

Structure of Mesozooplankton Communities in the Coastal Waters of Morocco

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Abstract—Mero- and holoplanktonic organisms from 23 large taxa have been detected in the coastal waters of Morocco. Seven Cladocera species and 164 Copepoda species were identified. Copepod fauna mostly consisted of oceanic epipelagic widely tropical species, but the constant species group (frequency of occurrence over 50%) included neritic and neritic–oceanic widely tropical species. The neritic community that formed a biotopic association with coastal upwelling waters and the distant-neritic community associated with Canary Current waters were the two major communities detected. The former community was characterized by a high abundance and biomass (5700 ind./m³ and 260 mg/m³) and predominance of neritic species. The trophic structure was dominated by thin filter feeders, mixed-food consumers, and small grabbers; the species structure was dominated by *Paracalanus indicus*, *Acartia clausi*, and *Oncaea curta*; the indices of species diversity (3.07 bit/ind.) and evenness (0.63) were relatively low. The latter community was characterized by low abundance and biomass (1150 ind./m³ and 90 mg/m³); variable biotopic, trophic, and species structure; and higher Shannon indices (3.99 bit/ind.) and Pielou (0.75). Seasonal variation of the abundance of organisms was not detected in the communities. Anomalous mesozooplankton states were observed in summer 1998 and winter 1998–1999.

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INTRODUCTION

The coastal waters of Morocco are an important area for international fishing and the largest area of the Canary Current upwelling ecosystem [35, 40]. This ecosystem is actively scrutinized by researchers in commercial fishing-related oceanology, since the intensity of international fishing has increased considerably during recent decades [5, 33]. However, the most important ecosystem components, especially zooplankton, remain less thoroughly characterized than analogous ecosystem components of the Atlantic and Pacific oceans [9, 33].

The main sources of Morocco's coastal waters are the North Atlantic Central Water mass (NACW), which is cold and more saline, but poorer in nutrients than the South Atlantic Central Water mass (SACW), which makes a smaller contribution, and surface modifications of the central water masses [33]. These water masses move within large-scale subtropical anticyclonic systems of the North and South Atlantic, with the Canary Current and Mauritanian Current being important components thereof. The Mauritanian Current meets the Canary Current near the Cap Blanc to form a frontal division known as the Senegal–Mauritania front (SMF). Coastal upwelling and the SMF are extremely important oceanographic phenomena that enrich the euphotic layer with nutrients and

largely determine the distinctive hydrological and ecological features of the entire area [1, 21]. These phenomena confer high productivity to the Canary Current upwelling ecosystem, the waters of which are eutrophic and hypertrophic with primary production greater than 1 gC/m² day, a chlorophyll concentration of 1 g/m² [1], and a phytoplankton abundance and biomass of 100 million cells/m³ and 400 mg/m³, respectively [29]. The mesozooplankton biomass and abundance are 800 mg/m³ and 36000 ind./m³ [17], and the shortness of the food chain determines the high production volume at the upper trophic levels and the high biomass of pelagic fish species, currently estimated at 9 million t [33].

Focused zooplankton studies near the Africa's Atlantic coast began a century ago [6, 8, 13]. Research in this area expanded the knowledge on mesoplankton fauna, distinctive features of the horizontal and vertical distributions of mesoplankton, regular patterns of plankton accumulation formation, and the biology of certain abundant species [11, 12, 18, 25, 27, 30, 42]. However, most results were obtained with incidental or individual samples collected in limited areas. Therefore, ecological questions on the theoretical and practical importance of the cenotic organization of zooplankton, distinctive features of the distribution of the zooplankton community, localization of cenotic

Table 1. Sampling periods and amount of material used in study

Trawler name	Voyage	Sampling season	Sampling period	Sample number
<i>AtlantNIRO</i>	No. 10	Winter 1993–1994	17.01–08.02.1994	85
	No. 11	Summer 1994	05.07–26.07.1994	64
	No. 12	Winter 1994–1995	25.01–25.02.1995	75
	No. 13	Summer 1995	19.07–10.08.1995	65
	No. 14	Summer 1996	06.06–22.06.1996	43
	No. 16	Winter 1996–1997	08.01–03.02.1997	68
	No. 17	Summer 1997	11.07–08.08.1997	83
	No. 19	Winter 1997–1998	27.02–30.03.1998	55
	No. 20	Summer 1998	09.07–12.08.1998	59
<i>Atlantida</i>	No. 21	Winter 1998–1999	27.03–25.04.1999	76

boundaries between these communities, and seasonal dynamics remain open today.

The aim of the present study was to analyze the composition and structure of mesoplankton fauna from the coastal waters of Morocco using materials from field studies performed in 1994–1999, and to characterize the distinctive features of the horizontal distribution of the plankton, including cenotic organization, distinctive features of the biotopic, trophic, and species structure of plankton communities, and seasonal dynamics of abundance and biomass.

MATERIAL AND METHODS

Mesozooplankton samples collected in the 200 NM exclusive economic zone of Morocco during research voyages of the freezer trawlers *Atlantida* and *AtlantNIRO* in 1994–1999 were used as the study material. Said material was collected within the framework of the Russian plan for resource research and monitoring of aquatic bioresources of the World Ocean and an inter-governmental agreement between the Russian Federation and the Kingdom of Morocco [6].

Results derived from the processing of 673 samples collected in 5 summer (June to October) and 5 winter (January to April) surveys (Table 1) were used.

The stations of the study range were located at sites with depths of 20 to 1000 m along parallel latitudinal profiles spaced approximately 15 NM apart (Fig. 1).

A Bongo 20 plankton collector with a grapple area of 0.03 m² and a filtering sieve with a 168 µm mesh size was used to collect the samples. Sampling was performed by stepwise-oblique trawling at the standard horizons in daytime in the 0–100 m (0–bottom) layer according to the procedural recommendations [24].

Laboratory inspection of the samples followed the conventional procedure [19]. Crustaceans of the subclass Copepoda and the order Cladocera received the most attention during the inspection. Synonymy was verified using ITIS (www.itis.gov). The abundance and

raw biomass of individual taxa (ind./m³ and mg/m³) in the sampling layer at each station was calculated in Fox-Pro 6.0 using software developed at the Atlantic Institute of Fisheries and Oceanography Research [20].

Three major mesozooplankton groups identified in the trophic structure according to the classifications presented in published studies [2, 26, 28] were filter feeders (fine and coarse), mixed-food consumers, and grabbers (large and small). The biotopic structure of mesozooplankton was inferred from the distribution of three ecological groups of Copepoda, namely, the neritic, nerito-oceanic, and oceanic organisms. Every species was assigned to a specific group according to the Vives classification [45], and Copepoda were divided into surface and interzonal organisms according to bathymetric associations [8, 45].

