanus elegans Andronov, 1972	4	xx	9	xxx	9	xxxx	x	
Mecynoceridae Andronov, 1973	Juveniles	5	xx	9	xx	6	xx		
	Mecynocera clausi Thompson, 1888	5	xx	4	xx	2	x		
Eucalanidae Giesbrecht, 1892	Juveniles	5	xxxx	10	xxx	7	xxx		
	Eucalanus sp.	1	x						
	Pareucalanus attenuatus Dana, 1849	5	xx						
	Pareucalanus sewelli Fleminger, 1973	2	x						
	Rhincalanus rostrifrons Dana, 1849	4	x						
	Subeucalanus crassus Giesbrecht, 1888	3	x						
	Subeucalanus mucronatus Giesbrecht, 1888	2	x			1	x		
	Subeucalanus pileatus Giesbrecht, 1888	5	xx	1	x				
	Subeucalanus subcrassus Giesbrecht, 1888	5	xx			1	x		
Clausocalanidae Giesbrecht, 1892	Juveniles	5	xxxx	10	xxx	6	xxx		
	Clausocalanus Males	5	xx	6	xx	2	x		
	Clausocalanus arcuicornis Dana, 1849	4	x						
	Clausocalanus farrani Sewell, 1929	5	xxx	4	x				
	Clausocalanus furcatus Brady, 1883	5	xx	5	x				
	Clausocalanus mastigophorus Claus, 1863	5	x						
	Clausocalanus minor Sewell, 1929	5	xx	6	xx	2	x	x	
	Clausocalanus parapergens Frost & Fleminger, 1968	1	x						
	Clausocalanus paululus Farran, 1926	5	xx	4	x				
	Ctenocalanus vanus Giesbrecht, 1888	4	x	1	x	1	x		
Aetideidae Giesbrecht, 1892	Juveniles	2	x						
	Aetideus acutus Cleve, 1904	2	x						
Euchaetidae Giesbrecht, 1893	Juveniles	5	xxx	2	x				
	Euchaeta concinna Dana, 1849	1	x						
	Euchaeta indica Wolfenden, 1905	3	x						
	Euchaeta longicornis Giesbrecht, 1888	1	x						
	Euchaeta rimana Bradford, 1973	3	x						
Phaennidae Sars, 1902	Juveniles	1	x						
	Xanthocalanus merica Grice, 1962	1	x						
Scolecitrichidae Giesbrecht, 1892	Juveniles	5	xxx	5	xx	2	x		
	Macandrewella joanae A. Scott, 1909	1	x						
	Scaphocalanus curtus Farran, 1926	4	xx						
	Scolecithricella longispinosa Chen & Zhang, 1965	5	xx						
	Scolecithricella tropica Grice, 1962	3	xx	1	x				
	Scolecithrix danae Lubbock, 1856	4	xx						
	Scolecitrichopsis ctenopus Giesbrecht, 1888	1	x						
Diaixidae Sars, 1902	Juveniles			1	x				
	Anawekia bilobata Othman & Greenwood, 1994	1	x						
	Anawekia sp. 1	1	x						
	Anawekia sp. 2			1	x				
Arietellidae Sars, 1902	Juveniles	3	x	6	xx	7	xxx		
	Metacalanus aurivilli Cleve, 1901			6	xx	6	xxx		

Table 3 (*continued*)

