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Biogeographic inferences of shifting copepod distribution during 1997-1999 El Niño and La Niña in the California Current

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ABSTRACT.- Geographic distribution is provided for the 72 most common copepod species observed in waters off Baja California through the period 1997-1999. In that time the region was subject to extreme changes as the rest of the Pacific basin due to El Niño event, which was followed by a rapid shift to La Niña conditions. Multidimensional Scaling ordination analysis was used to define general spatial patterns. Species were clearly separated in climatic groups. The major cluster corresponded to species covering an extensive area during El Niño (October 1997 and January 1998) disappearing thereafter, or drastically retreating to oceanic locations (e.g. *Undinula darwini*), or southward (e.g. *Pareucalanus attenuatus*). A second assemblage, less copious in species, showed a relative continuous occupancy of the area, increasing the coverage even more during La Niña (January and April 1999). In this group were the endemic species of the Transition-Zone as *Calanus pacificus*, *Eucalanus californicus* and *Rhincalanus nasutus*, as well as subarctic species (e.g. *Neocalanus cristatus*) and other broadly distributed in the central Pacific (e.g. *Pleuromamma*). Other species were scantily represented in warm and cold extremes of the study period, with one cluster showing higher coverage during the warm relaxation phase after El Niño (July 1998), and others in the prelude to cool conditions (October 1998). Most of the species congregated in La Niña group are known for some type of adaptation to regulate their vertical position in the water column, either by seasonal or daily long-distance vertical migration. In contrast most of the “invasive” species are epipelagic, and would be transported with the tropical water and further swept by the renewed strength of the California Current. Most of the cyclopoid and poecilostomatoid copepod species showed an El Niño-type distributional pattern or some climatic relaxation-phase pattern. The biogeographic status of the different species is discussed.

Key words: Copepods, California Current, El Niño, La Niña, biogeography.

Palabras clave: copépodos, corriente de California, El Niño, La Niña, biogeografía.

Introduction

Copepods are the most abundant and diverse invertebrates of the macrozooplankton. Planktonic communities of the California Current System (CCS) are particularly rich in copepod species due the confluence of temperate and tropical faunas. The CCS spans 27 degrees of latitude displaying a gradual physical and biological transition between subarctic and tropical waters. Coalescing with this gradient is an even stronger gradient from coast to ocean, driven by coastal upwelling (Lynn & Simpson 1987). The cooling of coastal waters extends the distribution of temperate species farther south than in any other area in the North Pacific. Both north-south and east-west gradients have complex time and space interactions and variability at different scales (seasonal, interannual, decadal, etc.).

Winds, circulation, and stratification of the water column change seasonally in the CCS. The strongest winds and equatorward flow occurs in spring-summer and the highest stratification takes place in fall-winter (Hickey 1979, Lynn & Simpson 1987). The physical environment and biological processes of the CCS are sensitive to interannual changes (Chelton et al. 1982). During the warm phase of the El Niño Southern Oscillation (ENSO), winds are weak and the water column off the coast is more strongly stratified; in coastal areas the sea level rises due to enhanced poleward flow. Coastal upwelling occurs but the input of nutrients is low due to the sinking of the pycnocline. In contrast, during the cool phase of the ENSO or La Niña, strengthened winds induce intense coastal upwelling activity; the flow toward the equator is also strong (Schwing & Moore 2000). Climate variability is superimposed to seasonal and interannual changes at longer time scales (Bograd & Lynn 2003). The Pacific Decadal Oscillation (PDO), derived from a climatic shift detected about 20-30 years ago in the sea surface temperature, seems to be linked to atmospheric pressure anomalies (Latif & Barnett 1994, Trenberth & Hurrel 1994, Mantua et al. 1997). This shift has generated a well justified interest.

Climatic variability produces changes in the oceanic habitat that are favorable to certain species over others. The biological variability in the CCS at the different time-scales is less well documented, due in part to a late development of methods for chlorophyll measurement and limited sustained efforts toward plankton species identification. Due to the importance of calanoid copepods, they have received more attention than other zooplankton taxa; seasonal changes in the species distribution have been described in detail (Fleminger 1964, 1967, Bowman & Johnson 1973). These CalCOFI atlases are the main source of information for large scale distribution of calanoids in the CCS. However, when analyzing other scales, these studies have limited use. Fleminger's atlases are based in quarterly cruises done between April 1958 and January 1959, a period far from being a normal one; a strong El Niño was active at that time and a relatively high influence of tropical species occurred. Seasonal changes were better tracked by Bowman and Johnson (1973) based on monthly surveys performed in 1949-1950. Unfortunately, the zone off Baja California is only partially included, the cruises covered higher latitudes (46°-28°N).

Interannual changes in the copepod community off southern Baja California were analyzed by Hernández-Trujillo (1999) for ten cruises performed between 1982 and 1989, but changes in the distribution of each species have been not published. Considering the scarce information available for the oceanic Baja California region, a monitoring program was created and is in operation since 1997. This program is known as IMECOCAL (Investigaciones Mexicanas de la Corriente de California) and has the mission of characterizing the pelagic ecosystem of a wide latitudinal fringe between 32-25°N off the Baja California Peninsula. The zooplankton collections from the first six IMECOCAL cruises were used in the present study; the changes in the distribution of copepods collected between October 1997 and April 1999 off north and central Baja California are described and analyzed. These data describe the abrupt changes that occurred during a two-year period (1997-1999), when an extreme El Niño and La Niña events took place (Durazo & Baumgartner 2002, Lavaniegos et al. 2002).

Study Area

The sampling region comprises a broad sector of the California Current system, extending between Ensenada (32°N) and Punta Abreojos (26°N), and from the coastline to 185-260 km offshore, with an additional distance of 150 km in the middle transect lines (Fig. 1). The coastal shelf is narrow along the western peninsular coast, expanding between Punta Baja and Punta Eugenia to configure the Vizcaino Bay, and south to Punta Abreojos forming the Gulf of Ulloa. The continental slope is steep and the bottom depth reaches 3000 m at distances of 150-185 km from the coast in the northern portion of the area, but as near as 60-120 km in the southern sector. The CCS is conformed by the main southward surface flow (California Current) and two poleward currents (coastal Countercurrent and California Undercurrent), which undergo seasonal, interannual and even decadal changes (Hickey 1979, Lynn & Simpson 1987, Bograd & Lynn 2003). The interaction of these currents in combination with coastal upwelling produces intense mixing processes and a mixed biological profile.

Methods and Material

Zooplankton sampling.- Zooplankton samples were collected on board of the R/V *Francisco de Ulloa*, during six IMECOCAL cruises carried out in 28 September-6 October 1997 (9710), 25 January-11 February 1998 (9801), 15-30 July 1998

(9807), 28 September-1 November 1998 (9810), 14-31 January 1999 (9901), and 30 March-16 April 1999 (9904). The sampling grid consisted of ten transect-lines (Fig 1) which were partially or fully covered depending on weather conditions. A total of 342 oblique tows were done with a Bongo net (61 cm mouth diameter, 505 µm mesh). The tow depth was approximately 210 m or 10 m above the bottom at shallow stations. The volume of water strained was measured with a flowmeter in the mouth of the net. The mean volume of filtered water in deep stations was 415 m^3.

Laboratory and data analysis.- Adult copepods were identified to species using sub-samples of 1/8 or 1/16 of the original sample, using the taxonomic keys by Grice (1961), Brodsky (1950), Dawson & Knatz (1980) and Palomares et al. (1998). Copepod abundance was standardized to individuals per volume (ind/1000 m^3).

Distribution maps were based in abundance ranks. Three types of scale were used (1000, 100 or 10 ind/1000 m^3) depending on the abundance of each species. These scales are easily identified in the maps with different color-tones. Multidimensional Scaling (MDS) analysis ordination (Clarke & Warwick 1994) was used in order to define distributional patterns. First a dissimilarity matrix was created with the Bray-Curtis index, based on data of presence-absence. Species selected for this analysis were those most commonly observed in samples (those species being present in 20% or more samples in at least one cruise).

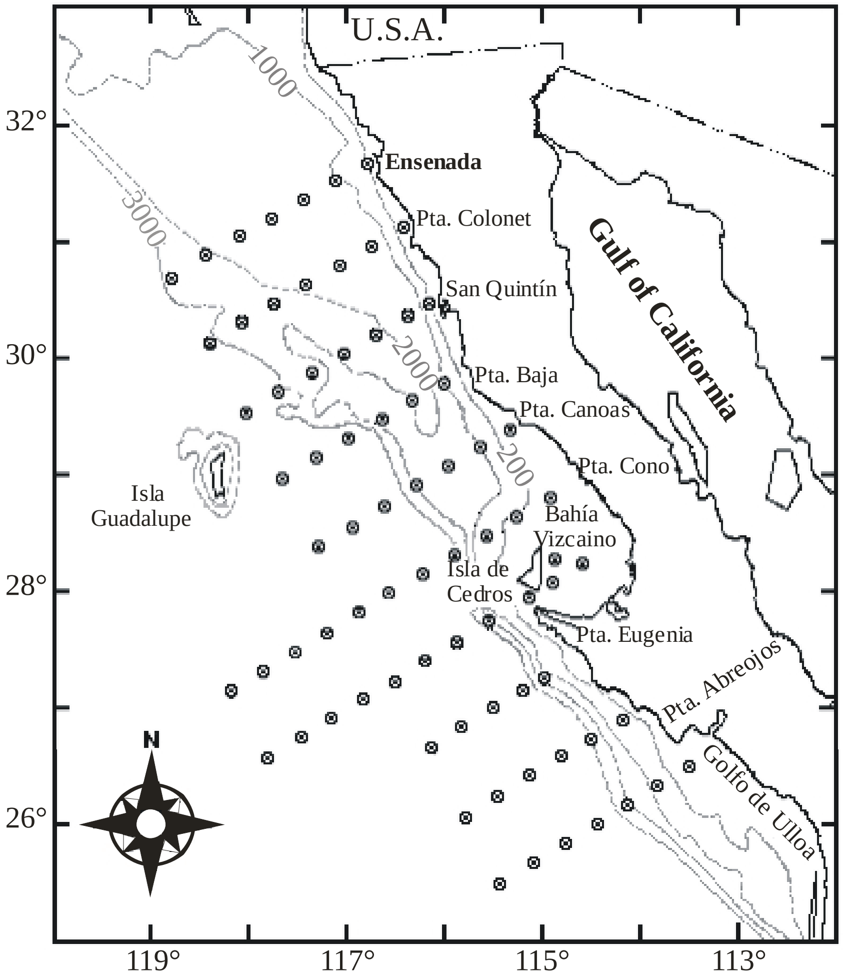

Fig. 1. Study area with IMECOCAL stations grid. Dashed lines indicate isobaths (m).

Results

The taxonomic analysis resulted in the identification of 169 species (the complete list is given in Jiménez-Pérez & Lavaniegos 2004). One half of the species were rare, appearing in less than 10% of the total samples. In the present study the 87 most frequent species were selected, which were present in 20% or more samples in at least one cruise (Table I). These will be referred to as "common species" hereafter. The only genus not identified to species level was included as *Clausocalanus* spp., due to its high occurrence in samples. Records of these species for other locations in the North Pacific are also shown in Table I. This is not an exhaustive list of sources, but includes the main studies treating the calanoid community or/and other planktonic copepod orders focusing in relatively large areas of the northeast Pacific.