The frequency of occurrence, calculated as the ratio between the number of stations where a taxon was found and the total number of stations, was used to assess the significance of individual species and higher taxa in the mesoplankton fauna. The following scale proposed by Bakanov [3] was used to characterize the frequency of occurrence: constant taxa, at a frequency of occurrence above 50%; secondary, at 25–50%; and incidental, at less than 25%.

Statistical analysis employed conventional procedures implemented in Microsoft Office Excel [34] and PRIMER[®]6 [38] software. Multidimensional non-parametric scaling and cluster analysis of standardized and square-root-transformed data on taxon abundance were used to identify mesozooplankton communities according to the Bray–Curtis similarity coefficient. Median values and errors thereof (m), Shannon diversity indices (H' , \log_2), and Pielou evenness indices (J') were calculated using taxon abundance data, and the significance of the differences in the species structure of communities (ANOSIM analysis, PRIMER[®]6) was assessed. Fischer's test was used to verify the hypothesis of the existence of seasonal variation in the abundance and biomass of mesozooplankton communities at a significance level of $p \leq 0.05$ [32].

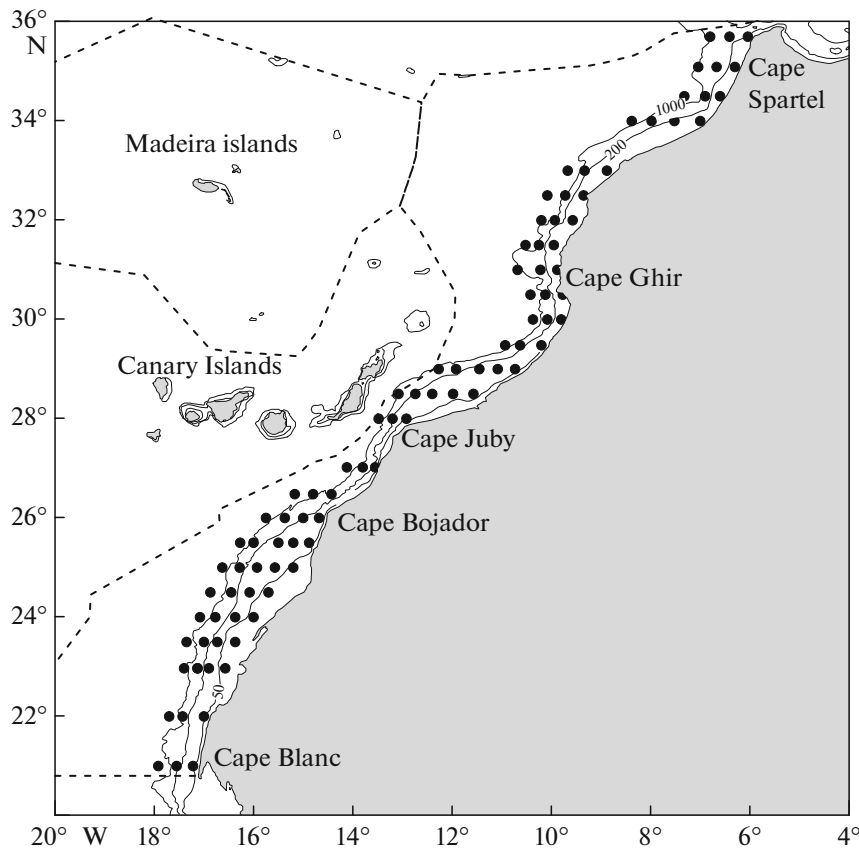


Fig. 1. Scheme of hydrobiological station location in coastal waters of Morocco.

RESULTS

Mesozooplankton composition and frequency of taxon occurrence. Mero- and holoplankton organisms found in the study area belonged to the following large taxa (ranking above genera): Polychaeta, Copepoda, Cladocera, Cirripedia, Ostracoda, Stomatopoda, Mysida, Cumacea, Isopoda, Amphipoda, Euphausiacea, Decapoda, Mollusca (Bivalvia, Gastropoda, and Cephalopoda), Echinodermata, Chaetognatha, Cephalochordata, Siphonophorae, Tunicata (Appendicularia, Doliolida, and Salpida), and fish eggs and larvae. Seven cladoceran species were identified, whereas 164 copepod species were identified and the species could not be identified for an additional seven representatives of specific copepod genera.

The large constant taxa (frequency of occurrence above 50%) were almost universally represented by chaetognathans and decapod crustacean larvae, in addition to Copepoda and Cladocera mentioned above; euphausiids, appendicularia, fish larvae and eggs, and gastropod mollusks occurred less frequently (Table 2). Representatives of six other large secondary taxa (frequency of occurrence 25–50%) were found over 30–40% of the study area. Incidental taxa (frequency of occurrence less than 25%) included mysids and salps found over 20% of the study area, isopods

found over 6% of the study area, and other species represented by individual organisms.

The cladocerans *Evadne spinifera* and *Podon intermedius* were found over 25–30% of the study area, and *Penilia avirostris* was found over 20% of the study area (Table 2). The remaining species (*Pseudevadne tergestina*, *Evadne nordmanni*, and *Pleopis polyphemoides*) were less common, and *Podon leuckartii* was represented by single individuals only.

Only 13 of the 164 copepod species were constant; i.e., they occurred continuously over more than half of the study area (Table 2). Epipelagic neritic and nerito-oceanic widely tropical species had a fundamental significance for this group. The secondary taxon group included 14 copepod species; two of these (*Oithona nana* and *Corycaeus giesbrechti*) were neritic and the others were widely tropical oceanic or nerito-oceanic epipelagic species. The incidental taxon group was represented by 137 copepod species, mostly oceanic (85%) widely tropical (76%) epipelagic (55%) species.