Taxa		Offshore (5)		Shelf (10)		Coastal (10)		MDFA	
		Freq.	Dom.	Freq.	Dom.	Freq.	Dom.	Incl.	Sign.
Augaptilidae Sars, 1905	Juveniles	3	x						
	Haloptilus longicornis Claus, 1863	1	x						
Heterorhabdidae Sars, 1902	Juveniles (*Heterorhabdus*)	3	x						
Lucicutiidae Sars, 1902	Juveniles	5	xxx	7	xx	1	x		
	Lucicutia flavicornis Claus, 1863	5	xx	2	x				
	Lucicutia gaussae Grice, 1963	3	x	1	x				
Metridinidae Sars, 1902	Juveniles (*Pleuromamma*)	5	xx	6	xx	3	x		
Centropagidae Giesbrecht, 1892	Juveniles	5	xxx	9	xxx	10	xxx		
	Centropages calaninus Dana, 1849	2	x						
	Centropages elongatus Giesbrecht, 1896	1	x						
	Centropages furcatus Dana, 1849	2	x	3	x	3	xx	x	
Pseudodiaptomidae Sars, 1902	Juveniles			1	x	7	xx		
	Pseudodiaptomus aurivilli Cleve, 1901					3	xx		
	Pseudodiaptomus clevei A. Scott, 1909			1	x				
Temoridae Giesbrecht, 1893	Juveniles	5	xxx	9	xxxx	10	xxxx		
	Temora discaudata Giesbrecht, 1889	5	xx	4	x	1	x	x	
	Temora stylifera Dana, 1849	4	x	1	x	1	x		
	Temora turbinata Dana, 1849	5	xx	5	xxx	10	xxxx	x	
Fosshageniidae Suarez-Morales and Iliffe, 1996	Juveniles	2	xx						
	Temeropia mayumbiensis T. Scott, 1894	2	x	1	x				
Candaciidae Giesbrecht, 1892	Juveniles	5	xxx	6	xx	1	x		
	Candacia catula Giesbrecht, 1889	5	xx						
	Candacia curta Dana, 1849	2	x						
	Candacia ethiopica Dana, 1849	1	x						
	Candacia pachydactyla Dana, 1849	2	x						
Pontellidae Dana, 1853	Juveniles	5	xxx	9	xxxx	10	xxxx		
	Calanopia americana F. Dahl, 1894	1	x			1	x		
	Calanopia aurivilli Cleve, 1901			1	x				
	Calanopia elliptica Dana, 1849	2	x	1	x				
	Calanopia herdmani A. Scott, 1909			1	x	1	xx		
	Calanopia minor A. Scott, 1902	5	xx	2	xx	1	xx	x	
	Labidocera acuta Dana, 1849	1	x						
	Labidocera bengalensis Krishnaswamy, 1952					1	x		
	Labidocera minuta Giesbrecht, 1989					1	x		
	Pontellopsis herdmani Thompson & Scott, 1903					1	x		
Acartiidae Sars, 1903	Juveniles	5	xxx	9	xxx	10	xxxx		
	Acartia centrura Giesbrecht, 1889					2	x		
	Acartia danae Giesbrecht, 1889	5	xx	1	x				
	Acartia erythraea Giesbrecht, 1889	1	x	5	xx	8	xxx	x	
	Acartia negligens Dana, 1849	5	xxx	7	xx	2	xx	x	
	Acartia pacifica Steuer, 1915			1	x	1	3		
	Acartia sp.			1	x				
Tortanidae Sars, 1902	Juveniles	1	x	8	xxx	10	xxxx		
	Tortanus barbatus Brady, 1883					1	x		
	Tortanus gracilis Brady, 1883	2	x	3	xx	9	xxx		
not identified	Juveniles	1	x						
Cyclopoida Burmeister, 1834									
Oithonidae Dana, 1853	Juveniles	5	xxxx	10	xxxx	10	xxxx		
	Oithona spp. adult	5	xxxx	10	xxxx	10	xxxx	x	
	Lubbockia sp.	2	x	2	x				
Oncaeidae Giesbrecht, 1892	Juveniles	5	xxxx	10	xxxx	10	xxx		
	Oncaea spp. adult	5	xxxx	10	xxxx	10	xxx	x	x
Corycaeidae Dana, 1852	Juveniles	5	xxx	10	xxxx	10	xxxx		
	Corycaeus spp. adult	5	xxx	10	xxx	10	xxxx	x	
	Farranula spp. adult	5	xxx	10	xxx	10	xxx	x	
Sapphirinidae Thorell, 1859	*Sapphirina* spp.	4	xx			1	x		
	Copilia spp.	5	xx	3	x				
Harpacticoida Sars, 1903									
Clytemnestridae A. Scott, 1909	*Clytemnestra* spp.	5	xx	5	xx	2	xx		
Ectinosomatidae Sars,1903; Olofsson, 1917	*Microsetella* sp.	5	xx	10	xxx	10	xxxx	x	
Miraciidae Dana, 1846	*Macrosetella gracilis* Dana, 1848	5	xx	7	xx	4	xx		
	Oculosetella gracilis Dana, 1852	5	x			1	x		
Euterpinidae Brian, 1921	*Euterpina acutifrons* Dana, 1848 adult	5	xxx	10	xxxx	10	xxxx	x	
not identified		5	xx	9	xx	5	xx		

At 3 m depth no difference was observed between the coastal and oceanic regions in chlorophyll *a* concentrations, whereas in 20 m or 45 m depth chlorophyll *a* was higher along the coastal and shelf stations.

3.2. *Spatial and vertical distribution*

The overall abundance of mesozooplankton varied highly throughout the Spermonde Archipelago (Fig. 2), from 3166 ind m^{-3}

Table 4
Classification matrices of the different MDFA models. A high discrimination success indicates significant differences and therefore different species compositions among the geographical zones.

	Observed	Cumulative percent	Predicted			Total
			Offshore p=0.32	Shelf p=0.42	Coastal p=0.26	1.00
INV (Higher Taxa)	Offshore	90.625	29	3	0	32
	Shelf	95.238	2	40	0	42
	Coast	73.077	0	7	19	26
	Total	88.000	31	50	19	100
COP (Copepoda)	Offshore	90.625	29	3	0	32
	Shelf	97.619	0	41	1	42
	Coastal	69.231	0	8	18	26
	Total	88.000	29	52	19	100

Table 5
Significance of the different MDFA models.

MDFA model	No. variables	Wilk's λ	*F*-Value	*p*-Value
INV	24	0.174	F(48, 148)=4.308	<0.001
COP	26	0.146	F(52, 144)=4.472	<0.001

at an offshore station and 23394 ind m^{-3} at a coastal station (mean 10061 ind m^{-3}). In general, abundance at the coastal stations was higher, station 4 (shelf) on the southernmost transect also showed an exceptionally high abundance compared to other shelf stations. Abundance was generally highest along the coast. Original abundance data of the cruise are available at the database PANGAEA (Schnack-Schiel and Cornils, 2009).