Table 1. Common copepod species found in the southern part of the California Current from September 1997 to April 1999. These species were found in 20% or more samples in at least one cruise. The table also shows records for other North Pacific Ocean ecosystems from studies based in relatively extense areas or transects. In these selected sources, most authors offer exhaustive lists of calanoids (B-E, H, K, M, O-Q), cyclopoids (A, I, K, O-Q) or poecilostomatoids (A, K, M, O-Q). Some limited to dominant (J, L) or large-size (F) species or families (G, N) are also included. Letters indicate the source: A= Olson (1949), B= Brodsky (1950), C= Grice (1961), D= Fleminger (1964, 1967), E= Park (1968), F= Gueredrat (1971), G= Brodsky (1972), H= Bowman & Johnson (1973), I= Nishida (1985), J= Arcos & Fleminger (1986), K= Brinton et al. (1986), L= Chen (1986), M= Dessier & Donguy (1987), N= Jiménez-Pérez & Lara-Lara (1988), O= Park (1995), P= Palomares et al. (1998), Q= Fernández-Álamo et al. (2000), R= Suárez-Morales et al. (2000).

SPECIES	SUBARCTIC PACIFIC	CENTRAL NORTH PACIFIC	EQUATORIAL PACIFIC	CALIFORNIA CURRENT	GULF OF CALIFORNIA	EASTERN TROPICAL PACIFIC
ORDER CALANOIDA Sars, 1903						
Family Acartiidae Sars, 1903						
Acartia clausi Giesbrecht, 1892	B			B, D		Q
Acartia danae Giesbrecht, 1889		E	C	D	K, N	M, Q, R
Acartia negligens Dana, 1852		E	C	D	K, N	M
Family Aetideidae Giesbrecht, 1892						
Aetideus acutus Farran, 1929		E	C	D, H	K	
Aetideus bradyi A. Scott, 1909			C	D, H	K, N, P	R
Euchirella curticauda Giesbrecht, 1888			C	B, D, H, P		
Gaetanus minor Farran, 1905			C	D, P		
Gaidius pungens Giesbrecht, 1895				B, D, H, P		
Undeuchaeta intermedia A. Scott, 1909			C	B, D, P		
Family Augaptilidae Sars, 1905						
Haloptilus longicornis (Claus, 1863)		B, E	C	D, H	K	L, Q
Haloptilus ornatus (Giesbrecht, 1892)			C	D, P	K, P	Q
Haloptilus spiniceps (Giesbrecht, 1892)		E	C	D		
Family Calanidae Dana, 1849						
Calanus pacificus Brodsky, 1948	G	E		B, D, H, P	K, N, P	
Mesocalanus tenuicornis (Dana, 1849)	B	B, E, G	C	D, H	K, N, P	J
Nannocalanus minor (Claus, 1863)		E, G	C	D, H, P	K, N, P	J, L, M, Q
Neocalanus cristatus (Kröyer, 1848)	B, G	B, E		B, D, H, P		
Neocalanus gracilis (Dana, 1852)		E, G	C	D	K	J, M
Undinula darwini (Lubbock, 1860)			C	D[1], P	K, N, P	J, L, M, P, Q, R
Undinula vulgaris (Dana, 1849)			C	D[1], P	K, N, P	J, M, P, Q, R

Table 1(continued)

Family Calocalanidae Bernard, 1958						
Calocalanus pavo (Dana, 1852)		E	C	D, P	K, N	M, P, Q
Family Candaciidae Giesbrecht, 1892						
Candacia aethiopica (Dana, 1849)		E	C	D, H, P	N, P	M
Candacia bipinnata (Giesbrecht, 1889)	B	E	C	D, H, P	K	M
Candacia curta (Dana, 1849)			C	D, H, P	K, N, P	M, Q, R
Candacia tenuimana (Giesbrecht, 1889)			C	D		
Paracandacia simplex (Giesbrecht, 1889)			C	D, H, P		M
Paracandacia truncata (Dana, 1849)			C	D[1], P	K, P	M, P, Q, R
Family Centropagidae Giesbrecht, 1892						
Centropages bradyi Wheeler, 1900		B, E		B, D, H, P		
Centropages elongatus Giesbrecht, 1896		E	C	D	P	M
Centropages furcatus (Dana, 1849)				D[1], P	K, N, P	J, L, M, P, Q, R
Centropages gracilis (Dana, 1849)			C	D[1], P	K, P	J, M, P, Q, R
Family Eucalanidae Giesbrecht, 1892						
Eucalanus californicus Johnson, 1938				B, D, H, P		
Eucalanus hyalinus (Claus, 1866)		B	F	B, D, H, P	P	J
Pareucalanus attenuatus (Dana, 1849)		B, E	C, F	D, H	K, N	J, L, M, Q
Rhincalanus nasutus Giesbrecht, 1888		B	C, F	D, H, P	K, N	J, L, Q, R
Subeucalanus crassus Giesbrecht, 1888				D, H	K	
Subeucalanus pileatus Giesbrecht, 1888			C	D	K, N, P	J, Q, R
Subeucalanus subcrassus Giesbrecht, 1888			C, F	P	K, N, P	J, L, M, P, Q, R
Subeucalanus subtenuis Giesbrecht, 1888			C, F	D, P	K, N	J, L, M, Q, R
Family Euchaetidae Giesbrecht, 1892						
Euchaeta acuta Giesbrecht, 1892	O	O		B, D	K, N	L, O
Euchaeta indica Wolfenden, 1905		O	C	D[1], P	K, P	M, P, R
Euchaeta longicornis Giesbrecht, 1888		O	C	D, P	K, N, P	M, Q, R
Euchaeta media Giesbrecht, 1888		E, O	C, F	B, D, P	K, N, P	L
Euchaeta rimana Bradford, 1974		B, E, O	C, F	D, P	K, N, P	L, M, P, Q, R
Paraeuchaeta elongata (Esterly, 1913)	B, O	B		B, O		
Family Heterorhabdidae Sars, 1902						
Heterorhabdus papilliger (Claus, 1863)		E	C	B, D, H, P	K, P	Q
Heterorhabdus tanneri (Giesbrecht, 1895)	B			D		
Heterostylites longicornis (Giesbrecht, 1889)		B, E		B, D, P	K, P	
Family Lucicutiidae Sars, 1902						
Lucicutia flavicornis (Claus, 1863)		B, E	C	D, H, P	K, N, P	L, M, Q
Family Mecynoceridae Andronov, 1973						
Mecynocera clausi Thompson, 1888		E		D, H, P	K	
Family Metridiniidae Sars, 1902						
Metridia pacifica Brodsky, 1950	B	B, E		B, D, H	P	
Pleuromamma abdominalis (Lubbock, 1856)		B	C, F	B, D, H, P	K, N, P	L, M, Q, R
Pleuromamma borealis (F. Dahl, 1893)		B	C	B, D, P	P	M
Pleuromamma gracilis (Claus, 1863)		B	C	D, H, P	K, N, P	L, M, Q
Pleuromamma piseki Farran, 1929				H		M
Pleuromamma quadrungulata (F. Dahl, 1893)			C, F	B, D, P		

Table 1 (continued)

Pleuromamma xiphias (Giesbrecht, 1889)		B	C, F	B, D, H, P	P	
Family Paracalanidae Giesbrecht, 1892						
Acrocalanus longicornis Giesbrecht, 1888			C	D^1	K, N	M, Q
Paracalanus parvus (Claus, 1863)	B	B, E	C	B, D, P	K, N, P	M, Q
Family Phaennidae Sars, 1902						
Phaenna spinifera Claus, 1863		E	C	B, D, H, P	K, N, P	
Family Pontellidae Dana, 1852						
Labidocera acuta (Dana, 1849)				D, P	K, N, P	P, Q, R
Labidocera acutifrons (Dana, 1849)				D^1, P	K, P	M
Labidocera euchaeta Giesbrecht, 1889						
Pontellina plumata (Dana, 1849)		E	C	D, P	K, N, P	M, P, Q, R
Family Scolecithricidae Giesbrecht, 1892						
Lophothrix frontalis Giesbrecht, 1895				B, D, P		
Scolecithricella abyssalis (Giesbrecht, 1888)			C	D	K, N	Q
Scolecithricella dentata (Giesbrecht, 1892)		E		D		
Scolecithricella ovata (Farran, 1905)	B	E		D		
Scolecithrix bradyi Giesbrecht, 1888		E	C	D, P	K, N, P	Q, R
Scolecithrix danae (Lubbock, 1856)		E	C	D, H, P	K, N, P	L, M, P, Q, R
Family Temoridae Giesbrecht, 1892						
Temora discaudata Giesbrecht, 1889				D, P	K, N, P	J, L, M, P, Q, R
ORDER CYCLOPOIDA Burmeister, 1835						
Family Oithonidae Dana, 1852						
Oithona plumífera Baird, 1843		I	I	A, I, P	K, P	I, Q, R
Oithona spinirostris Claus, 1863		I	I	A, I		I
ORDER POECILLOSTOMATOIDA Thorell, 1859						
Family Corycaeidae Dana, 1852						
Corycaeus amazonicus F. Dahl, 1894				A, P	P	
Corycaeus anglicus Lubbock, 1857				A	K	
Corycaeus clausi F. Dahl, 1894					K, N	M
Corycaeus flaccus Giesbrecht, 1891				A^1, P	K, N	M, Q, R
Corycaeus furcifer (Claus, 1863)				A		P
Corycaeus limbatus Brady, 1883				A^1		
Corycaeus speciosus Dana, 1849				P	K, N, P	M, P, Q, R
Family Oncaeidae Giesbrecht, 1892						
Oncaea mediterranea (Claus, 1863)				A		M
Family Sapphirinidae Thorell, 1859						
Copilia mirabilis Dana, 1852				P	K, N, P	P, Q, R
Copilia quadrata Dana, 1849				A^1	K, P	
Sapphirina angusta Dana, 1849					P	
Sapphirina gastrica Giesbrecht, 1891				A^1, P	P	P
Sapphirina gemma Dana, 1852				P	K, P	P, R
Sapphirina nigromaculata Claus, 1863				A	K, N, P	Q, R
Sapphirina stellata Giesbrecht, 1891				P	P	

[1] Recorded only south of Punta Eugenia.

The distribution of all the common species collected through the six analyzed cruises is shown in the appendix. Some of the common species presented wide distribution during El Niño (cruises 9710, 9801) followed by a retraction in subsequent cruises, either offshore (e.g. *Subeucalanus subtenuis*, *Undinula darwini*), southward (e.g. *Pareucalanus attenuatus*, *Candacia curta*), and some disappeared (e.g. *Centropages furcatus*, *Undinula vulgaris*). The opposite tendency would then be expected in temperate species during La Niña, i.e., increased distribution during January and April 1999 (cruises 9901, 9904). This tendency was present but less evident due in part to the limitations of sampling. We have two contrasting falls and two winters to compare, but we lack an April cruise in 1998. It is difficult to discriminate clearly the seasonal or the interannual effects. Many tropical species experienced a reduction of their distributional rank in July 1998, but increased again in October 1998 (e.g. *Neocalanus gracilis*, *Oithona spinirostris*).

Some species such as *Acartia danae* and *Clausocalanus* spp. showed a wider distribution in the region during the intermediate cruises (9807, 9810) than during the climatic extremes. The same problem of a mixed influence of the seasonal and interannual scales exists for spring, but April 1999 was deemed as a cool spring. Most of the species well distributed in the area during La Niña (e.g. *Eucalanus californicus*, *Heterorhabdus papilliger*) were equally well distributed since the relaxation period.

None distribution of one species was exactly equal to the other, but some general patterns can be stated. In order to avoid a detailed species-by-species description, a classification of patterns will be described in the next section using multivariated techniques.