Cenotic organization, community structure, and distribution of mesozooplankton from Moroccan coastal waters. Results of cluster analysis and multidimensional scaling of data on the relative abundance of mesozooplankton taxa, not presented here because due to size constraints, demonstrated statistically reli-

Table 2. Composition of constant and secondary taxonomic groups

Taxon	Association		Species habitat range	Frequency of occurrence, %
	biotopic	bathymetric		
Constant taxa				
<i>Paracalanus indicus</i>	N	E	WT	95
Chaetognatha				92
Decapoda				90
<i>Oncaea curta</i>	N	E	WT	89
<i>Centropages chierchiae</i>	N–O	E	WT	88
<i>Calanus helgolandicus</i>	N–O	Int	NC	88
<i>Acartia clausi</i>	N	E	WT	86
<i>Temora stylifera</i>	N	E	WT	83
Euphausiacea				78
Appendicularia				72
Pisces (eggs and larvae)				69
<i>Calanoides carinatus</i>	N–O	Int	SC	62
<i>Oithona plumifera</i>	N–O	Int	WT, carryover to h.l.	61
<i>Oncaea media</i>	N–O	Int	WT, carryover to b.z.	58
<i>Oithona brevicornis</i>	N–O	E	NC	56
Gastropoda				55
<i>Nannocalanus minor</i>	N–O	E	WT, carryover to h.l.	55
<i>Euterpina acutifrons</i>	N	E	WT	54
<i>Ctenocalanus vanus</i>	N–O	E	WT, carryover to h.l.	52
Secondary taxa				
<i>Clausocalanus jobei</i>	N–O	E	WT, carryover to b.z.	46
Polychaeta				43
<i>Oncaea mediterranea</i>	O	E	WT, carryover to h.l.	42
Ostracoda				42
Bivalvia				42
<i>Farranula rostrata</i>	N–O	E	WT	39
Amphipoda				37
<i>Oithona nana</i>	N	E	WT	36
<i>Calocalanus contractus</i>	O	E	WT, carryover to h.l.	34
<i>Clausocalanus furcatus</i>	N–O	E	WT	34
<i>Mecynocera clausi</i>	O	E	WT, carryover to h.l.	33
Siphonophorae				32
Doliolida				32
<i>Acartia danae</i>	O	E	WT	32
<i>Paraeuchaeta hebes</i>	O	E	WT	32
<i>Corycaeus latus</i>	O	E	WT	30
<i>Evadne spinifera</i>				30
<i>Calocalanus styliremis</i>	N–O	E	WT, carryover to h.l.	29
<i>Eucalanus monachus</i>	O	Int	WT	26
<i>Podon intermedius</i>				25
<i>Corycaeus giesbrechti</i>	N	E	WT	25
<i>Clausocalanus paululus</i>	O	E	WT	25

Ecological characteristics indicated for copepod species: N, neritic; N–O, neritic–oceanic; O, oceanic; E, epipelagic; Int, interzonal; WT, widely tropical; NC, northern central; SC, southern central; high latitudes (h.l.), boreal zone (b.z.).

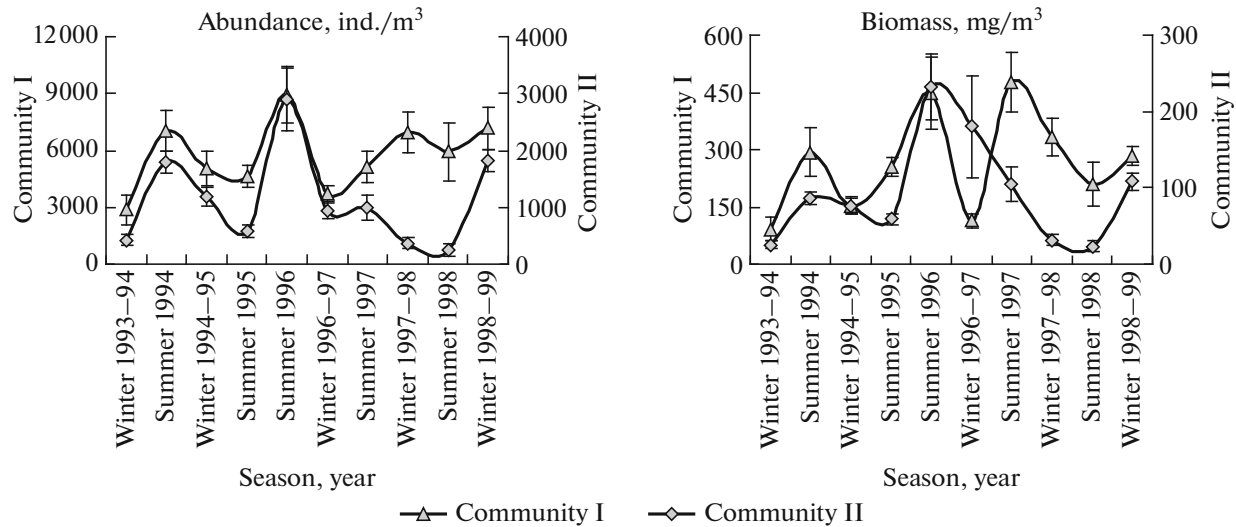


Fig. 2. Abundance and biomass dynamics for major mesozooplankton communities in coastal waters of Morocco.

able (ANOSIM analysis) and stable segregation of two large zooplankton clusters I and II throughout the study period and incidental segregation of one (III) or two (III and IV) small additional clusters. The identified clusters were assigned the ecological status of distinct mesozooplankton communities [38].

Community I. This community was characterized by a high abundance and biomass (5700 ± 860 ind./m³ and 260 ± 40 mg/m³) (Fig. 2). These parameters were 1.5 times higher in summer than in winter, but no statistically significant seasonal differences were identified (Fischer's test result for abundance $F = 2.1$, significance level $p = 0.2$, critical value of Fischer's test result $F_{cr} = 7.7$; for the biomass: $F = 1.5$; $p = 0.3$; $F_{cr} = 7.7$).

Neritic copepod species predominated in the community in summer and winter: the relative abundance of these organisms ranged from 60 to 80% (Table 3). The trophic structure was dominated by fine filter feeders (31%), mixed-food consumers (29%), and small grabbers (25%). Coarse filter feeders acquired a more important role in summer 1996 and in the winter 1996–1997 only. The average values of species diversity and evenness indices were 3.07 bit/ind. and 0.63, respectively.

The dominant function in the species structure of the community was stably fulfilled by three neritic widely tropical copepod crustacean species with a constant frequency of occurrence: *Acartia clausi*, *Paracalanus indicus*, and *Oncaea curta* (Table 4). The subdominant nerito-oceanic constant species *Centropages chierchiaie* acquired a codominant status in rare instances only, since it replaced *P. indicus* (in summer 1995) or *O. curta* (in summer 1997 and in winter 1997–1998).

Community I was usually located above the shelf and the continental slope (Fig. 3). As a rule, this com-

munity spread offshore, far beyond the shelf boundaries, south of Cape Bojador (26° N), where the shelf became much broader and the Canary Current was usually displaced westwards. Biologically, community I gravitated to coastal upwelling waters characterized by lower temperature and salinity; this phenomenon did not depend on season. Moreover, the community distribution boundary largely coincided with the spatial distribution of the isotherm that separated upwelling waters from Canary Current waters (Fig. 3).

Community II. This community was characterized by a relatively low abundance and biomass (1150 ± 190 ind./m³ and 90 ± 20 mg/m³) (Fig. 2). An increase in the values in summer (1.7 times on average) did not attain statistical significance, similar to the case described earlier (for abundance: $F = 3.1$, $p = 0.2$, $F_{cr} = 7.7$; for biomass: $F = 1.1$; $p = 0.4$; $F_{cr} = 7.7$).