The vertical distribution of total mesozooplankton did not show distinct differences between the three geographical zones (Fig. 3). Zooplankton within the water column was highly variable. At the offshore stations the depth interval with the highest abundance was always below 10 m depth. Station 50 had a bimodal distribution with peaks at 20-30 m and 100-200 m depth intervals. At the shelf stations the highest occurrence was below 5 m depth, except for station 4 where the highest density of zooplankton was in the upper 5 m. At the coast stations the peak in relative zooplankton abundance was mostly at the deepest depth interval (10-15/20 m, 5–10 m), except for station 43 and 1 where most zooplankton occurred in the upper 5 m.

3.3. *Higher taxonomic groups*

In total, 47 higher mesozooplankton taxa were identified on different systematic levels (Table 2). Copepods outnumbered the other taxa with 29 to 53% (mean 41%) at coastal stations, 29 to 52% (mean 43%) at shelf stations and 51 to 69% (mean 58%) at offshore stations (Table 8), increasing in importance at the offshore stations. Appendicularians ranked second at all three geographical zones with means of 16% (coast), 27% (shelf) and 24% (offshore) followed at the offshore zone by chaetognaths (4.5%) and, at shelf and coastal zones by echinoderm pluteus larvae (11% and 15%, respectively). The latter did not appear within the 10 most abundant taxa at the offshore stations. Ostracods and doliolids were only of higher importance offshore whereas polychaete trochophora and meroplankton (only larger polychaete larvae) appeared in higher ranks only at shelf and coastal stations.

34 taxa occurred at least at one station in each geographical zone of which 18 mesozooplankton taxa occurred at all sampled stations. They varied in dominance and frequency of occurrence (Table 2). Some taxa increased in abundance from coast to offshore (ostracods, doliolids, salps) whereas others were more abundant at coastal stations (e.g. *Pilidium* larvae, bivalve larvae, echinoderm pluteus larvae, *Pseudevadne tergestina*, actinotrocha larvae).

3.4. *Copepoda*

Calanoids were the most abundant taxa of copepods (mean: 66% (coastal zone), 72% (shelf zone), 64% (offshore zone)). They comprised 89 species in 23 families and 42 genera (Table 3). Half of the species (44) occurred in more than one of the three geographical zones, and many of these showed a tendency to increase in abundance towards the offshore zone (Table 3). However, there were also species with higher densities at coastal stations (e.g. *Temora turbinata*, *Parvocalanus* spp., *Metacalanus aurivilli*, *Acartia erythraea*, *Tortanus gracilis*). 34 species occurred only at the offshore stations of which 14 occurred just at one station. Five species were only once found at shelf stations (*Acartia* sp., *Acrocalanus monachus*, *Anawekia bilobata*, *Calanopia aurivilli*, *Pseudodiaptomus clevei*). Six species were restricted to the coastal stations (*Acartia centrura*, *Labidocera bengalensis*, *Labidocera minuta*, *Pontellopsis herdmani*, *Pseudodiaptomus aurivilli*, *Tortanus barbatus*) but apart from *P. aurivilli* and *A. centrura* they were single occurrences.

The most abundant family was the Paracalanidae with 61 to 75% of all calanoids in all three geographical zones (Table 9). This family was represented by 14 species and some unidentified *Calocalanus* spp. (Table 3). The Temoridae were ranked second at the coastal and shelf zone with 3 species (17% and 6.5%, respectively) while Clausocalanidae (8.7%) were more abundant in the offshore zone with 8 species. The third rank varied among the three geographical zones: in the offshore zone it was the Calanidae with 6.7%, in the shelf zone Pontellidae occurred with 6.2% and in the coast zone the Acartiidae were abundant with 7.2%.

Other copepod taxa were the cyclopoids and harpacticoids (Table 3) represented by 12 genera. In cyclopoids the genera *Oithona* and *Oncaea* were most abundant, while in harpacticoids *Euterpina acutifrons* and *Microsetella* sp. were found in higher numbers. The less abundant harpacticoids were mainly found at the offshore stations as well as the cyclopoids *Sapphirina* spp. and *Copilia* spp.

3.5. *Multivariate discriminant function analysis*

The classification matrices of the Multivariate Discriminant Function Analyses (MDFA) models show a discrimination success of 88% for both the higher mesozooplankton taxa (INV) and the copepods (COP) (Table 4). Only few samples were misplaced in another geographical zone by the MDFA models and more than

Table 6
Step down χ^2 test for successively removed canonical roots. As each successive root contributes less to further separation their significance was tested with a step down χ^2-test. The first rows indicate significance including all roots. Each further line gives the significance with the preceding ones removed and is an indicator for the number of functions to interpret. From the Eigenvalues the cumulative proportion of explained variance can be calculated for each root.

MDFA model	Root	Eigenvalue	Wilk's λ	χ^2	DF	*p*-Value	Cum. %
INV	1	1.848	0.174	149.497	48	< 0.0001	0.645
	2	1.017	0.496	60.001	23	< 0.001	1.000
COP	1	2.524	0.146	162.457	52	< 0.0001	0.729
	2	0.940	0.696	56.016	25	< 0.0004	1.000

Table 7
Mean values of the canonical analyses for the two MDFA models.