Multidimensional Scaling ordination analysis.- Shifts in spatial distribution throughout the study period were not always clear and each species show particularities related not only to their optimal thermohaline range but also to behavior. Vertical migration contributes to the inaccuracy of the statement of real absence of some species (p. ex. *Pleuromamma*). The MDS ordination analysis is a useful tool to find spatial patterns among the diverse species distributions. In order to maximize the interannual contrast we performed this analysis using separated set of data, one for fall-winter (cruises 9710, 9801, 9810, 9901) and the other for spring-summer (9807, 9904). In the fall-winter group all 88 common species were represented, whereas the spring-summer set contained only 77. The resultant MDS (Fig. 2) indicated a configuration highly influenced by the number of zero values (absence) in the data. The species with a mean occurrence per cruise higher than 50% were strongly concentrated in the nucleus of the MDS ordination, and the species decreasing in occurrence moving away to the periphery. Therefore, it appears appropriate to separate the analysis at levels of major or minor relative occurrence to minimize the zero values effect, thus magnifying the geographic differences of the species.

High frequency species.- In the first level, there were 16 nuclear species, i.e., those with mean occurrence per cruise higher than 50% (Fig. 3). The resultimg MDS for fall-winter may be better explained by quadrants where the x-axis is the climate and the y-axis is the onshore-offshore gradient (Fig. 3a). As can be verified in the distributional maps (Appendix), the species in the lower quadrants presented even distributions, with those falling rightward covering more area in the warm period (9710-9801), and those to the left more extended during the cool period (9810-9901). *Undinula darwini* and *Eucalanus californicus* represented the extremes of this tendency. The former species invaded the whole region during El Niño and moved offshore in La Niña, whereas the latter was restricted to the northern sector, progressing subsequently to cover the complete region. *Calanus pacificus* and *Rhincalanus californicus* presented wide covertures during both climatic extremes. Therefore, these could be considered the nucleii of the endemic species, well adapted to the extreme changes of this sector of the California Current.

The upper quadrants of the fall-winter MDS (Fig. 3a) presented an uneven distribution. Species to the right (*Pleuromamma abdominalis*, *P. borealis*, *P. gracilis*) were patchy, evidencing the vertical migratory activity of this genus. Species to the left (*Haloptilus longicornis*, *Heterorhabdus papilliger*, *Scolecithrix bradyi*) showed a peripheral distribution during El Niño, avoiding the shallow region of Vizcaino Bay and the immediate offshore area. *Haloptilus longicornis* also avoided coastal locations during cruises 9810 and 9901.

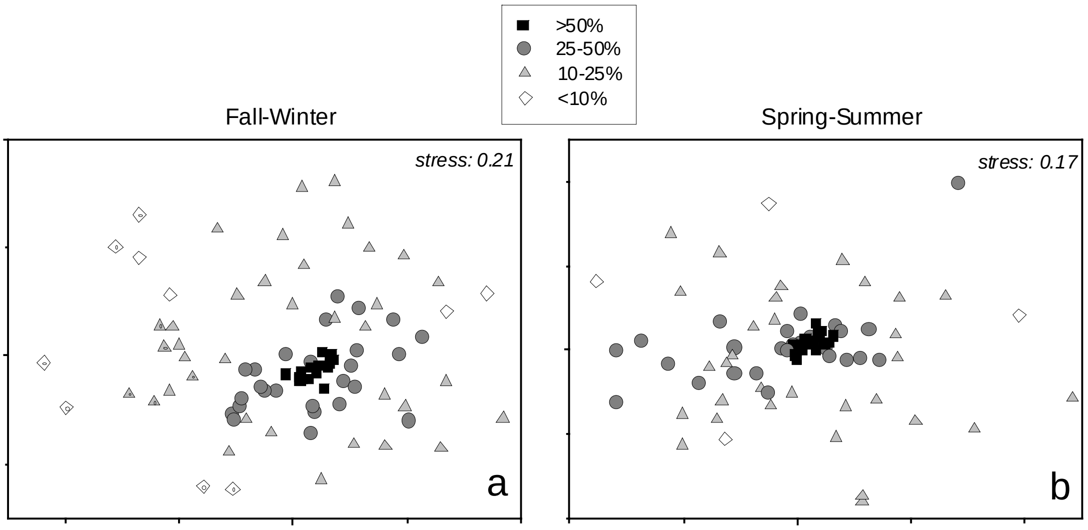

Fig. 2. MDS ordination of the common copepod species (N=88) based on Bray-Curtis dissimilarity index. The fall-winter MDS (a) included cruises 9710, 9801, 9810, 9901, and the spring-summer MDS (b), cruises 9807, 9904. Symbols represent mean percentage of occurrence per cruise taken the complete study period. Symbols with points were species absent in spring-summer.

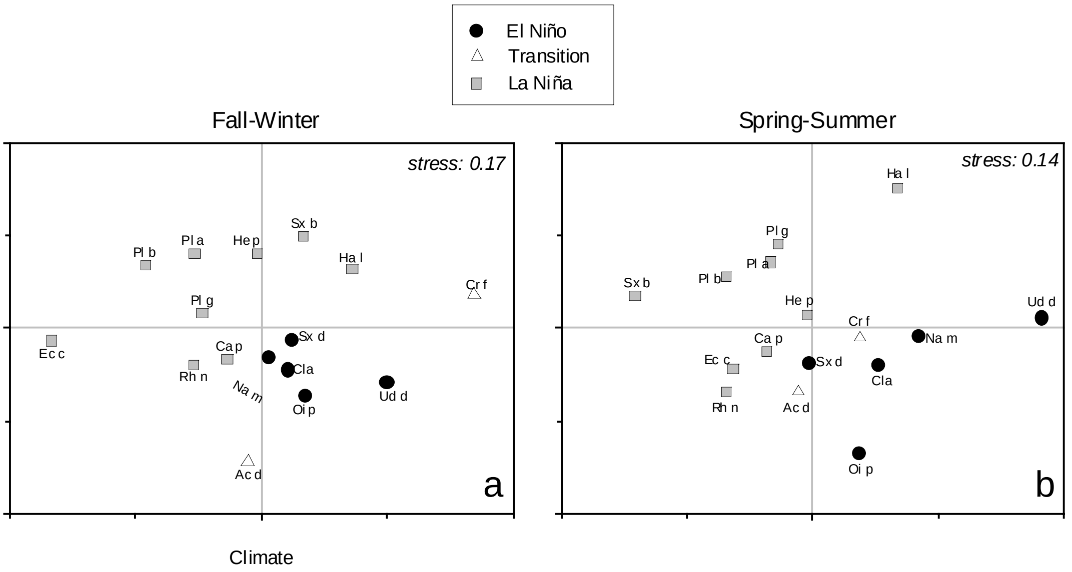

Figure 3. MDS ordination of the common species with high occurrence (mean per cruise >50%) during fall-winter (a) and spring-summer (b). The species were *Acartia danae* (Ac d), *Calanus pacificus* (Ca p), *Clausocalanus* spp. (Cla), *Eucalanus californicus* (Ec c), *Haloptilus longicornis* (Ha l), *Heterorhabdrus papilliger* (He p), *Nannocalanus minor* (Na m), *Pleuromamma abdominalis* (Pl a), *P. borealis* (Pl b), *P. gracilis* (Pl g), *Rhincalanus nasutus* (Rh n), *Scolecithrix bradyi* (Sx b), *S. danae* (Sx d), *Undinula darwini* (Ud d), *Oithona plumífera* (Oi p), and *Corycaeus flaccus* (Cr f).

Species from El Niño group appeared dispersed to the right in the spring-summer MDS (Fig. 3b), excepting *Scolecithrix danae*, widely distributed during July 1998. However, it is retained in El Niño group due to its transgression to the neritic region in the warm period. In contrast, species from La Niña group remained together in the spring-summer MDS (Fig. 3b), excepting *H. longicornis* that was absent in the shallow stations.

Regular frequency species.- There were 26 species with mean occurrence between 25 and 50% per cruise. In the fall-winter MDS (Fig. 4a) the species kept a bipolar arrangement with the species better distributed during El Niño aggregated to the right along the climate axis (x-axis). Species less spatially represented during El Niño fall and/or winter appeared more disperse on the left side of the MDS. The y-axis did not show in this case any relation with the distance to the coast, but appeared to be more related with coverage during October 1998. Thus, *Metridia pacifica* and *Gaidius pungens* were poorly distributed in October 1998 whereas *Mesocalanus tenuicornis* and *Corycaeus furcifer* were equally distributed both in 9810 and 9901.

Four species (*Acartia negligens*, *Paracandacia simplex*, *Candacia aethiopica*, and *C. bipinnata*) were better distributed in October 1998 than other fall-winter cruises. Their maximal occurrence in the phase between El Niño and La Niña was confirmed also in the spring-summer MDS (Fig. 4b). These species were well distributed in the oceanic region during July 1998 (*A. negligens* in less degree) denoting affinity to the upwelling season and proximity to La Niña group in the MDS. *Aetideus bradyi* was kept in La Niña group despite its central position in the fall-winter MDS (Fig. 4a), because it was well distributed in 9904, approaching to La Niña group in the spring-summer MDS (Fig. 4b). *Euchaeta media* and *Pleuromamma piseki* are difficult to fit in a particular group. Both species were in the center of the fall-winter MDS (Fig. 4a) and approached to La Niña group in the spring-summer MDS (Fig. 4b). However, if fall to fall and winter to winter are compared they moved as tropical species. *Euchaeta media* retreated southward in 9810 compared to 9710, and moved offshore in 9901 compared to 9801; *P. piseki* retreated southward in 9901 compared to 9801.

Species virtually absent in 9807 and 9904 must be included in El Niño assemblage despite their dispersion in the spring-summer MDS (Fig. 4b). Moreover, *Neocalanus gracilis*, with a unique record in 9904 was excluded from the MDS plot to avoid the collapse of the remainder species under consideration. Other species maintained limited occurrence in July 1998 (*Euchaeta rimana*, *Subeucalanus subtenuis*, *S. subcrassus*, and *Pareucalanus attenuatus*).

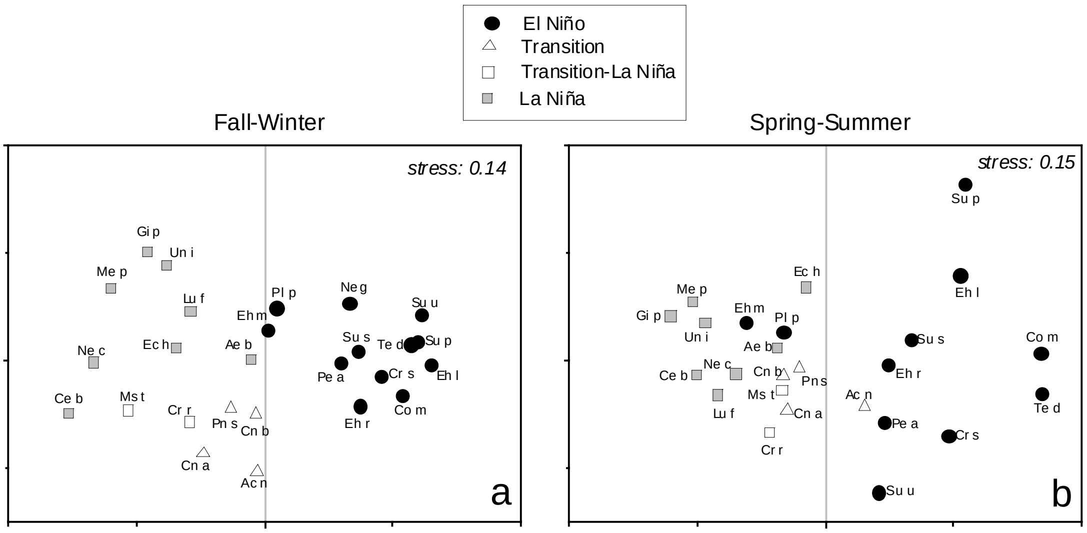

Fig. 4. MDS ordination of the common species with medium occurrence (mean per cruise 25-50%) during fall-winter (a) and spring-summer (b). The species were *Acartia negligens* (Ac n), *Aetideus bradyi* (Ae b), *Candacia aethiopica* (Cn a), *C. bipinnata* (Cn b), *Centropages bradyi* (Ce b), *Eucalanus hyalinus* (Ec h), *Euchaeta longicornis* (Eh l), *E. media* (Eh m), *E. rimana* (Eh r), *Gaidius pungens* (Gi p), *Lucicutia flavicornis* (Lu f), *Mesocalanus tenuicornis* (Ms t), *Metridia pacifica* (Me p), *Neocalanus cristatus* (Ne c), *N. gracilis* (Ne g), *Paracandacia simplex* (Pn s), *Pareucalanus attenuatus* (Pe a), *Pleuromamma piseki* (Pl p), *Subeucalanus pileatus* (Su p), *S. subcrassus* (Su u), *S. subtenuis* (Su s), *Temora discaudata* (Te d), *Undeuchaeta intermedia* (Un i), *Copilia mirabilis* (Co m), *Corycaeus furcifer* (Cr r), and *C. speciosus* (Cr s).