The relative abundance of oceanic species in this community (32% on average) was always several times higher than in community I (Table 3). Fine filter feeders (44%) and small grabbers (29%) made a fundamental contribution to the trophic structure; the role of mixed-food consumers was less significant and that of coarse filter feeders was more significant than in community I. The species diversity index was on average 1.3 times higher than in community I and ranged from 3.73 to 4.19 bit/ind.; the evenness index was also higher (1.2 times) and varied in a narrow range of 0.71–0.79.

The species structure was more variable, whereas dominant and subdominant composition was less stable than in community I (Table 5). However, the structure-forming species were usually represented by oceanic and nerito-oceanic organisms from the genus *Clausocalanus* and species *Oithona plumifera*, *Temora stylifera*, and *Centropages chierchiaie*. Neritic commu-

Table 3. Structure of mesozooplankton communities from coastal waters of Morocco, %

Parameter	Winter 1993–1994			Summer 1994		Winter 1994–1995				Summer 1995		Summer 1996	
	community												
	I	II	III	I	II	I	II	III	IV	I	II	I	II
Shannon index, bit/ind.	2.97	4.19	3.51	3.18	3.73	2.84	4.19	2.95	3.91	3.37	3.85	3.18	3.81
Pielou evenness index	0.60	0.76	0.72	0.66	0.71	0.61	0.79	0.61	0.77	0.68	0.76	0.64	0.72
Relative abundance, %													
—neritic species	71	22	53	71	41	84	38	66	32	62	29	76	55
—nerito-oceanic species	19	42	28	23	40	11	37	31	37	27	35	18	23
—oceanic species	10	36	19	6	19	5	25	3	31	11	36	6	22
—fine filter feeders	31	54	33	29	41	24	35	45	47	28	38	31	37
—coarse filter feeders	7	6	15	11	14	10	14	18	28	10	6	14	20
—mixed-food consumers	41	9	16	30	10	39	14	17	10	26	20	16	11
—small grabbers	19	28	18	28	32	25	34	18	13	34	32	37	29
—large grabbers	1	2	4	1	2	1	1	1	1	1	3	1	2
—nonfeeding	1	1	14	1	1	1	2	1	1	1	1	1	1
Parameter	Winter 1996–1997		Summer 1997		Winter 1997–1998		Summer 1998			Winter 1998–1999			
	community												
	I	II	I	II	I	II	I	II	III	I	II	III	
Shannon index, bit/ind.	2.71	4.07	3.26	4.18	3.17	3.96	2.99	3.82	1.41	3.07	4.09	2.21	
Pielou evenness index	0.58	0.73	0.65	0.74	0.67	0.75	0.64	0.76	0.54	0.57	0.75	0.46	
Relative abundance, %													
—neritic species	80	31	61	26	65	13	68	30	26	78	39	92	
—nerito-oceanic species	16	37	28	38	28	44	25	24	70	16	42	2	
—oceanic species	4	32	11	36	7	43	7	46	4	6	19	6	
—fine filter feeders	27	53	40	44	35	48	34	42	9	34	48	9	
—coarse filter feeders	28	9	10	10	13	9	8	13	16	12	11	15	
—mixed-food consumers	25	7	26	16	29	10	27	17	40	29	11	2	
—small grabbers	18	27	21	26	20	27	29	24	5	23	26	72	
—large grabbers	1	3	2	3	2	5	1	3	7	1	3	1	
—nonfeeding	1	1	1	1	1	1	1	1	23	1	1	1	

nity codominants (*P. indicus*, *A. clausi*, and *O. curta*) were also among the structure-forming species in many cases, and sometimes they even played a dominant role. Appendicularia (in summer 1995, 1996, and 1997 and in winter 1997–1998), *Penilia avirostris* cladocerans (in summer 1995) and salps (in winter 1997–1998 and in summer 1998) played an important role in species structure along with copepod crustaceans.

Community II was usually distributed in the oceanic zone and above the continental slope. It was usually displaced by community I (Fig. 3) in areas south of Cape Bohador. Expansion of community II to the shelf was also observed quite often (for example, in winter 1994–1995 and 1996–1997 and in summer 1996). This com-

munity was biotopically associated with oceanic waters of the Canary Current. As mentioned earlier, the boundary between communities I and II largely coincided with the spatial distribution of the isotherm that separated upwelling waters from Canary Current waters (Fig. 3).

Winter mesozooplankton communities near the Cap Blanc. Small communities III and IV became sporadically segregated in the southern coastal waters of Morocco, between the Cap Blanc and Cape Barbas, in winter (Fig. 3, Table 3). If community III appeared alone, it was able to spread both over the shelf and the oceanic part (in winter 1993–1994), and if two communities were segregated (in winter 1994–1995), com-

Table 4. Relative abundance of structure-forming species of neritic community I from coastal waters of Morocco, %

Winter 1993–1994		Summer 1994		Winter 1994–1995	
<i>Acartia clausi</i>	36	<i>Acartia clausi</i>	22	<i>Acartia clausi</i>	36
<i>Paracalanus indicus</i>	15	<i>Oncaea curta</i>	15	<i>Oncaea curta</i>	17
<i>Oncaea curta</i>	10	<i>Paracalanus indicus</i>	14	<i>Paracalanus indicus</i>	14
Clausocalanus sp. cop.	7	<i>Centropages chierchiae</i>	8	Clausocalanus spp. cop.	4
<i>Centropages chierchiae</i>	4	Clausocalanus spp. cop.	5	<i>Temora stylifera</i>	3
<i>Oithona plumifera</i>	2	<i>Evadne spinifera</i>	4	Nauplia Calanus	3
Others	26	Others	32	Others	23
Summer 1995		Summer 1996		Winter 1996–1997	
<i>Oncaea curta</i>	19	<i>Oncaea curta</i>	23	<i>Acartia clausi</i>	24
<i>Acartia clausi</i>	13	<i>Paracalanus indicus</i>	15	<i>Paracalanus indicus</i>	16
<i>Centropages chierchiae</i>	12	<i>Acartia clausi</i>	11	<i>Oncaea curta</i>	9
<i>Paracalanus indicus</i>	7	Appendicularia	4	<i>Temora stylifera</i>	8
<i>Oithona plumifera</i>	4	<i>Calanus helgolandicus</i>	4	<i>Centropages chierchiae</i>	7
Appendicularia	4	<i>Centropages chierchiae</i>	4	<i>Euterpina acutifrons</i>	5
Others	41	Others	39	Others	31
Summer 1997		Winter 1997–1998		Summer 1998	
<i>Paracalanus indicus</i>	17	<i>Paracalanus indicus</i>	20	<i>Acartia clausi</i>	24
<i>Acartia clausi</i>	13	<i>Acartia clausi</i>	14	<i>Paracalanus indicus</i>	21
<i>Centropages chierchiae</i>	12	<i>Centropages chierchiae</i>	13	<i>Oncaea curta</i>	11
Appendicularia	7	<i>Oncaea curta</i>	8	<i>Pleopis polyphemoides</i>	6
<i>Penilia avirostris</i>	6	Appendicularia	6	<i>Evadne spinifera</i>	4
<i>Oncaea curta</i>	6	<i>Calanus helgolandicus</i>	3	Nauplia Calanus	3
Others	39	Others	36	Others	31
		Winter 1998–1999			
		<i>Paracalanus indicus</i>	24		
		<i>Acartia clausi</i>	23		
		<i>Oncaea curta</i>	9		
		<i>Centropages chierchiae</i>	5		
		Appendicularia	3		
		<i>Euterpina acutifrons</i>	3		
		Others	33		