MDFA model	Root	Offshore	Midshelf	Coast
INV	1	-1.955	0.614	1.290
	2	-0.303	1.075	-1.324
COP	1	-2.249	0.604	1.642
	2	0.383	-1.060	1.209

half of these were samples of the surface layer (0-5 m). Fewer intersections were found between offshore and shelf clusters than between offshore and coast clusters. No intersection were found between offshore and coast.

Both Wilk's λ and F-test indicate significance for the two models (Table 5). Thus, it is possible to discriminate samples from different geographical zones by the included variables in both the mesozooplankton and copepod models.

For all MDFA analyses algebraic signs of the canonical means show that the first root separates the offshore zone from the residuals (Table 7). In both analyses the first roots contribute with 77% to 80% to the observed variance (Table 6). Results imply that the strongest differences in zooplankton community are found between the offshore zone and those closer to the coastline. The second root then separates the remaining shelf and coast zone. The step-down χ^2-tests show that all roots are significant. Wilk's λ advises caution as it shows high values for the second roots in both models.

The INV-CFSC values show that variables of higher taxonomic groups are scattered in all four quadrants of the plot (Fig. 3). Algebraic signs of the canonical means (Table 7) show that the first root separates offshore from shelf and coast samples (inshore). Variables having a higher numerical importance for identification of offshore samples, respectively species with higher abundances in the respective geographical zones, are located in quadrants II and III. The second root separates variables dominant in the shelf zone in quadrant I from those of the coast zone in quadrant IV. All variables being significant in the INV-MDFA show higher relative loadings off the origin. The variable Appendicularia is located in the shelf quadrant and its perpendicular distance to the axes is higher for the coastal, than for the offshore zone. The high loading of the variable Doliolida on the first root indicates higher dominance in offshore waters. The location of the variable *Pseudevadne tergestina* shows dominance in shelf waters. Pteropoda are found at the intersection between quadrants I and II. In general, meroplanktonic larvae were found abundant mainly in coastal, but also in shelf waters.

COP-CFSC values (Fig. 4) again show a separation of copepod taxa among all three geographical zones. Variables in quadrant II and III represent species more common in offshore waters. Quadrant I includes species variables being dominant in samples close to the coast and quadrant IV those dominant in shelf samples. The low CFSC value on the second root for *Paracalanus* cf. *parvus* implies dominance in shelf samples. *Oncaea* spp. is significantly located in the offshore segment.

4. Discussion

This is the first comprehensive study on mesozooplankton distribution in southwest Sulawesi. It provides an insight into the distribution of mesozooplankton taxa and calanoid copepods on four cross-shelf and one coastal transect in the Spermonde Archipelago. Early expeditions went through Makassar Strait, but did not sample the reef-based shelf of the Spermonde Archipelago (e.g. Scott, 1909). This short-term study revealed a remarkable difference in taxa composition between the three chosen geographical zones: coast, shelf and offshore. The obtained data can serve as a base for future pelagic research at the Spermonde Archipelago.

4.1. Environmental variables

In September 2005 the water column of the Spermonde Archipelago was well mixed with slightly higher temperatures at the coastal sites. Salinity was high (34.42 to 34.48), and did not show any cross-shelf differences suggesting that river input during the end of the dry season (SE monsoon) was negligible. Kinkade et al. (1997) proposed that the salinity changes between wet season (NW monsoon, salinity: 31.23) and dry season (SE monsoon, salinity 34.45) might be partly due to the differences in river runoff. During the NW monsoon the wind drives low-salinity surface water from the Java Sea into the southern Makassar Strait, while the reversal SE monsoon wind eliminates the northward pressure gradient by transferring more saline Banda Sea water into the southern Makassar Strait.

Chlorophyll *a* values are higher compared to the values from the Sulu and Celebes Seas during the NW monsoon. In the Sulu and Celebes Sea Nishikawa et al. (2007) reported that chlorophyll *a* concentrations were less than 0.5 $\mu g\ L^{-1}$ at surface and 0.27 to 0.68 $\mu g\ L^{-1}$ at 50-70 m. The discrepancy to our chlorophyll *a* values might be due to changes between seasons as discussed by Kinkade et al. (1997). They found an increase of up to an order of magnitude between NW monsoon (0.25 $mg\ m^{-3}$) and SE monsoon (2.5 $mg\ m^{-3}$) in the Spermonde Archipelago. However, additional chlorophyll *a* data from March 2005 were in the same magnitude as those from our study (Schnack-Schiel, unpublished data).