Low frequency species.- The MDS analysis for species present between 10 and 25% (mean per cruise) included inside the El Niño cluster many species exclusive or almost exclusive of one cruise. Some of these species covered the area completely in October 1997, showing a drastic reduction afterwards. Only scarce remnants persisted during January 1998, confined to Vizcaino Bay (*Centropages furcatus*, *Labidocera acutrifrons*, *Undinula vulgaris*) or adjacent stations (*Paracalanus parvus*, *Corycaeus amazonicus*). Other species (*Euchaeta indica*, *Heterorhabdus tanneri*, *Corycaeus anglicus*) were relatively extended in both El Niño cruises, and *Scolecithricella abyssalis* had the best coverage in 9801. These nine species appeared grouped to the right in the fall-winter MDS (Fig. 5a) and were completely absent in the cruises 9807 and 9904. With only one record in 9807, *S. abyssalis*, had to be excluded in the spring-summer MDS (Fig. 5b) to avoid collapse of the plot. The rest (*Euchaeta indica*, *Corycaeus amazonicus* and *Paracalanus parvus*) also with few records resulted displaced to the edge of the MDS (Fig. 5b).

A subgroup of species within the El Niño assemblage (Fig. 5a) was also relatively important in October 1998, but their warm affinity is apparent in their southward displacement (*Sapphirina gastrica*, *Candacia curta*). *Pontellina plumata* was distributed in January 1999, though was mainly displayed during El Niño cruises. The subgroup split in two in the spring-summer MDS (Fig. 5b), due to some species (*Candacia curta*, *Centropages gracilis*, *Sapphirina nigromaculata*) were partially distributed in July 1998.

La Niña group was small. However, there were many species difficult to label, though in general appeared to be better distributed during the El Niño-La Niña transition (Fig. 5). The species clearly favored by La Niña conditions were *Scolecithricella ovata* and *Aetideus acutus*. Other species close to *S. ovata* and *A. acutus* in the MDS plots (Fig. 5) were scattered throughout the study period. They had a coverage slightly higher in 9901 (*Gaetanus minor*, *Lophothrix frontalis*, *Pleuromamma quadrangulata*) or 9904 (*Pleuromamma xiphias*), and the special case of *Corycaeus limbatus* which was well distributed in 9801, 9810, and 9904.

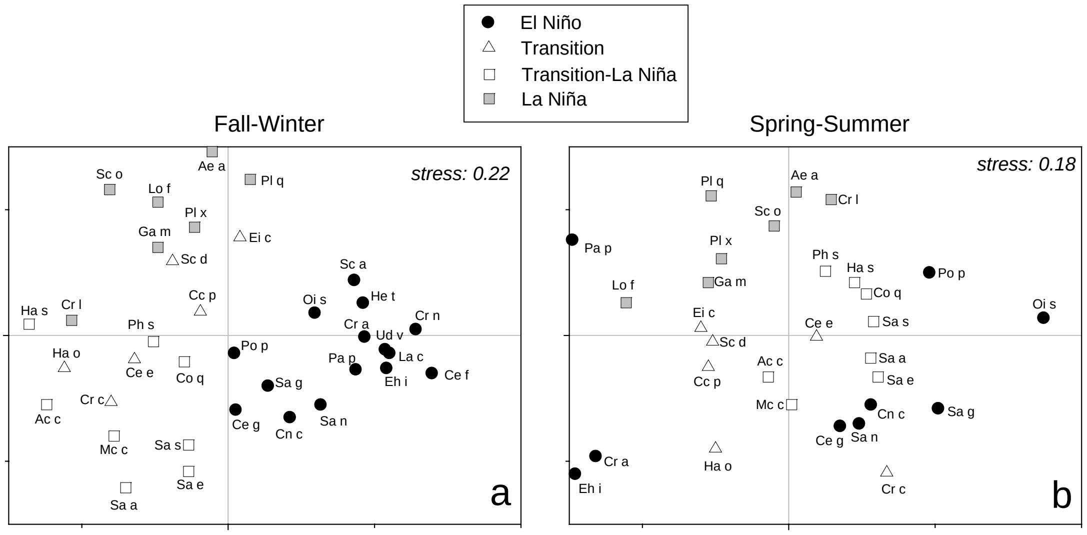

Fig. 5. MDS ordination of the common species with low occurrence (mean per cruise 10-25%) during fall-winter (a) and spring-summer (b). The species were *Acartia clausi* (Ac c), *Aetideus acutus* (Ae a), *Calococalanus pavo* (Cc p), *Candacia curta* (Cn c), *Centropages elongatus* (Ce e), *C. furcatus* (Ce f), *C. gracilis* (Ce g), *Euchaeta indica* (Eh i), *Euchirella curticauda* (Ei c), *Gaetanus minor* (Ga m), *Haloptilus ornatus* (Ha o), *H. spiniceps* (Ha s), *Heterorhabdus tanneri* (He t), *Labidocera acutífrons* (La c), *Lophothrix frontalis* (Lo f), *Mecynocra clausi* (Mc c), *Paracalanus parvus* (Pa p), *Phaenna spinífera* (Ph s), *Pleuromamma quadrungulata* (Pl q), *P. xiphias* (Pl x), *Pontellina plumata* (Po p), *Scolecithricella abyssalis* (Sc a), *S. dentata* (Sc d), *S. ovata* (Sc o), *Undinula vulgaris* (Ud v), *Oithona spinirostris* (Oi s), *Copilia quadrata* (Co q), *Corycaeus amazonicus* (Cr a), *C. anglicus* (Cr n), *C. clausi* (Cr c), *C. limbatus* (Cr l), *Sapphirina angusta* (Sa a), *S. gastrica* (Sa g), *S. gemma* (Sa e), *S. nigromaculata* (Sa n), and *S. stellata* (Sa s).

Species distributed within the relaxation period presented two general tendencies: 1) species with the best coverage in October 1998 and partial distribution during 9807 northward (*Euchirella curticauda*, *Scolecithricella dentata*, *Calocalanus pavo*) or southward (*Centropages elongatus*, *Haloptilus ornatus*, *Corycaeus clausi*); 2) species with the best coverage in one or both transition cruises and also during La Niña. Those better distributed during 9904 (*Phaenna spinifera*, *Haloptilus spiniceps*, *Copilia quadrata*, *Sapphirina angusta*, *S. gemma*, *S. stellata*) fall together in the spring-summer MDS (Fig. 5b), separated from *Mecynocera clausi* and *Acartia clausi*, with main occurrence in 9807.

Rare species.- Ten species had less than 10% mean occurrence per cruise, most of them contained in El Niño group (Fig. 6b) and being predominantly observed in October 1997 (*Acrocalanus longicornis Labidocera acuta*, *L. euchaeta*, *Paraeuchaeta elongata*, *Paracandacia truncata*, *Subeucalanus crassus*) or January 1998 (*Euchaeta acuta*, *Candacia tenuimana*). Most of the species from El Niño group were absent in 9807 and 9904 cruises and did not take part in the spring-summer MDS (Fig. 6b). Only *Heterostylites longicornis* and *Oncaea mediterranea* were separated from the rest in the fall-winter MDS (Fig. 6a). Both were observed mainly in October 1998 and January 1999.

Climatic groups.- Resuming the MDS analysis, four climatic groups were defined, two for species better distributed in one of the extreme phases of the ENSO cycle (El Niño and La Niña), and two more groups for species with better spatial coverage during the shift between the extreme events (warm-phase and cool-phase). El Niño group contained more species (39), but most of them had regular, low or rare occurrence (Table 2). This group reached around 60% of the copepods abundance in most of the area during fall 1997, and up to 80% inside and around Vizcaino Bay (Fig. 7). Only few north offshore stations recorded less than 40% of the copepod abundance from this group. It is impossible to define how far north did these species reach influence due to lack of samples in the northern transects during 9710. January 1998 had also high percentages of El Niño species, but the spatial pattern was different, with more influence in the southwest offshore region. This suggests a strong input of North Pacific Central water in 9801 (Fig. 7). Relative abundance of El Niño group was below 60% in the northern area, with the minimal percentages near the coast, contrasting with the coastal trend in 9710.

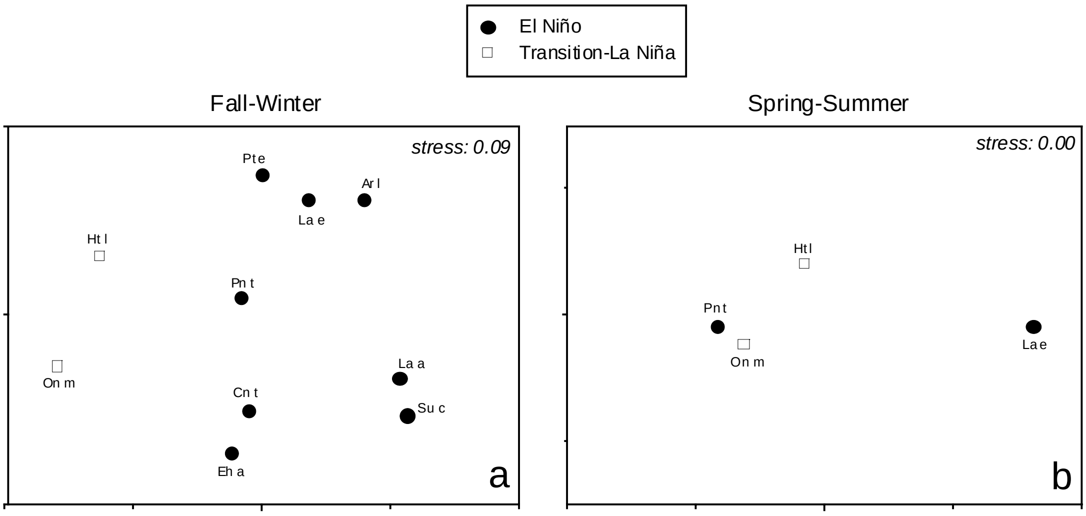

Fig. 6. MDS ordination of the common species with limited occurrence (mean per cruise <10%) during fall-winter (a) and spring-summer (b). The species were *Acrocalanus longicornis* (Ar l), *Candacia tenuimana* (Cn t), *Euchaeta acuta* (Eh a), *Heterostilytes longicornis* (Ht l), *Labidocera acuta* (La a), *L. euchaeta* (La e), *Paraeuchaeta elongata* (Pt e), *Paracandacia truncata* (Pn t), *Subeucalanus crassus* (Su c), and *Oncaea mediterranea* (On m).