munity III spread over the shelf and community IV spread in the oceanic zone.

The abundance and biomass of community III that developed in winter 1993–1994 were 2050 ± 1050 ind./m³ and 170 ± 80 mg/m³, respectively. The abundance and biomass of similar communities III and IV, which became segregated in winter 1994–1995, were 6450 ± 1100 ind./m³ and 500 ± 190 mg/m³ and 980 ± 430 ind./m³ and 90 ± 20 mg/m³, respectively. The values obtained were comparable to the abundance values for the neighboring major communities I and II that developed at the same time (Fig. 2).

Neritic species predominated in community structure (53–66%), with nerito-oceanic species playing a considerable role in community IV in winter 1994–1995 only (Table 3). The trophic structure was defined by the dominance of fine filter feeders (33–47%). The species diversity and evenness indices were in the ranges of 2.95–3.91 bit/ind. and 0.61–0.77, respectively, and were thus higher than those for neighboring community I and lower than those for neighboring community II.

The major features of the species structure of the community near the Cap Blanc were similar to those

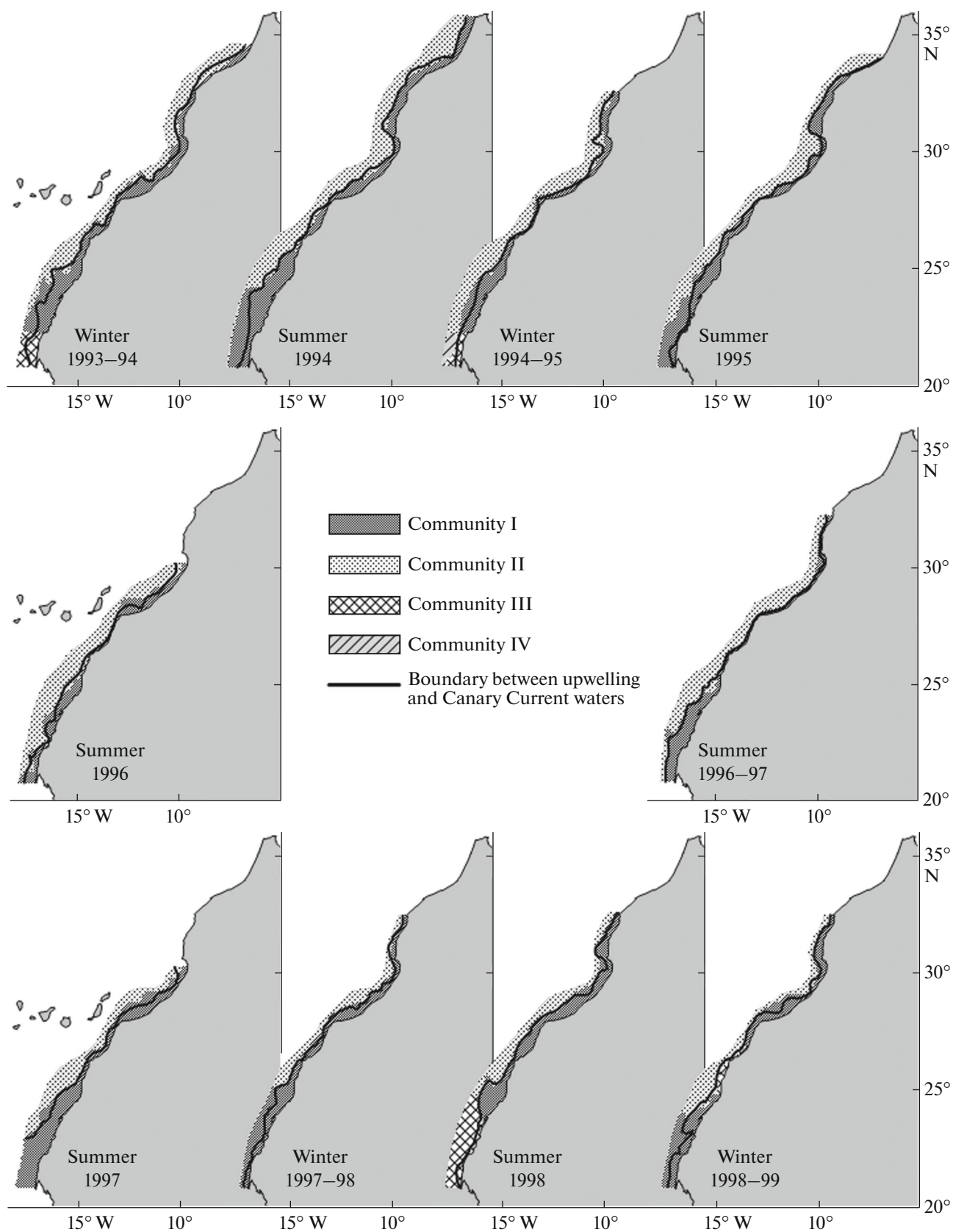


Fig. 3. Spatial distribution of mesozooplankton communities in coastal waters of Morocco in winter and summer 1994–1999.