4.2. Mesozooplankton composition

Similar to the chlorophyll *a* values the mesozooplankton concentration was high, comparable to eutrophic tropical areas (e.g. Kingston Harbor, Jamaica: Dunbar and Webber, 2003; Webber et al., 2003; Bay of Bengal: Rakesh et al., 2008) and much higher than in offshore waters of the Sulu and Celebes Seas

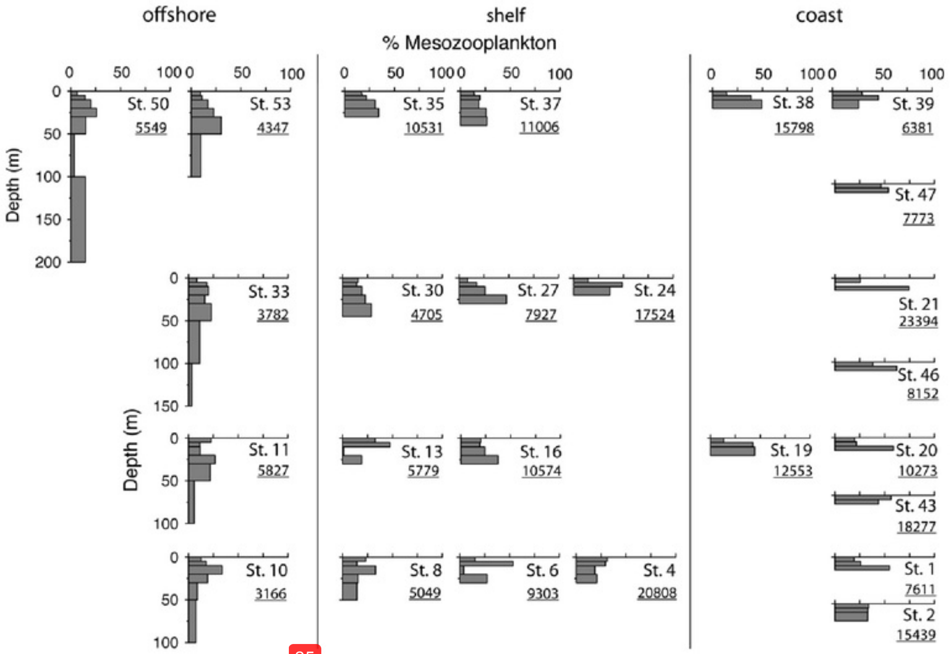

Fig. 2. Vertical distribution of total mesozooplankton (%) as a percentage of the total abundance at the given station numbers (St.). Underlined numbers denote the total abundance (individuals m^{-3}) for the entire water column sampled (Table 1).

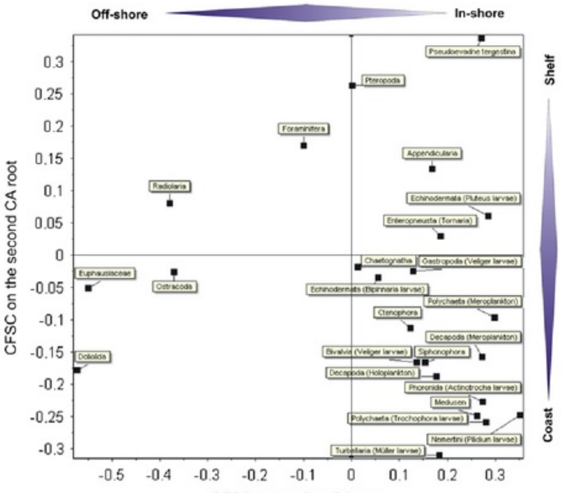

Fig. 3. Canonical factor structure coefficients (CFSC) values of the canonical analysis for the invertebrate zooplankton MDFA (INV-CFSC).

(Nishikawa et al., 2007). Therefore, it can be assumed that the Spermonde Archipelago is an area of elevated primary and secondary production.

As in most marine subtropical and tropical waters the mesozooplankton community was dominated by copepods and appendicularians (e.g. Deevey, 1971; Mazzocchi and Ribera d'Alcalą, 1995; Cornils et al., 2005; Rakesh et al., 2008; Satapoomin et al., 2004, Jaspers et al. 2009). However, copepods were less dominant comprising only 41–57% of the mesozooplankton abundance compared to other reef-based shelf areas, e.g. in the Caribbean (Moore and Sander, 1976) where they accounted for at least 75% of the total mesozooplankton abundance. Baars et al. (1990) show that the dominance of copepods in the Banda Sea changed between the seasons. During cruises in August the dominance was higher (83% at offshore stations and 70% at shelf stations) than in February (77% and 57%, respectively). Unfortunately investigations from other Indonesian regions are based on biomass rather than on abundance.

The high abundance of meroplanktonic larvae, especially in coastal and shelf waters of the Spermonde Archipelago, might be responsible for the lower relative importance of copepods. As observed during our study the relative abundance of copepods increased with distance offshore while that of meroplanktonic larvae decreased. Meroplanktonic larvae often play an important role in coastal waters as many benthic species produce pelagic larvae (e.g. Fetzer, 2002; Fernandez de Puelles et al., 2003; Kirby et al., 2008).

It has to be taken into account that the present study shows only a snapshot of the zooplankton composition at the Spermonde Archipelago. Earlier studies in the Banda Sea have shown that the biomass concentration was twice as high in the upper 300 m during the SE monsoon (August) as during the NW monsoon (February) (Schalk, 1987). Hence, abundance and composition might differ greatly between seasons.

The usage of a smaller mesh size (55 μ m) will also increase the abundance by ten-fold (e.g. Paffenhöfer and Mazzocchi, 2003). During the present study a 55 μm net was also used, which especially at the coastal stations, was often clogged due to high particle concentration. The samples contained mainly copepod nauplii and copepodites (Schnack-Schiel, unpublished data). The importance of cyclopoid copepods will probably also increase

Table 8
Ranking of the 10 most abundant mesozooplankton taxa in each geographical zone.