Table 2.- Climatic groups resultant from the MDS ordinations analysis based in presence-absence of common species (N=88). Percentages are mean occurrence per cruise.

OCCUR-RENCE	EL NIÑO	SHIFT		LA NIÑA
	(9710, 9801)	WARM PHASE (9807)	COOL PHASE (9810)	(9901, 9904)
High (>50%)	*Nannocalanus minor* *Undinula darwini* *Clausocalanus* spp. *Scolecithrix danae* *Oithona plumifera*[1]	*Acartia danae* *Corycaeus flaccus*[1]		*Calanus pacificus*[3] *Eucalanus californicus*[3] *Rhincalanus nasutus*[3] *Haloptilus longicornis*[2] *Heterorhabdus papilliger*[1,2] *Pleuromamma abdominalis*[2] *Pleuromamma borelais*[2] *Pleuromamma gracilis*[2] *Scolecithrix bradyi*[2]
Medium (25-50%)	*Neocalanus gracilis* *Pareucalanus attenuatus* *Subeucalanus pileatus* *Subeucalanus subcrassus* *Subeucalanus subtenuis* *Euchaeta longicornis*[1,2] *Euchaeta media*[1] *Euchaeta rimana*[1] *Pleuromamma piseki*[2] *Temora discaudata* *Corycaeus speciosus*[1] *Copilia mirabilis*[1]	*Acartia negligens* *Candacia aethiopica*[1] *Candacia bipinnata*[1] *Paracandacia simplex*[1]	*Mesocalanus tenuicornis*[2] *Corycaeus furcifer*[1]	*Aetideus bradyi* *Gaidius pungens* *Undeuchaeta intermedia*[1] *Neocalanus cristatus*[3] *Centropages bradyi* *Eucalanus hyalinus*[2] *Metridia pacifica*[3] *Lucicutia flavicornis*
Low (10-25%)	*Undinula vulgaris* *Candacia curta*[1] *Centropages furcatus* *Centropages gracilis* *Euchaeta indica*[1] *Heterorhabdus tanneri*[1,2] *Paracalanus parvus* *Labidocera acutrifrons*[1] *Pontellina plumata*[1] *Scolecithricella abyssalis* *Oithona spinirostris* *Corycaeus amazonicus*[1] *Corycaeus anglicus*[1] *Sapphirina gastrica*[1] *Sapphirina nigromaculata*[1]	*Euchirella curticauda*[2] *Haloptilus ornatus*[2] *Calocalanus pavo* *Centropages elongatus* *Scolecithricella dentata* *Corycaeus clausi*[1]	*Acartia clausi* *Haloptilus spiniceps* *Mecynocera clausi* *Phaenna spinifera*[1,2] *Copilia quadrata*[1] *Sapphirina angusta*[1] *Sapphirina gemma*[1] *Sapphirina stellata*[1]	*Aetideus acutus*[2] *Gaetanus minor*[2] *Pleuromamma quadrangulata* *Pleuromamma xiphias*[2] *Lophothrix frontalis*[2] *Scolecithricella ovata*[2] *Corycaeus limbatus*[1]
Rare (<10%)	*Candacia tenuimana*[1] *Paracandacia truncata*[1] *Subeucalanus crassus* *Euchaeta acuta*[1] *Paraeuchaeta elongata*[1,2] *Acrocalanus longicornis* *Labidocera acuta*[1] *Labidocera euchaeta*[1]		*Heterostylites longicornis*[1] *Oncaea mediterranea*[1]	

[1] Carnivore species

[2] Mesopelagic or long-distance vertical migrating species

[3] Species performing seasonal migrations

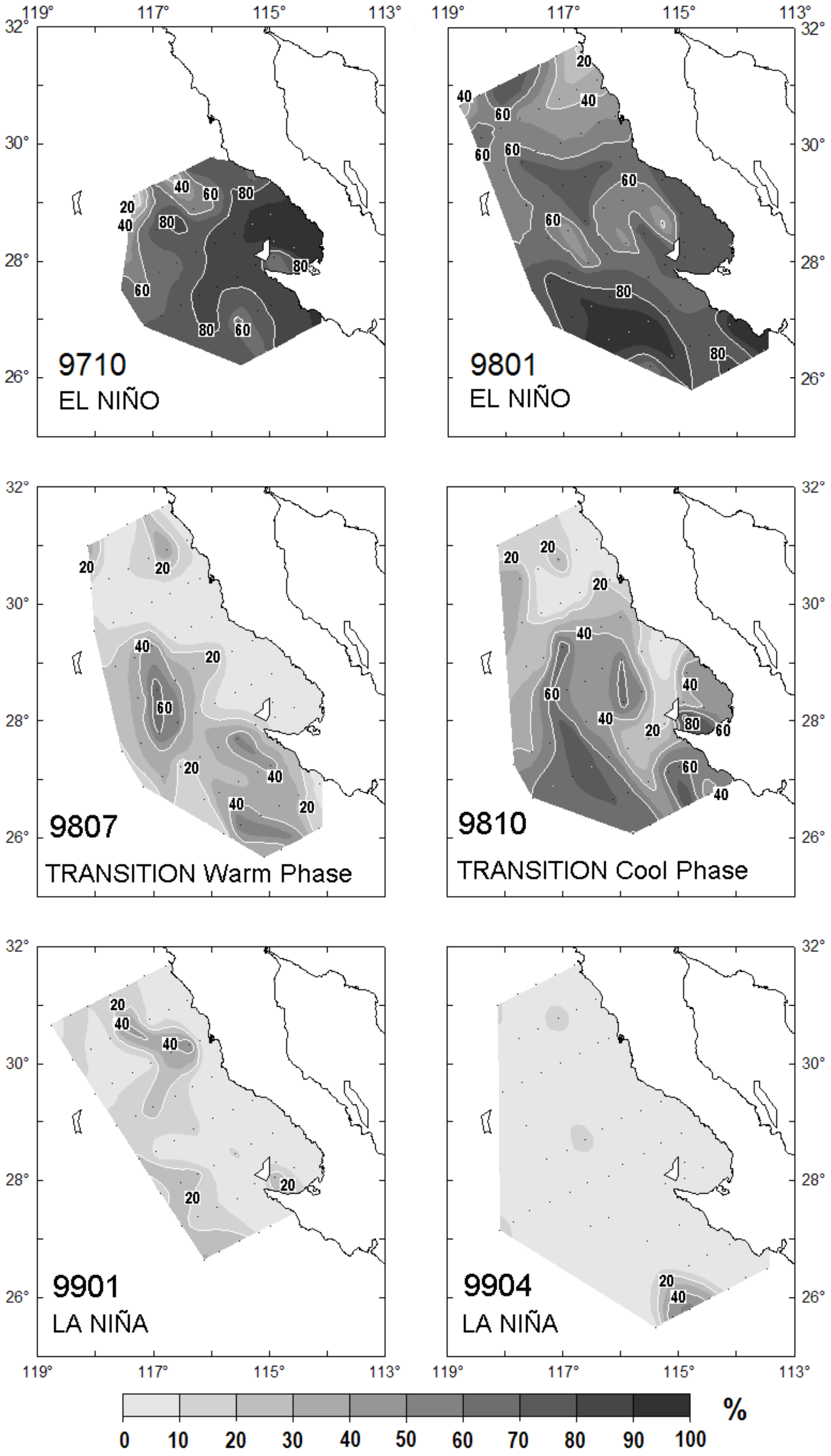

Fig. 7. Progressive decrease in relative abundance of El Niño group species (enlisted in Table 2) through 1997-1999.

Table 3. Calanoid species defined in biogeographic groups by Fleminger (1967) and changes proposed based in the response of species to extreme climate events in the present study.

OCEANIC SPECIES

Fleminger (1967)		Status change
SUBARCTIC	TRANSITIONAL	
Neocalanus cristatus	*Calanus pacificus* [1]	
EQUATORIAL	*Candacia bipinnata*	*C. bipinnata* to Warm-Temperate Cosmopolite Group
Paracandacia truncata	*Eucalanus californicus*	
Centropages gracilis	*Heterorhabdus tanneri*	*H. tanneri* to Equatorial or Central Group
Euchaeta acuta	*Rhincalanus nasutus*	
Euchaeta longicornis	*Metridia pacifica* [1]	
Scolecithricella abyssalis	*Pleuromamma borealis*	
	Scolecithricella ovata	
CENTRAL	CENTRAL + EQUATORIAL	
Neocalanus gracilis	*Pleuromamma abdominalis*	
Paracandacia simplex	*Pleuromamma gracilis*	*L. acutifrons* to Coastal-Neritic Tropical
Centropages elongatus	*Scolecithrix bradyi*	
Eucalanus hyalinus	*Nannocalanus minor*	
Euchaeta media	*Pareucalanus attenuatus*	
Mecynocera clausi	*Euchaeta rimana* [1]	
Pleurommama xiphias	*Scolecithrix danae*	
	Labidocera acutifrons	

COASTAL-NERITIC SPECIES

Fleminger (1967)		Status change
BOREAL	TEMPERATE-SUBTROPICAL	
Acartia clausi	*Candacia curta*	*C. curta* to Oceanic Equatorial Group;
TROPICAL	*Paracalanus parvus*	*P. parvus* and *T. discaudata* to Tropical Group
Centropages furcatus	*Temora discaudata*	
Subeucalanus pileatus		
Euchaeta indica [1]		
Labidocera acuta		

[1] Recorded as *C. helgolandicus*, *M. lucens*, *E. marina*, and *E. wolfendeni*, respectively.

Relative abundance of El Niño group was drastically reduced in July 1998, with half of the area showing percentages below 40% (Fig. 7). A relative increase of El Niño species occurred in October 1998 only in the southern part, which is their usual area of influence in that season. In the cool period only 10% of copepods were from El Niño group, in half of the area parallel to the coast during 9901, and all over the place in 9904.

The tendencies observed in La Niña group present an inverse projection of Fig. 7. A lower number of species were contained in this assemblage, but more of them had high occurrence. Particularly, endemic species (*Calanus pacificus*, *Rhincalanus nasutus*, *Pleuromamma borealis*) showed a notable increase during La Niña and exhibit their preference for cool temperatures along the upwelling region.

Trophic composition.- Many of the common species from El Niño assemblage were carnivorous. There was a high range of size classes: small carnivores as *Oithona* (1-1.3 mm) and *Corycaeus* (1-2 mm), medium-sized such as Candacidae (2-2.5 mm) and Sapphirinidae (2-3 mm), and the large carnivores *Labidocera* (2.5-4 mm), *Euchaeta* (2.5-4 mm), *Heterorhabdus tanneri* (4 mm), and *Pareuchaeta elongata* (6.8 mm). In total the carnivore species represented 55% of the species from El Niño group, contrasting with the 9% in La Niña group (Fig. 8, Table 2).