Table 5. Relative abundance of structure-forming species in distant neritic community II from coastal waters of Morocco, %

Winter 1993–1994		Summer 1994		Winter 1994–1995	
<i>Clausocalanus</i> spp. cop.	18	<i>Clausocalanus</i> spp. cop.	15	<i>Clausocalanus</i> spp. cop.	11
<i>Paracalanus indicus</i>	8	<i>Temora stylifera</i>	10	<i>Oncaea curta</i>	10
<i>Oithona plumifera</i>	7	<i>Oncaea curta</i>	9	<i>Paracalanus indicus</i>	7
<i>Oncaea media</i>	6	<i>Paracalanus indicus</i>	9	<i>Temora stylifera</i>	7
<i>Oncaea curta</i>	5	<i>Centropages chierchiae</i>	6	<i>Acartia clausi</i>	6
<i>Acartia clausi</i>	4	<i>Evadne spinifera</i>	5	<i>Oithona plumifera</i>	5
Others	52	Others	46	Others	54
Summer 1995		Summer 1996		Winter 1996–1997	
Appendicularia	12	<i>Temora stylifera</i>	17	<i>Clausocalanus</i> spp. cop.	11
<i>Temora stylifera</i>	8	Appendicularia	10	<i>Paracalanus indicus</i>	8
<i>Clausocalanus</i> spp. cop.	8	<i>Oncaea curta</i>	9	<i>Oncaea curta</i>	6
<i>Oithona plumifera</i>	6	<i>Paracalanus indicus</i>	6	<i>Oithona plumifera</i>	6
<i>Penilia avirostris</i>	6	<i>Centropages chierchiae</i>	5	<i>Oncaea media</i>	5
<i>Oncaea curta</i>	6	<i>Clausocalanus</i> spp. cop.	4	<i>Temora stylifera</i>	4
Others	54	Others	49	Others	60
Summer 1997		Winter 1997–1998		Summer 1998	
<i>Oithona plumifera</i>	9	<i>Oithona plumifera</i>	16	<i>Oithona plumifera</i>	12
<i>Clausocalanus</i> spp. cop.	8	Salpidae	10	<i>Pleuromamma borealis</i>	8
Appendicularia	6	<i>Clausocalanus</i> spp. cop.	7	<i>Acartia danae</i>	8
<i>Acartia clausi</i>	5	Appendicularia	5	<i>Clausocalanus</i> spp. cop.	7
<i>Paracalanus indicus</i>	5	<i>Mecynocera clausi</i>	4	Salpidae	6
<i>Centropages chierchiae</i>	5	<i>Calocalanus contractus</i>	3	<i>Mecynocera clausi</i>	4
Others	62	Others	55	Others	55
		Winter 1998–1999			
		<i>Paracalanus indicus</i>	14		
		<i>Oithona plumifera</i>	9		
		<i>Oncaea curta</i>	9		
		<i>Clausocalanus</i> sp. cop.	9		
		<i>Ctenocalanus vanus</i>	7		
		Nauplia Calanus	6		
		Others	46		

of the major distant neritic communities (Table 6), with neritic species (*P. indicus*, *A. clausi*, and/or *O. curta*), nerito-oceanic species, and oceanic species (*Clausocalanus* spp., *Oithona plumifera*, *Oncaea media*, and others) acting together as structure-forming species.

However, the essential presence of *Temora turbinata* (in addition to the composition and relative abundance of structure-forming species) distinguished the communities of the Cap Blanc from the neighboring major communities I and II. This species could be subdominant (in winter 1994–1995) or secondary (in winter 1993–1994) in the communities

mentioned above, but it was hardly ever detected in major communities I and II.

Atypical mesozooplankton community in summer 1998. The state of zooplankton in summer 1998 (Fig. 3) did not fit the typical spatial distribution and community structure patterns. Communities I and II did not spread south beyond 24° N during this period, and an atypical community III developed in both the shelf and oceanic zones to the south of these communities and spread over a large territory all the way to the Cap Blanc.

Communities I and II had a typical structure. Community III was characterized by anomalously low abundance parameters (140 ± 40 ind./m³ and

Table 6. Relative abundance of structure-forming species in the communities III and IV from coastal waters of Morocco, %

Winter 1993–1994			Winter 1994–1995					
Community III	<i>Paracalanus indicus</i>	17	Community III	<i>Paracalanus indicus</i>	36	Community IV	<i>Paracalanus indicus</i>	15
	Ova Pisces	14		<i>Acartia clausi</i>	11		Clausocalanus sp. I–V cop.	11
	<i>Acartia clausi</i>	12		<i>Temora turbinata</i>	10		<i>Oithona plumifera</i>	6
	<i>Oithona plumifera</i>	10		<i>Oncaea curta</i>	10		<i>Oncaea curta</i>	5
	<i>Calanoides carinatus</i>	8		<i>Calanoides carinatus</i>	6		Nauplia Eucalanus	4
	<i>Oncaea media</i>	5		<i>Centropages chierchiae</i>	6		<i>Centropages chierchiae</i>	4
	<i>Temora turbinata</i>	4		<i>Podon leuckartii</i>	5		<i>Temora turbinata</i>	4
	Others	29		Others	16		Others	51
Summer 1998			Winter 1998–1999					
Community III	<i>Centropages chierchiae</i>	30	Community III	<i>Oncaea curta</i>	55			
	Ova Pisces	13		Bivalvia	9			
	<i>Calanoides carinatus</i>	9		<i>Oithona nana</i>	7			
	<i>Podon leuckartii</i>	5		<i>Paracalanus indicus</i>	7			
	Appendicularia	5		<i>Euterpina acutifrons</i>	5			
	Decapoda larvae	5		Nauplia Cirripedia	3			
	<i>Temora stylifera</i>	4		<i>Podon leuckartii</i>	3			
	Others	29		Others	11			

$25 \pm 20 \text{ mg/m}^3$). The community mostly consisted of neritic-oceanic species (Table 3). Mixed-food consumers were the fundamental constituents of the trophic structure (40%). Extremely low species diversity (1.41 bit/ind.) and evenness (0.54) indices were the major structural features. They reflected the impoverished character of the species composition and the high degree of dominance of a single neritic-oceanic copepod species *Centropages chierchiae* (Table 6), as well as a high relative abundance of fish eggs. Ichthyoplankton sample analysis performed by V.A. Sedletskaya showed that the eggs belonged to round sardinella (*Sardinella aurita*), a species characteristic of the warmer waters of Mauritania exposed to the influence of SACW [15]. *Calanoides carinatus*, which also showed biotopic association with SACW, had a subdominant status in the community [42].

Analysis of hydrological data showed that the SACW, characterized by relatively high temperature and salinity, spread south along the coast of Morocco (both in the oceanic zone and above the continental slope) with the Canary Current (Figs. 4a–4c). Colder upwelling water with a lower salinity was confined to a broad zone of intensive coastal water uplift that actively developed in the central part of the study area (24° – 29° N). The Canary Current took a sharp westward turn at 25° N in the oceanic zone, and a powerful cyclonic upwelling circulation developed in the coastal zone, which carried the waters offshore, far from the vicinity of the coast. Specific dynamic conditions emerged in the southern part of the study area between 21° N and 24° N. First, advection to the shelf and the

subsequent downward motion of ocean waters with a low nutrient content predominated. Second, a broad convergence zone emerged between the adjacent cyclonic and anticyclonic circulating cells at 24° N. Downwelling also occurred in this zone, and a local transverse blocking dynamic front was formed. The SMF usually located near 21° N in summer was not observed, as it was shifted anomalously to the south (17° – 19° N) during the study period.