Rank	offshore		shelf		coastal	
	Taxa	%	Taxa	%	Taxa	%
1	Copepoda	57.6	Copepoda	42.8	Copepoda	40.9
2	Appendicularia	23.6	Appendicularia	26.6	Appendicularia	16.1
3	Chaetognatha	4.5	Echinodermata, Pluteus-Larvae	11.3	Echinodermata, Pluteus-Larvae	15.4
4	Gastropoda, Larvae	1.9	Cladocera, Evadne	4.6	Medusae	4.1
5	Medusae	1.6	Chaetognatha	2.2	Polychaeta, Trochophora	3.5
6	Ostracoda	1.4	Gastropoda, Larvae	2.1	Polychaeta, Meroplankton	2.9
7	Cladocera, Evadne	1.4	Polychaeta, Meroplankton	1.9	Chaetognatha	2.6
8	Siphonophora	1.2	Medusae	1.8	Gastropoda, Larvae	2.1
9	Doliolida	1.0	Polychaeta, Trochophora	1.2	Cladocera, Evadne	2.0
10	Decapoda, Holoplankton	0.9	Decapoda, Holoplankton	1.0	Siphonophora	1.9

Table 9
Ranking of the 10 most abundant calanoid families in each geographical zone.

Rank	offshore		shelf		coastal	
	Taxa	%	Taxa	%	Taxa	%
1	Paracalanidae	67.4	Paracalanidae	75.2	Paracalanidae	60.5
2	Clausocalanidae	8.7	Temoridae	6.5	Temoridae	17.1
3	Calanidae	6.7	Pontellidae	6.2	Acartiidae	7.2
4	Eucalanidae	4.3	Calanidae	3.9	Pontellidae	5.0
5	Temoridae	2.7	Clausocalanidae	2.7	Tortanidae	4.0
6	Acartiidae	2.2	Acartiidae	1.8	Calanidae	2.4
7	Scolecitrichidae	2.0	Eucalanidae	1.4	Arietellidae	0.9
8	Pontellidae	1.6	Tortanidae	0.9	Clausocalanidae	0.9
9	Lucicutiidae	1.5	Centropagidae	0.6	Centropagidae	0.8

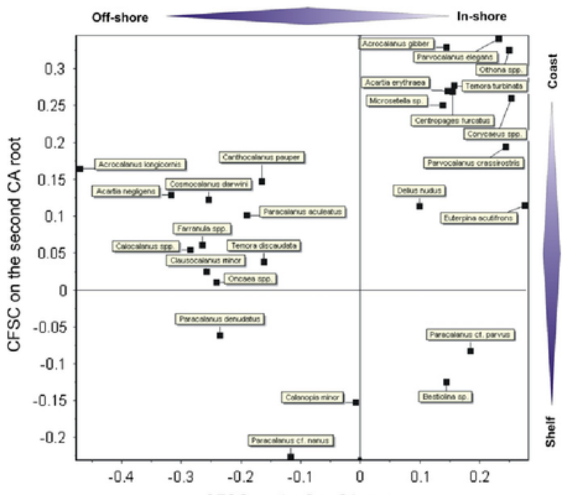

Fig. 4. Canonical factor structure coefficients (CFSC) values of the canonical analysis for the copepod MDFA (COP-CFSC).

with the use of a smaller mesh size (Satapoomin et al., 2004; McKinnon et al., 2008).

In the Spermonde Archipelago 89 calanoid species and genera, and 12 other copepod genera have been found which is only a small fraction of the species recorded in the Indonesian seas and their adjacent regions where about 450 calanoid copepod species have been recorded (Razouls et al., 2005-2009). The species number is in the same range as that of Mulyadi, 2004 who sampled the surface waters (0–25 m) throughout the Indonesian Archipelago (99 calanoid species from 33 genera and 17 families) and in the NE Taiwan Strait (94 species: Lee et al., 2006), but higher than in other near shore regions (NW Australia: 60 species: McKinnon et al., 2008; Gulf of Carpentaria: 68 species: Othman et al., 1990; SE Taiwan Strait: 75 species: Hwang et al., 2006).

In total 77 of the 81 identified calanoid species (not including species only identified on generic level) had already been found in the cited literature in the Indonesian Seas and adjacent seas (Cleve, 1901; Carl, 1907; Scott, 1909; Früchtl, 1924; Vervoort, 1946; Mulyadi, 2002; 2004; Wilson, 1950; Wickstead, 1961; Grice, 1962; Arinardi, 1991; Othman et al., 1990; Hirota, 1995). First records for Indonesian waters are *Clausocalanus paululus*, *Paracalanus* cf. *nanus*, *Acartia centrura*, *Xanthocaanus dilatus* and *Scolecithricella longispinosa*. The genus *Anawekia* has so far been only reported from the Gulf of Carpentaria in North Australia by Othman and Greenwood (1994). Only one species could be identified (*Anawekia bilobata*), the other two are possible new species, the individuals occurred at the deepest samples at two offshore and one shelf station.