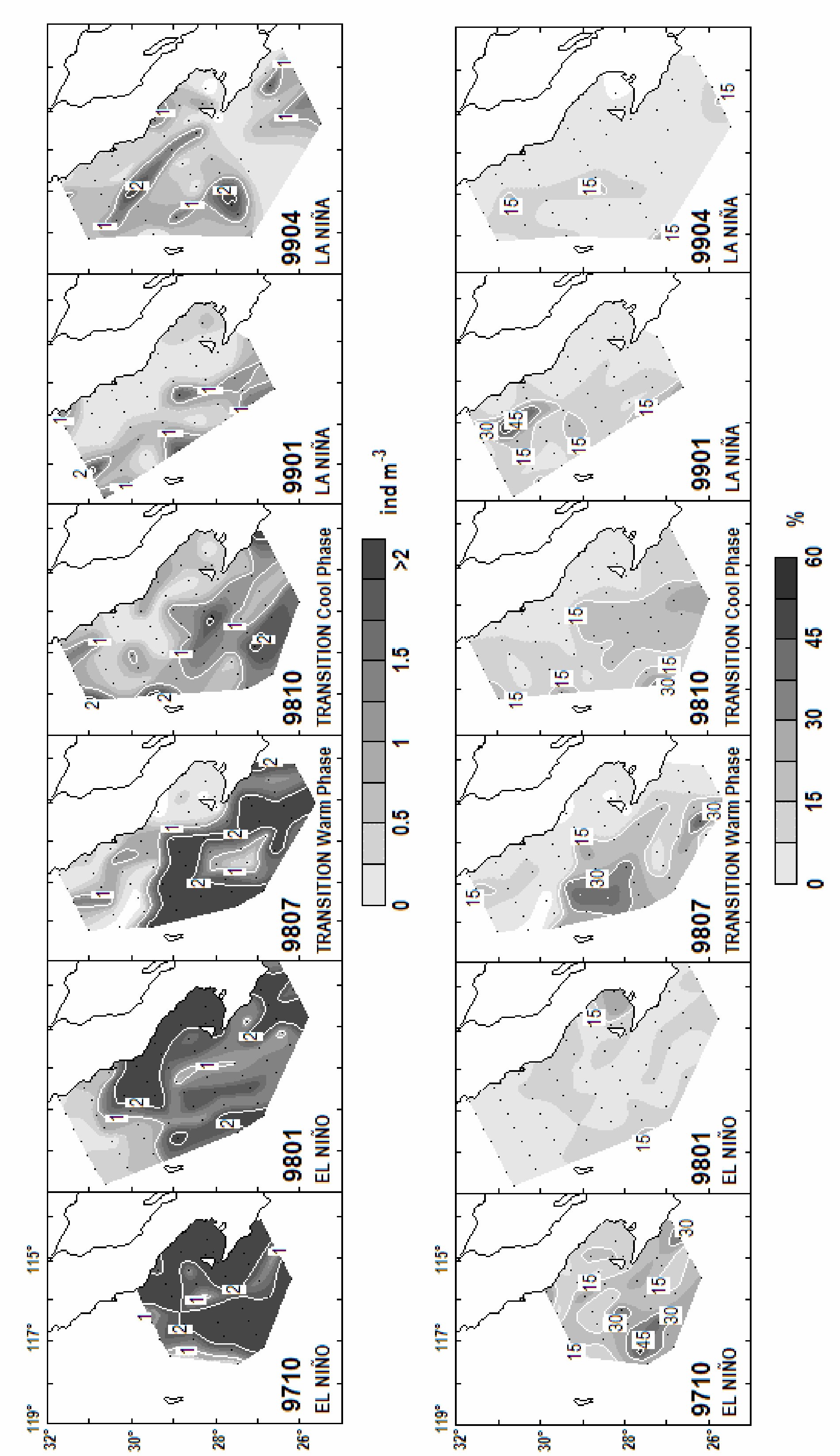

Fig. 8. Absolute and relative abundance of carnivore species through 1997-1999 (upper and lower panels respectively).

Discussion

The rapid and extreme change from a strong El Niño in 1997-1998 to an equally strong La Niña affecting the CCS since fall 1998, provided an excellent opportunity to define biogeographic groups and their succesional profiles. We will discuss with some detail the biogeographic classification by Fleminger (1967), the most complete for the Calanoida in the CCS. This author defined five oceanic groups: Subarctic, Transitional, Central, Equatorial, and Central-Equatorial; and four coastal-neritic groups: endemic, boreal-temperate, temperate-subtropical and tropical. He did not give explanation on the nature of his biogeographic groups but justified their insertion in the general faunal patterns described by Johnson & Brinton (1963). These last authors used the concept of water masses and currents to delimit marine biomes in the Pacific Ocean. Thus, the subarctic ecological zone has cold and low salinity water, circumscribed between 40° and 60°N by a semi-closed circulation. Warm and saline water occurs in the equatorial system of currents, while central water corresponds to large subtropical gyres in both hemispheres. In the northern hemisphere a transition region, where subarctic, central and equatorial waters converge is the California Current, where some widely distributed species maintain high concentrations and some others are endemic to it (Johnson & Brinton 1963).

Among the common species analyzed in the present study 38 were classified in either of the Fleminger's biogeographic groups (Table 3). In general, the response observed by these species during 1997-1999 agreed with his classification. We found discrepancies in six species only: *Candacia bipinnata*, *Heterorhabdus tanneri*, *Labidocera acutifrons*, *Candacia curta*, *Paracalanus parvus*, and *Temora discaudata*.

In the transitional group (TG) we found divergence in the status of *Candacia bipinnata* and *Heterorhabdus tanneri*, which were not included in La Niña cluster (Table 2) as the rest of the TG species did. This biogeographic group contains species characteristic of the California Current (Fleminger 1967), a bridge between the temperate and the tropical zones. The MDS analysis indicated that *C. bipinnata* was best represented during the warm phase of the shifting between El Niño and La Niña. This species recovered presence in April 1999, which indicates occupancy of the region during upwelling seasons. Besides, records in warm and temperate regions (see Table 1) indicate a wide distribution not coherent with a transitional form. Therefore, *C. bipinnata* should not be kept in the TG. A deeper discrepancy was found with respect to *Heterorhabdus tanneri*, which in our analysis belonged to El Niño group. Though observed in low abundance, the occurrence of *H. tanneri* during El Niño was unexpected as it inhabits the subarctic Pacific (Brodsky 1950, Koeller 1977, Yamaguchi & Ikeda 2000). Probably, as a carnivorous mesopelagic species, it could be less affected by warming of the upper sea layers and moderate productivity, but the oceanic occurrence of *H. tanneri* off Baja California suggests that it was carried to the region from the west, not from the north.

A high number of species in the Central group (CG) and the Central-Equatorial Group (CEG) appeared as part of La Niña cluster, whereas others were assigned to El Niño (Table 2). The different response to climate could be explained in part by the vertical distribution of the species in those groups. The mesopelagic habit or the long distance vertical migration in those species with cool-temperature affinity, as is the case of *Pleuromamma* (Haury 1988) could avoid the upper layer during the warm event. In contrast, the epipelagic *Nannocalanus minor* and *Scolecithrix danae* (Ambler & Miller 1987) living in warmer layers, would be transported toward the coast during El Niño. This invasive process was even more evident for the Equatorial group (EG) species. With the renewed strength of the southward flow during La Niña, epipelagic species from EG, CEG and CG were swept out of the area, conserving a limited presence offshore.

Labidocera acutifrons in Fleminger's CEG was the only species showing a different response compared to the rest of the species in the CEG. The distributional pattern of *L. acutifrons* was more in agreement with the Coastal-Neritic Tropical group (CNTG), as *Centropages furcatus*, *Euchaeta indica*, and *Labidocera acuta*, relevant in October 1997, scarce in January 1998, and disappearing thereafter. Therefore, *L. acutifrons* must be placed in the CNTG. Similarly, *Paracalanus parvus* and *Temora discaudata* also must place in the CNTG instead the Temperate-Subtropical group (Table 3). The response of *T. discaudata* in our study confirms the further reallocation of this species as a tropical neritic form (Fleminger 1975). The species of the CNTG seems to have replaced the neritic endemics (*Labidocera trispinosa*, *L. jollae* and *Pontellopsis occidentalis*), which were very rare in the region during 1997-1999. In contrast, *Candacia curta* showed an EG-type pattern. In the Indian Ocean also was reported as an offshore copepod more than coastal (Kasmi 2004). Probably Fleminger (1967) considered an extended distribution in the neritic zone due to the presence of this species near the coast in 1958-1959. However, during that time another El Niño event was taking place, and *C. curta* featured the same kind of intrusion observed in other equatorial species. The retreat of this species toward the oceanic zone was confirmed in distributional charts from the cold year of 1949 (Bowman & Johnson 1973).

Up to 47% of the common calanoid species did not receive a biogeographic category in Fleminger's classification. We propose the assignation of these species in the biogeographic groups as shown in Table 4, based on their response to extreme climatic events during 1997-1999. Most of them were allocated in the CEG and corresponded to species best represented during the climatic relaxation after El Niño or during La Niña. The only species from the El Niño cluster (Table 2) were *Pleuromamma piseki* and *Pontellina plumata*. The circumglobal distribution of *P. plumata* between latitudes 40°N and 40°S was established by Fleminger & Hulsemann (1973).

The category of Subarctic was assigned to *Lophothrix frontalis* because it was in La Niña cluster and has been recorded in the Gulf of Alaska and Canada (Sloan et al. 2001). The species in the CG and the warm-temperate cosmopolites in Table 4 were also part of La Niña or the climatic shift clusters (Table 2).

All the species allocated in the EG were from El Niño cluster, except for *Haloptilus ornatus* that corresponded to the warm-phase of the shifting period. *Subeucalanus subtenuis* agrees with the circumglobal equatorial distribution described by Fleminger (1973), but *S. subcrassus* does not correspond to the tropical neritic category proposed by him. In regard to *S. crassus*, its neritic nature is confirmed; Fleminger (1973) described its distribution as tropical-subtropical, but we found it as part of the CNTG, as it was observed exclusively in October 1997.

Although the species richness in El Niño cluster (39) was higher than in La Niña cluster (24), many of the latter had a high occurrence, among them several large-size herbivores. The ability of temperate herbivores to regulate their vertical distribution is suggested as the best way to explain their perma-

Table 4. Biogeographic status assigned to calanoid species not classified by Fleminger (1967), based in their response to extreme climate events in the present study.

OCEANIC		COASTAL-NERITIC
SUBARCTIC	CENTRAL + EQUATORIAL	TEMPERATE-SUBTROPICAL
Lophotrix frontalis	*Acartia danae*	*Centropages bradyi*
EQUATORIAL	*Acartia negligens*	TROPICAL
Haloptilus ornatus	*Aetideus acutus*	*Undinula vulgaris*
Undinula darwini	*Undeuchaeta intermedia*	*Paraeuchaeta elongata*
Candacia tenuimana	*Haloptilus longicornis*	*Subeucalanus crassus*
Subeucalanus subcrassus	*Haloptilus spiniceps*	*Acrocalanus longicornis*
Subeucalanus subtenuis	*Calocalanus pavo*	*Labidocera euchaeta*
	Candacia aethiopica	
	Heterorhabdus papilliger	
CENTRAL	*Heterostylites longicornis*	
Euchirella curticauda	*Lucicutia flavicornis*	
Gaetanus minor	*Pleuromamma piseki*	
Gaidius pungens	*Pleuromamma quadrungulata*	
Scolecithricella dentata	*Phaenna spinifera*	
WARM-TEMPERATE COSMOPOLITE	*Pontellina plumata*	
Aetideus bradyi		
Mesocalanus tenuicornis		

manence in the region despite the warming of the surface layer. In contrast, the invasive nature of the tropical epipelagic species was evident, entering in the region with the strong poleward flow from the south and the southwest observed during El Niño (Durazo & Baumgartner 2002). Equatorial species, such as *Subeucalanus subtenuis* and *Undinula darwini*, are considered herbivores sustained by equatorial upwellings (Fleminger & Hulseman 1973). During 1997-1998 off Baja California, the equatorial species had the advantage of water less affected by the low primary production reported for other locations in the central Pacific (Chavez et al. 1999). There is evidence of a decreased abundance of *U. darwini* during other strong El Niño (1982-1983) due to the low productivity in the eastern tropical Pacific (Dessier & Donguy 1987). The Baja California region was aside from a dramatic drop in productivity during the 1997-1998 El Niño (Kahru & Mitchell 2000, Lavaniegos et al. 2002); this region represented a refuge for the herbivorous immigrants from the eastern tropical Pacific.