These specific dynamic conditions in the area between 21° N and 24° N obviously prevented the southward spreading of communities I and II, on the one hand, and promoted the formation of the atypical community III, on the other hand.

Atypical mesozooplankton community in winter 1998–1999. The state of zooplankton in winter 1998–1999 did not fit the typical pattern either. Another atypical community III that disrupted the spatial distribution of community I (Fig. 3) was segregated on the shelf between 25° – 27° N during this time.

The abundance and biomass ($3950 \pm 2060 \text{ ind./m}^3$ and $100 \pm 60 \text{ mg/m}^3$) of this community did not drop as low as those for the atypical community observed in summer 1998, but on average they still were 1.5 times lower than those of the neighboring community I (Fig. 2). Neritic species dominated this community, with small grabbers dominating the trophic structure (Table 3). The species diversity and evenness indices were low (2.21 bit/ind. and 0.46, respectively), and the neritic species *Oncaea curta*, with a relative abundance

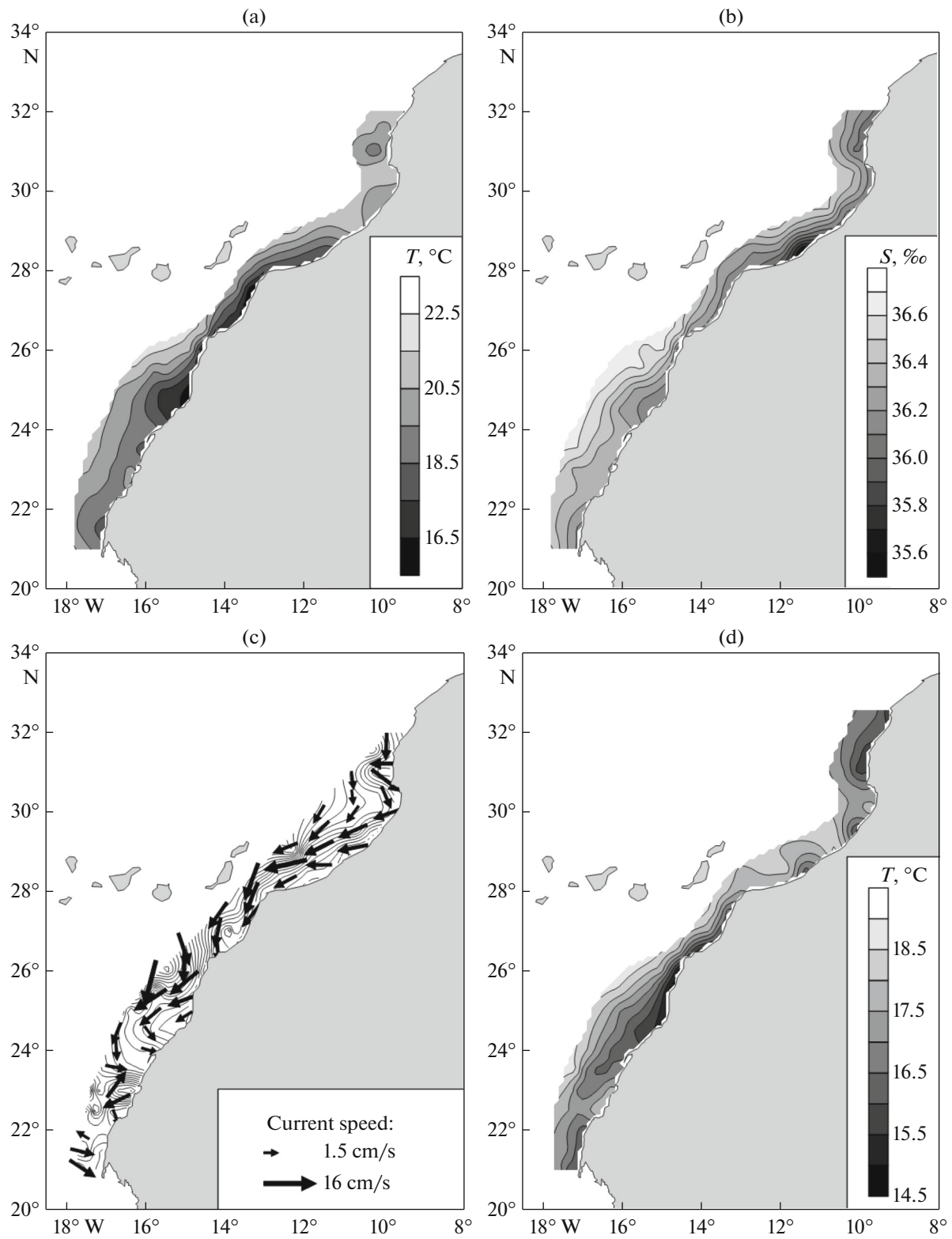


Fig. 4. Distribution of (a) temperature and (b) salinity, current speed and (c) direction at 0 m horizon relatively to 500 m “zero surface” in summer 1998 and (d) temperature distribution at 0 m level in winter 1998–1999 in coastal waters of Morocco.

of approximately 55%, dominated the species structure (Table 6).

The distribution of this community in the temperature field of the ocean surface (Fig. 4d) is evidence of biotopic association of the community with very intensive local upwelling waters with a thermal upwelling index of -4.17°C , or two times higher than the long-term average winter index for the Morocco area (-1.99°C) reported in [16].

DISCUSSION

The faunistic list of mesoplankton from the coastal waters of Morocco compiled by us [22] and partially presented in Table 2 is comparable to the lists reported by other authors [11, 12, 14, 45]. For example, all representatives of large taxa and cladoceran species were typical of Canary upwelling waters [11]. Some of them played an important role in the community structure. Chaetognathans, appendicularia, and decapod larvae usually formed the base of the biomass [11, 30], whereas *P. intermedius* and *E. spinifera* cladocerans often acted as subdominants [22]. Local population bursts were observed for other species, so that they became dominant within a limited area (for example, *P. avirostris*) [22] or acquired a codominant status (for example, Gastropoda) [21].

Our faunistic list of Copepoda included approximately 40% of species from the Copepoda list compiled by Vives [45]. This difference between our results and the data from an earlier study are primarily due to the smaller size of the study area explored by us and the confinement of this area to the epipelagic zone. Therefore, for exactly this reason, the overwhelming majority of species found in the list by Vives [45], but not in our list, were oceanic interzonal or bathypelagic.