Demersal, meso- and bathypelagic calanoids were rare in the samples due to the fact that during daytime only the upper 200 m (at the offshore stations) were sampled. Hence, only few mesopelagic species have been found (*Scaphocalanus curtus*, *Haloptilus longicornis*, *Lucicutia* spp., *Temeropia mayumbiensis*, *Candacia ethiopica*, *Candacia pachydactyla*; Bradford-Grieve et al., 1999; Razouls et al., 2005-2009).

According to Bradford-Grieve et al. (1999) and Razouls et al. (2005-2009) most of the identified species from SW Sulawesi have a wide distribution in subtropical and tropical realms of all oceans. This is true for the calanoids and for cyclopoid and harpacticoids copepods. However, there are a number of species that seem to be restricted to the Indian and Pacific Oceans (all *Euchaeta* and *Scolecithricella* species, *Centropages calaninus*, *Centropages elongatus*, *Temora discaudata*, *Candacia catula*, *Rhincalanus rostrifrons*, *Canthocalanus pauper*, *Bestiolina* sp., *Labidocera acuta*, *Labidocera minuta*, *Tortanus barbatus*) and others with an even narrower distribution, having so far only been found in the Indian Ocean and the Indo-west-Pacific (Australia, Indonesian Seas, South China Sea) (*Macandrewella joanae*, *Metacalanus aurivilli*, *Calanopia "americana"*, *Calanopia aurivilli*, *Calanopia herdmani*, *Labidocera herdmani*, *Pontellopsis herdmani*).

Within the copepods the family Paracalanidae was predominant at all stations and with > 14 species the most species as also found in other coastal regions (e.g. McKinnon et al., 2008). The genus *Paracalanus* is known to contribute greatly to calanoid assemblages in subtropical and tropical shelf waters (e.g. Bahia Magdalena: Palomares-García and Gómez-Gutiérrez, 1996; Straits of Malacca: Rezai et al. (2004); Yellow Sea: Zuo et al., 2006; Sun et al., 2008; Great Barrier Reef: McKinnon and Duggan, 2001).

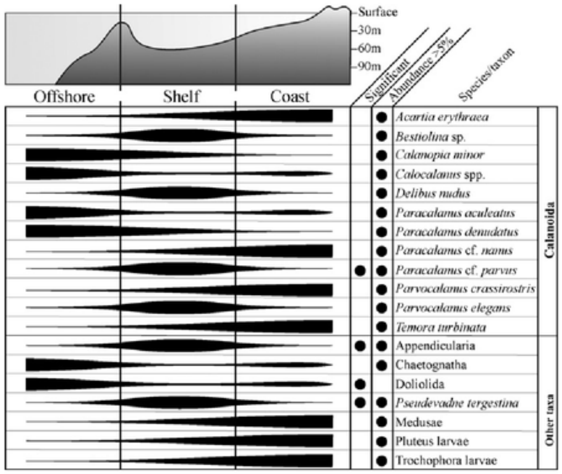

Fig. 5. Horizontal distribution of abundant and/or significantly occurring taxa summarised from the results of the multivariate analysis.

4.3. Spatial distribution

Fig. 5 summarises the results of the multivariate analysis and revealed that the abundant taxa are to a large extent associated with the three geographical zones. It shows that the plankton community changed considerably across the shelf as has also been stated from other investigations on cross-shelf distributions (e.g. Williams et al., 1988; Lopes et al., 1999; Morgan et al., 2003, Rezai et al., 2004, Lee et al., 2006). The use of different models for the mesozooplankton taxa and the calanoid copepods avoided overestimation of the numerically dominant copepods. Not all taxa were included because many taxa and calanoid species occurred only at stations of one geographical zone.

The mesozooplankton of the coastal stations is characterized by high abundance of meroplanktonic larvae (e.g. *Pilidium* larvae), cnidarians and neritic copepods such as *Acartia erythraea*, *Temora turbinata*, *Centropages furcatus*, *Paracalanus* cf. *nanus*, *Parvocalanus crassirostris*, and *Parvocalanus elegans*. Species of *Acartia* and *Parvocalanus crassirostris* are often found in tropical inshore waters (e.g. McKinnon and Klumpp, 1998; Sampey et al., 2007). The genus *Acartia* occurred with 6 species. It is a characteristic neritic genus throughout the world; only *A. negligens* and *A. danae* inhabit the open ocean (Tranter and Abraham, 1971). This confirms our findings for the abundant coastal species *Acartia erythraea* and the offshore species *A. negligens*. *Calanopia* was the most abundant pontellid genus during the present study. *Temora turbinata* is often found abundantly in coastal waters (e.g. Brazil: Lopes et al., 1999; Bay of Bengal: Rakesh et al., 2008).

Species occurring almost only at the coastal stations are, e.g., species of *Pseudodiaptomus* and *Tortanus* and can hence serve as indicator taxa for shallow coastal waters. They occur within a wide range of salinities and are often dominant in the plankton of brackish coastal lagoons and estuaries (Walter, 1989; Boxshall and Halsey, 2004). *Pseudodiaptomus* species are also mainly demersal and have thus not been sampled quantitatively due to the daytime sampling. The coastal assemblage of the Spermonde Archipelago has to cope with rather high nutrient and seston concentrations (Schmitt, 2007) due to the river runoffs and the vicinity to Makassar. Additionally the water depth exceeds 20 m, hence, larger copepods might be prevented from colonizing the coastal zone by the shallow depth (Uye, 1994; Hopcroft and Roff, 1998).