Despite their great abundance and importance in marine food webs (Turner 2004), cyclopoid and poecilostomatoid copepods have received relatively low attention in the California Current (Olson 1949). These small copepods have been undersampled in most of the plankton prospective studies due to the use of nets with large mesh-size. Though unreliable their quantification, a substantial number of species in these orders were retained in our nets during El Niño period, being the most abundant *Oithona plumifera*. This species is considered oceanic in tropical and subtropical waters (Nishida 1985). A study on the fecal pellets of *O. plumifera* suggest that this cyclopoid is a fine-particle feeder (Turner 1986). However, lipid reserves of polar copepods *Oithona* and *Oncaea* pointed a carnivore diet (Kattner et al. 2003). In any case, the ability of cyclopoid and poecilostomatoid copepods to exploit the lower portion of the food size spectrum appeared to be an important factor for the success of these organisms during El Niño and the transition to cool conditions.

Copepod biogeography is probably one of the most difficult to confront due to morphological confusion and information gaps in geographic and vertical distribution. Few species have received attention at a global spatial scale. Additionally, the introduction and proliferation of exotic species contribute to obscure the coupling between marine currents and animal locomotion to maintain or disperse populations in the marine environment. Copepod identification is increasingly requiring the support of genetic tools. Presumedly cosmopolitan marine species are being revealed as cryptic species complexes (Goetze 2003). Consequently, the use of indicator species is coming less reliable; hence biogeographic assemblages is recommended to describe the effect of climatic events as El Niño (Jiménez-Pérez & Lavaniegos 2004).

Studies of species composition is far to be complete; there are still important sampling gaps to fill. The response of species to changing climate, as observed in the present study, provides an excellent opportunity to improve understanding in the biogeographic affinity of the species. However, the best way to improve our conception of the entire species distribution requires more information from all regions. Recently important efforts have been done in this direction. A significant number of species records dispersed through the scientific literature are now available through comprehensible systems in internet (Razouls & De-Bovée 1998, IT IS 2005, OBIS 2005). The enrichment of these systems with more records and complemental information about vertical distribution of the species will contibute to better delineate old biogeographic problems and raise new hypothesis.

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Resumen

Se provee la distribución geográfica de las 72 especies más comunes de copépodos observadas en aguas de Baja California a través del periodo 1997-1999. En ese tiempo la región estuvo sujeta a cambios extremos, como el resto de la cuenca del Pacifico debido a El Niño, el cual fue seguido por un rápido cambio a condiciones de La Niña. Se usó el método de ordenación por escalamiento multidimensional para definir patrones espaciales generales. Las especies se separaron claramente en grupos climáticos. El conglomerado principal correspondió a especies que cubrieron una extensa área durante El Niño (octubre 1997 y enero 1998), desapareciendo posteriormente, o retrayéndose drásticamente a localidades oceánicas (e.g. *Undinula darwini*) o hacia el sur (e.g. *Pareucalanus attenuatus*). Un segundo ensamblaje, menos copioso en especies, presentó una ocupación del área más o menos continua, incrementando su cobertura aún más durante La Niña (enero y abril 1999). En este grupo estuvieron las especies endémicas de la Zona de Transición como *Calanus pacificus*, *Eucalanus californicus* y *Rhincalanus nasutus*, así como las especies subárticas (e.g. *Neocalanus cristatus*) y otras ampliamente distribuidas en el Pacifico central (e.g. *Pleuromamma*). Otras especies estuvieron escasamente representadas en los extremos cálido y frió del periodo de estudio, con un conglomerado mostrando una amplia cobertura durante la fase de relajamiento después de El Niño (julio 1998) y otro en el preludio de la condición fría (octubre 1998). La mayoría de las especies congregadas en el grupo La Niña son conocidas por presentar algún tipo de adaptación para regular su posición vertical en la columna de agua, ya sea por migración vertical estacional o circadiana sobre largas distancias. En contraste la mayoría de las especies "invasoras" son epipelágicas y habrían sido transportadas por agua tropical, para ser barridas posteriormente por la renovada fuerza de la corriente de California. La mayor parte de las especies de copépodos ciclopoides y poecilostomatoides presentaron un patrón de distribución tipo El Niño o patrones propios de la fase de relajación climática. Se discute el estatus biogeográfico de las diferentes especies.

Literature Cited

Ambler, J.W., & C.B. Miller. 1987. Vertical habitat-partitioning by copepodites and adults of subtropical oceanic copepods.– Marine Biology 94 (4): 561-577.

Arcos, F., & A. Fleminger. 1986. Distribution of filter-feeding calanoid copepods in the eastern equatorial Pacific.– California Cooperative Oceanic Fisheries Investigations Reports 27: 170-187.

Bograd, S.J., & R.J. Lynn. 2003. Long-term variability in the Southern California Current System.– Deep-Sea Research, Part II 50: 2355-2370.

Bowman, T.E., & M.W. Johnson. 1973. Distributional atlas of calanoid copepods in the California Current region, 1949 and 1950.– California Cooperative Oceanic Fisheries Investigations Atlas 19: 1-239.

Brinton, E., A. Fleminger, & D. Siegel-Causey. 1986. The temperate and tropical biotas of the Gulf of California.– California Cooperative Oceanic Fisheries Investigations Reports 27: 228-266.

Brodsky, K. A. 1950 [1967]. Calanoida of the Far Eastern Seas and Polar Basin of USSR. Keys to the Fauna of the USSR. Academy of Sciences USSR. Israel Program for Scientific Translations, 440pp.

Brodsky, K. A. 1972 [1975]. Phylogeny of the family Calanidae (Copepoda) on the basis of a comparative morphological analysis of its characters. Pp. 1-127 in Z. A. Zvereva, ed., Geographical and seasonal variability of marine plankton. Studies of marine fauna, Academy of Sciences of the USSR 12:1-303. Israel Program for Scientific Translations.

Chavez, F.P., P.G. Strutton, G.E. Friederich, R.A. Feely, G.C. Feldman, D.G. Foley & M.J. McPhaden. 1999. El Niño.– Science 286: 2126-2131.

Chelton, D.B., P.A. Bernal, & J.A. McGowan. 1982. Large-scale interannual physical and biological interaction in the California Current.– Journal of Marine Research 40: 1095-1125.

Chen, Y.Q. 1986. Vertical distribution of some pelagic copepods in the Eastern Tropical Pacific.– California Cooperative Oceanic Fisheries Investigations Reports 27: 205-227.

Clarke, K.R, & R.M. Warwick. 1994. Change in marine communities: an approach to statistical analysis and interpretation. Plymouth Marine Laboratory, 144 pp.

Dawson, K.J., & G. Knatz. 1980. Illustrated key to planktonic copepods of San Pedro Bay, California.– Allan Hancock Foundation Technical Report, Los Angeles 2: 1-106.

Dessier, A., & J.R. Donguy. 1987. Response to El Niño signals of the epiplanktonic copepod populations in the eastern tropical Pacific.– Journal of Geophysical Research 92: 14393-

14403.

Durazo, R., & T.R. Baumgartner, 2002. Evolution of oceanographic conditions off Baja California: 1997-1999.– Progress in Oceanography 54: 7-31.

Fernández-Álamo, M.A., L. Sanvicente-Añorve, & G. Alameda-dela-Mora, 2000. Copepod assemblages in the Gulf of Tehuantepec, Mexico.– Crustaceana 73: 1139-1153.

Fleminger, A. 1964. Distributional Atlas of calanoid copepods in the California Current region, Part 1.– California Cooperative Oceanic Fisheries Investigations Atlas 2: 1-313.

———. 1967. Distributional Atlas of calanoid copepods in the California Current region, Part 2.– California Cooperative Oceanic Fisheries Investigations Atlas 7: 1-213.

———. 1973. Pattern, number, variability and taxonomic significance of integumental organs (sensilla and glandular pores) in the genus *Eucalanus* (Copepoda: Calanoida).– Fishery Bulletin 71: 965-1010.

———. 1975. Geographical distribution and morphological divergence in American coastal-zone planktonic copepods of the genus *Labidocera*. Pp. 392-419 *in* L. E. Cronin, ed., Chemistry, biology and the estuarine system. Estuarine Research, Academic Press, New York Vol. 1, 738 pp.

———, & K. Hulsemann. 1973. Relationship of Indian Ocean epiplanktonic calanoids to the World Oceans. Pp. 339-347 *in* B. Zeitschel, ed., Ecological Studies: Analysis and Synthesis, Springer-Verlag, Berlin Vol. 3, 549 pp.

Goetze, E. 2003. Cryptic speciation on the high seas; global phylogenetics of the copepod family Eucalanidae.– Proceedings of the Royal Society of London Series B 270: 2321-2331.

Grice, G.D. 1961. Calanoid copepods from equatorial waters of the Pacific Ocean.– Fishery Bulletin 61: 171-246.

Gueredrat, J. A. 1971. Evolution d'une population de copépodes dans le système des courants équatoriaux de l'Océan Pacifique. Zoogéographie, écologie et diversité spécifique.– Marine Biology 9: 300-314.

Haury, L.R. 1988. Vertical distribution of *Pleuromamma* (Copepoda: Metridinidae) across the eastern North Pacific Ocean.– Hydrobiologia 167/168: 335-342.

Hernández-Trujillo, S. 1999. Variability of community structure of Copepoda related to El Niño 1982-83 and 1987-88 along the west coast of Baja California Peninsula, Mexico.– Fisheries Oceanography 8: 284-295.

Hickey, B. 1979. The California current system: hypothesis and facts.– Progress in Oceanography 8: 191-279.

IT IS. Integrated Taxonomic Information System. [2005] http://www.itis.usda.gov

Jiménez-Pérez L.C., & J.R. Lara-Lara. 1988. Zooplankton biomass and copepod community structure in the Gulf of California during the 1982-1983 El Niño event.– California Cooperative Oceanic Fisheries Investigations Reports 29: 122-128.

———, & B.E. Lavaniegos, 2004. Changes in dominance of copepods off Baja California during the 1997-1999 El Niño and La Niña.– Marine Ecology Progress Series 277: 147-165.

Johnson, M.W., & E. Brinton, 1963. Biological species, water-masses and currents. Pp. 381-414 *in* M. N. Hill, ed., The Composition of Seawater. The Sea, Interscience, New York, Vol. 2, 554 pp.

Kahru, M., & G. Mitchell, 2000. Influence of the 1997-98 El Niño on the surface chlorophyll in the California Current.– Geophysical Research Letters 27: 2937-2940.

Kasmi, Q.B. 2004. Copepods from shore and offshore waters of Pakistan.– Journal of Marine Science and Technology 12: 223-238.

Kattner, G., C. Albers, M. Graeve, & S.B. Schnack-Schiel. 2003. Fatty acid and alcohol composition of the small polar copepods, *Oithona* and *Oncaea*: indication on feeding modes.– Polar Biology 26: 666-671.