Comparison of our results on the frequency of occurrence of mesozooplankton organisms to the materials of earlier studies [14] showed that the constant, secondary, and incidental taxon composition remained unchanged for at least five years. Moreover, the frequency of occurrence of the most thoroughly characterized copepod species in the coastal waters of Morocco was largely similar to that of these species in the coastal areas of the entire North Atlantic subtropical gyre [31]. All these facts point to the high spatio-temporal stability of the faunal distribution in the study area.

The conclusions made by certain authors who performed faunistic studies provide indirect proof for the possible organization of mesozooplankton into two distinct major communities. Differences between zooplankton species composition in the coastal and oceanic zones were reported in [40]. The authors of another study characterized a neritic species complex associated with the shelf zone and an oceanic species complex associated with Canary Current waters [14]. Our results fit the general pattern outlined by the

authors of the studies cited above. Moreover, the neritic species complex characterized by these authors plays a structure-forming role in community I, whereas the oceanic species complex plays a structure-forming role in community II.

As mentioned above, community I (biotopically associated with coastal upwelling waters) mostly consisted of neritic species. The characteristics of this community included a high abundance and biomass, relatively low species diversity and evenness indices, and a stable species structure dominated by *P. indicus*, *A. clausi*, and *O. curta*, three neritic widely tropical species with a constant frequency of occurrence in the community. It is apparently a typical neritic community [4].

Community II, biotopically associated with Canary Current waters, was characterized by a relatively low abundance and biomass, a more variable structure, higher species diversity and evenness indices, and a less stable composition of dominant and subdominant species, with codominants of neritic community I often occupying an important position among these species. All these features allow the conclusion that community II is a distant neritic community that develops between the primary oceanic community of the chalcid zone and the coastal neritic community [4]. This community is subject to the strong influence of coastal fauna and (judging by the above) possesses all properties of ecotonic type communities, such as high species diversity and a variable structure determined by the degree of impact from neritic fauna. This community is expected to include specific boundary species, which are probably represented by *Calanus helgolandicus*, *Calanoides carinatus*, and other nerito-oceanic species that have not been characterized yet in this regard.

Our analysis of the abundance and biomass dynamics for neritic and distant neritic communities I and II did not reveal statistically significant seasonal differences, even though the average values for summer were 1.5 and 1.7 times higher than for winter. Coastal upwelling activity is a principal factor that determines the plankton development intensity in the eastern boundary waters of the ecosystem; this activity, in turn, depends on the wind regime [9]. The seasonal dynamics of these two interrelated factors governs the variability of zooplankton abundance. Thus, the seasonal cycle of the intensity and position of trade wind transfer and the activity and width of the water uplift zone near the coast of Morocco are well studied [33]. This cycle determines the stable impact of the northeast trade wind and maximal upwelling activity along the entire coast of Morocco in spring and summer. This is reflected by the trend to a higher mesozooplankton abundance in summer 1994–1998 reported in the present study. The zone exposed to the trade wind becomes smaller and shifts to the south in winter, so that water uplift remains more active in the south. This apparently led to a slight decrease in meso-

zooplankton abundance and biomass recorded in winters of 1993–1994 to 1998–1999.

Changes in zooplankton abundance in the distant-neritic community II biotopically associated with Canary Current waters were, as a rule, synchronized with similar changes in neritic community I that developed in coastal waters exposed to the direct impact of upwelling. This phenomenon illustrates the effect of coastal upwelling processes on oceanic inhabitants in eastern boundary current waters [9, 40]. The impact is apparently realized along two major pathways [39, 40]. The first pathway is mediated by upwelling cell destruction after weakening of the trade wind, whereas the second involves upwelling filaments.

On the whole, the questions related to the seasonal dynamics of zooplankton abundance in the upwelling ecosystems of the World Ocean remain a matter of discussion. Some authors managed to identify cyclic annual changes in zooplankton associated with the seasonal upwelling cycle [37, 44]. Other authors detected neither strong seasonal changes nor a dependence of zooplankton abundance on abiotic factor dynamics in the same areas [36, 41]. Chelton et al. [37] showed that interannual changes comparable to seasonal changes or even exceeding them in intensity occurred in the upwelling ecosystem along with seasonal zooplankton variability. Interannual variability that masked the seasonal variability predominated in cases when seasonal cycles could not be detected. The predominance of interannual variability in the Canary upwelling ecosystem apparently precluded reliable identification of seasonal variability of the mesozooplankton abundance based on analysis of data available to us.

In discussing the winter communities periodically identified near the Cap Blanc, let us again note that the abundance and biomass of these communities were comparable to those of neighboring major communities I and II, whereas the structure was variable and distinct, but, as a rule, formed by neritic species, with fine filter feeders predominating in the trophic structure. The essential and exclusive presence of *Temora turbinata* was a distinctive feature of the species structure in these communities. It is assumed that this epipelagic neritic-oceanic species develops in warm water only [43] and is characteristic of areas located more to the south and influenced by SACW.

Zooplankton analysis in the coastal waters of Mauritania showed that the studied communities occupied the entire water mass near the Cap Blanc in autumn and winter, so that they could be distinguished both in the coastal waters of Morocco and farther south, down to 20° N [10]. Mixed waters of the subsurface frontal zone that divides the North and South Atlantic central water masses are found below depths of 40 m in this area in autumn and winter. The effect of these waters apparently enables the individualization of these communities. Thus, the association of communities near

the Cap Blanc with the area where NACW and SACW are mixed and the contribution of characteristic SACW species to community structure formation allow the assumption that these communities belong to the ecotone type, segregated from the neritic and distant-neritic communities of Moroccan coastal waters, on one hand, and those of the coastal waters of Mauritania, on the other hand.

Finally, the atypical community III identified in summer 1998 in the waters south of 24° N developed in an area characterized by strong advection of oligotrophic ocean waters to the shelf. The abundance and biomass values were anomalously low in this community, and the biotopic, trophic, and species structures were substantially simplified. These features of the community were apparently reflective of a state of zooplankton degradation due to an abrupt disturbance in the biotope evoked by specific dynamic processes.

Another atypical community identified in winter 1998–1999 was biotopically associated with the “fresh” waters of intensive local upwelling. These conditions are known to provide massive local input of additional external energy, which usually disturbs the spatial uniformity of any community and enhances its heterogeneity [7]. The highly intensive local rise of waters apparently led to differentiation of the neritic community and the formation of a new distinct community characterized by lower abundance and biomass and a simplified structure defined by the predominance of a single neritic species *O. curta*.

Overall, the results obtained corroborate the relationship between the structure of the biotope and formation of the plankton community, with hydrodynamic factors assumed to exert the strongest influence on the structuring of marine and oceanic communities [7, 23]. Moreover, the relatively stable structure and dynamics of the waters ensured a stable spatiotemporal distribution of fauna in the coastal waters of Morocco and stable differentiation of mesozooplankton into two major communities.

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