The "shelf" assemblages are characterized by appendicularians, the cladoceran *Pseudevadne tergestina*, and the copepods *Paracalanus* cf. *parvus* and *Bestiolina* sp. *Paracalanus* cf. *parvus* is known as a widely distributed and abundant species in coastal waters (Zuo et al., 2006; Sun et al., 2008; McKinnon and Duggan, 2001). The taxonomic status of this species, however, is unclear. Other species of *Bestiolina* are known to occur abundantly in tropical mangrove zooplankton (McKinnon and Klumpp, 1998). The cladoceran *Pseudevadne tergestina* occurs circumglobally, but is particularly abundant in warm eutrophic embayments (Onbe, 1999).

The offshore zone is characterized by a high number of adult species occurring only at these stations. In abundance, Paracalanidae, Clausocalanidae and Calanidae were predominant, similar to the results of Nishikawa et al. (2007) from the Sulu and Celebes Sea. There Calanidae, Clausocalanidae, Paracalanidae and Acartiidae dominated the upper 100 m of the water column. This confirms the opinion that species of *Clausocalanus* are often predominant in the epipelagic zone of temperate and tropical oceanic regions (e.g. Peralba and Mazzocchi, 2004; Cornils et al., 2007).

Other "offshore" groups were *Paracalanus aculeatus*, *Cosmocalanus darwini*, chaetognaths and Doliolida. Chaetognaths belong to the abundant open-ocean species, often ranking second or third in abundance after copepods as in the offshore samples of the Spermonde Archipelago (e.g. Longhurst, 1985; Cornils et al., 2005). Doliolids are warm-water cosmopolitans (Esnal, 1999), and similar to chaetognaths they are evenly distributed throughout the water column. The offshore stations are situated at the boundary of the Indonesian throughflow at Makassar Strait. Sampling the Makassar Strait proper will lead to a much better understanding of the offshore mesozooplankton population in the Indonesian waters. Only a few species inhabit the neritic realms.

The MDFA also revealed that the species of the Paracalanidae showed distinctly different horizontal distributions across the shelf as shown in Fig. 4. The reason for this possible niche portioning might be to avoid feeding competition also known from other closely related species (e.g. *Clausocalanus* in Peralba and Mazzocchi, 2004).

Differences in plankton communities are often related to temperature or salinity gradients (e.g. Cornils et al., 2005, 2007). However, during the present study the water column was well mixed. Hence, the strong differences in taxa composition between the coastal and offshore zones are probably connected to other factors such as the distance offshore, total depth of the station and higher particle concentration at the coastal stations (Schmitt, 2007). Also the water depth decreases greatly between offshore and shelf stations. Oceanic zooplankton species might be incapable of feeding in particle-rich waters because they are adapted to relatively particle-free water and thus occur mainly at the offshore stations (Morgan et al., 2003). Other factors for the rare occurrence of larger plankton might be the small net opening or the increased susceptibility of large plankton to visual predators (e.g. Ueda, 1991).

Tides are also an important parameter which unfortunately was not recorded for the various islands on the Spermonde Archipelago during the sampling period. Tidal currents enable a regular exchange of zooplankton organisms across the outer barrier and the incoming zooplankton thus provides an additional food resource for planktivorous fishes, and benthic invertebrates. Their selective feeding might also affect the distribution of zooplankton on a reef-based shelf (Heidelberg et al., 2004; Hamner et al., 2007; Sampey et al., 2007).

Meroplanktonic larvae are often passively distributed by tides and currents (Belgrano and Dewarumez, 1995). With the distance offshore the community changes from a high percentage of meroplanktonic larvae (mainly echinopluteus) to higher abundance of oceanic holoplanktonic taxa (e.g. chaetognaths, ostracods). Generally it seems that meroplanktonic larvae are restricted by the 40 m isobath where strong changes occur within the benthic community (Renema and Troelstra, 2001; Cleary et al., 2005). It has also been postulated that meroplanktonic populations may be more related to differences in the benthic habitat than in the pelagic environment (Uriarte and Villate, 2004). Shanks et al. (2002) proved that bivalve larvae in the water column showed a similar distribution pattern to the respective adult populations. The discontinuous barrier reef at the boundary between the offshore and shelf communities might prevent organisms from being washed on the shelf by currents and tides.

Acknowledgments

We would like to thank the scientific crew of the vessel "Ciska" for their help in data sampling. We also thank K. Bremer and S. Wilken for their phytoplankton analysis, Ruth Alheit for the english revision and two anonymous reviewers for their comments and suggestions. This work was supported by the SPICE project (Science for the Protection of Indonesian Coastal Ecosystems) financed by the German Federal Ministry of Education and Research (BMBF). This study was also funded by the Census of Marine Zooplankton project, a Census of Marine Life project by the Alfred P. Sloan Foundation.

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