Koeller, P.A. 1977. Observations on some bathypelagic copepods living in the British Columbia Mainland Inlets.– Journal of Oceanographic Society of Japan 33: 219-226.

Latif, M., & T. P.Barnett. 1994. Causes of Decadal Climate Variability over the North Pacific and North America.– Science 266: 634-637.

Lavaniegos, B.E., L.C. Jiménez-Pérez, & G. Gaxiola-Castro, 2002. Plankton Response to El Niño 97-98 and La Niña 99 in the Southern region of the California Current.– Progress in Oceanography 54: 33-58.

Lynn, R.J., & J.J. Simpson. 1987. The California

Current system: The seasonal variability of physical characteristics.– Journal of Geophysical Research 92: 12947-12966.

Mantua, N.J., S.R. Hare, Y. Zhang, J.M. Wallace, & R.C. Francis. 1997. A Pacific interdecadal climate oscillation with impacts on salmon production.– Bulletin of the American Meteorological Society 78: 1069-1079.

Nishida, S. 1985. Taxonomy and distribution of the family Oithonidae (Copepoda, Cyclopoida) in the Pacific and Indian Oceans.– Bulletin of the Ocean Research Institute of the University of Tokyo 20: 1-167.

OBIS. Ocean Biogeographic Information System. [2005] www.iobis.org

Olson, J. B. 1949. The pelagic cyclopoid copepods of the coastal waters of Oregon, California and Lower California. Unpublished Ph.D. dissertation, University of California, Los Angeles, 208 pp.

Palomares, R., E. Suárez-Morales, & S. Hernández-Trujillo. 1998. Catálogo de los copépodos (Crustacea) pelágicos del Pacífico mexicano. Centro Interdisciplinario de Ciencias Marinas/El Colegio de la Frontera Sur, México 352 pp.

Park, T.S. 1968. Calanoid copepods from the central North Pacific Ocean.– Fishery Bulletin 66: 527-572.

———. 1993. Taxonomy and distribution of the marine calanoid copepod family Euchaetidae.– Bulletin of the Scripps Institution of Oceanography of the University of California 29: 1-203.

Razouls, C., & F. De-Bovée. 1998 [2002]. Diversity and geographical distribution of pelagic Copepoda. 3- An overview and initial interpretation.– Annales de l'Institut Océanographique, Paris 74: 139-200. (http://copepodes.obsbanyuls.fr/index.php)

Schwing, F.B., & C.S. Moore. 2000. A year without summer for California, or a harbinger of a climate shift?– Transactions of the American Geophysical Union 81 (27): 301.

Sloan, N.A., P.M. Bartier, & W.C. Austin. 2001. Living marine legacy of Gwaii Haanas. II: Marine invertebrate baseline to 2000 and invertebrate-related management issues. Parks Canada - Technical Reports in Ecosystem Science, Halifax, 35: 331 pp. Retrieved [September 21, 2005] from www.iobis.or

Suárez-Morales, E., C. Franco-Gordo, & M. Saucedo-Lozano. 2000. On the pelagic copepod community of the central Mexican tropical Pacific (Autumn, 1990).– Crustaceana 73: 751-761.

Trenberth, K.E., & J.W. Hurrel. 1994. Decadal atmosphere-ocean variations in the Pacific.– Climate Dynamics 9:303-319.

Turner, J.T. 1986. Zooplankton feeding ecology: Contents of fecal pellets of the cyclopoid copepods *Oncaea venusta*, *Corycaeus amazonicus*, *Oithona plumifera,* and *O. simplex* from the northern Gulf of Mexico.– Marine Ecology 7: 289-302.

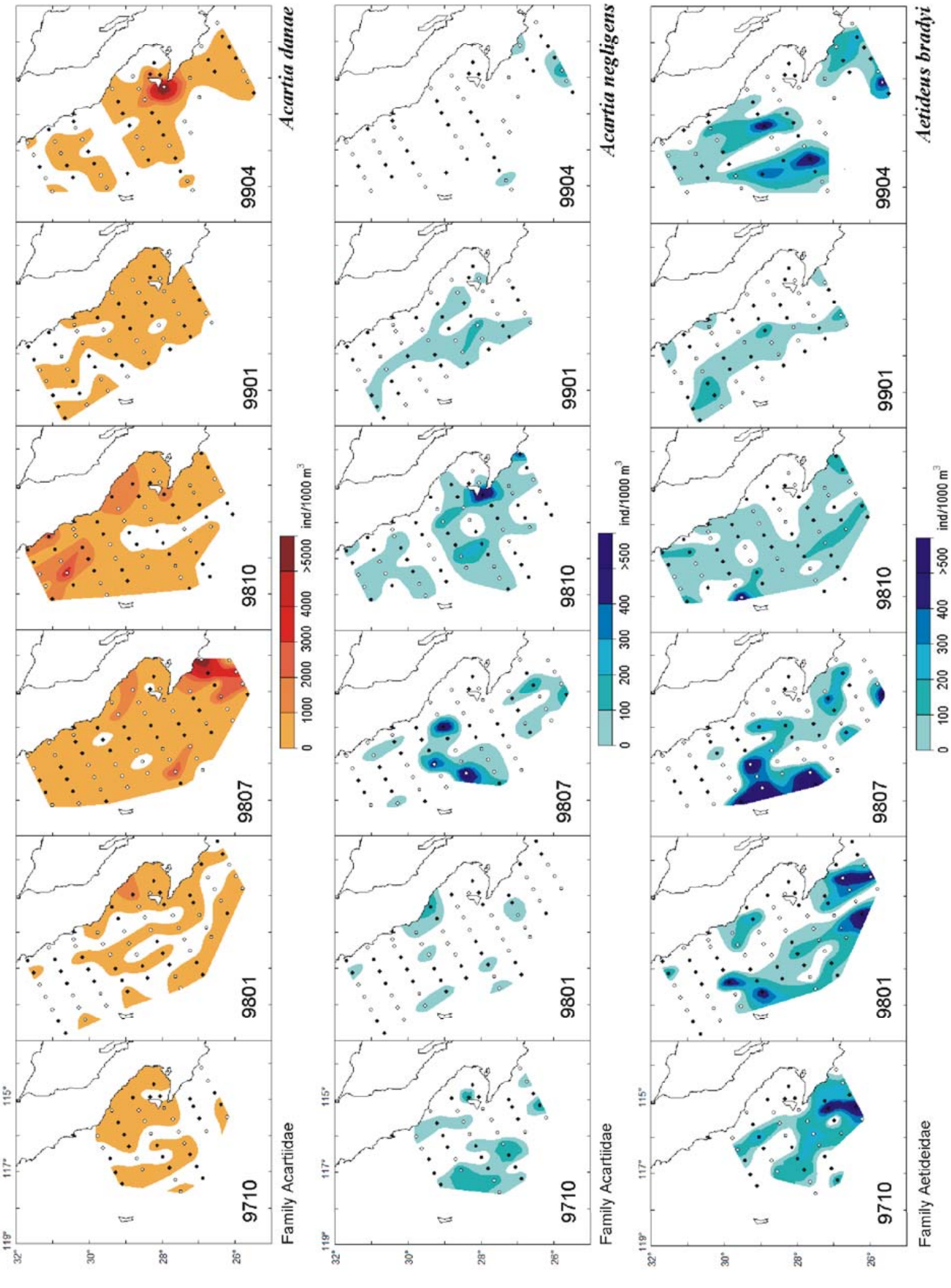
———. 2004. The importance of small planktonic copepods and their roles in pelagic marine food webs.– Zoological Studies 43: 255-266.

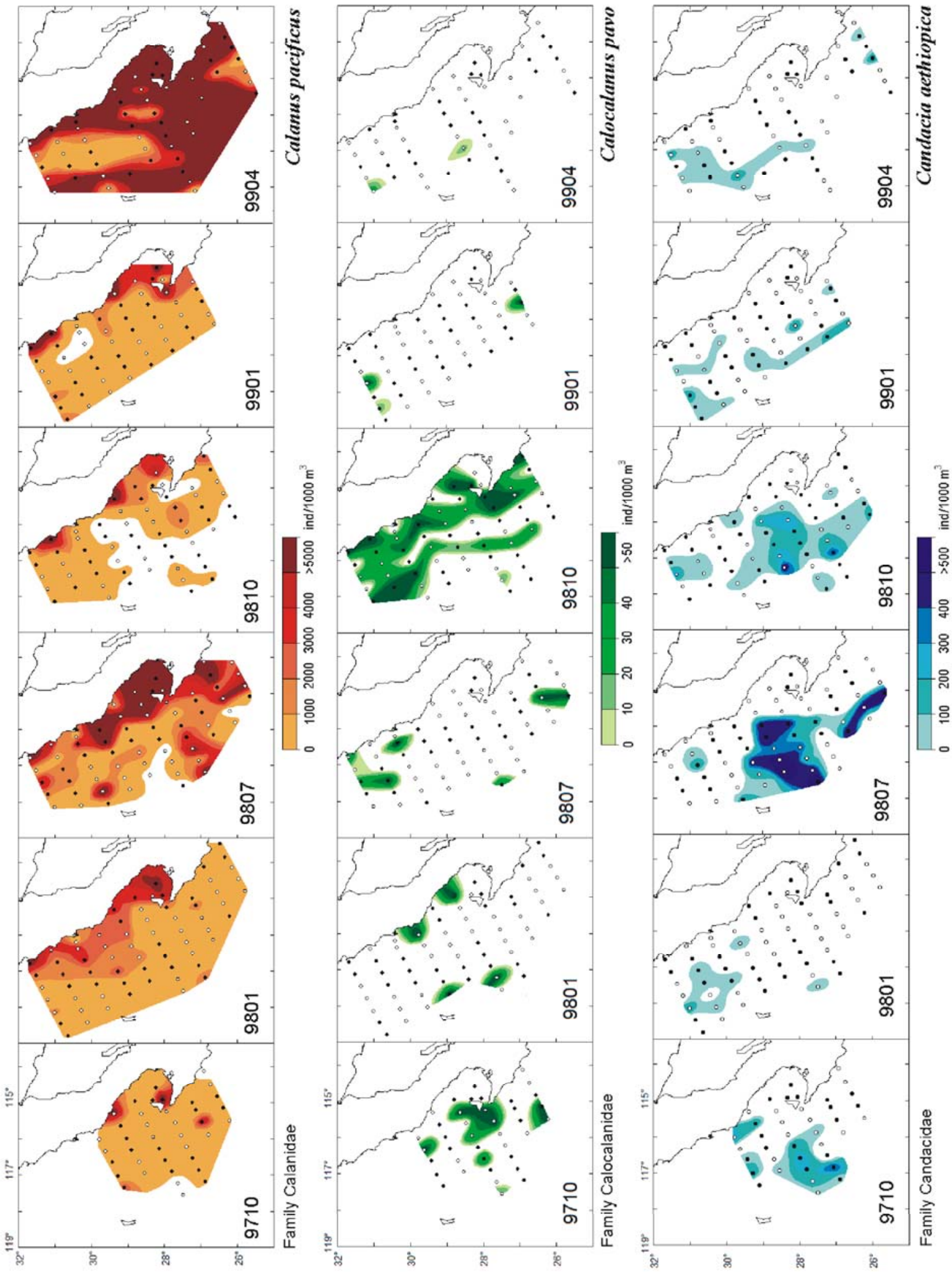
Yamaguchi, A., & T. Ikeda. 2000. Vertical distribution, life cycle and body allometry of two oceanic calanoid copepods (*Pleuromamma scutullata* and *Heterorhabdus tanneri*) in the Oyashio region, western North Pacific Ocean.– Journal of Plankton Research 22: 29-46.

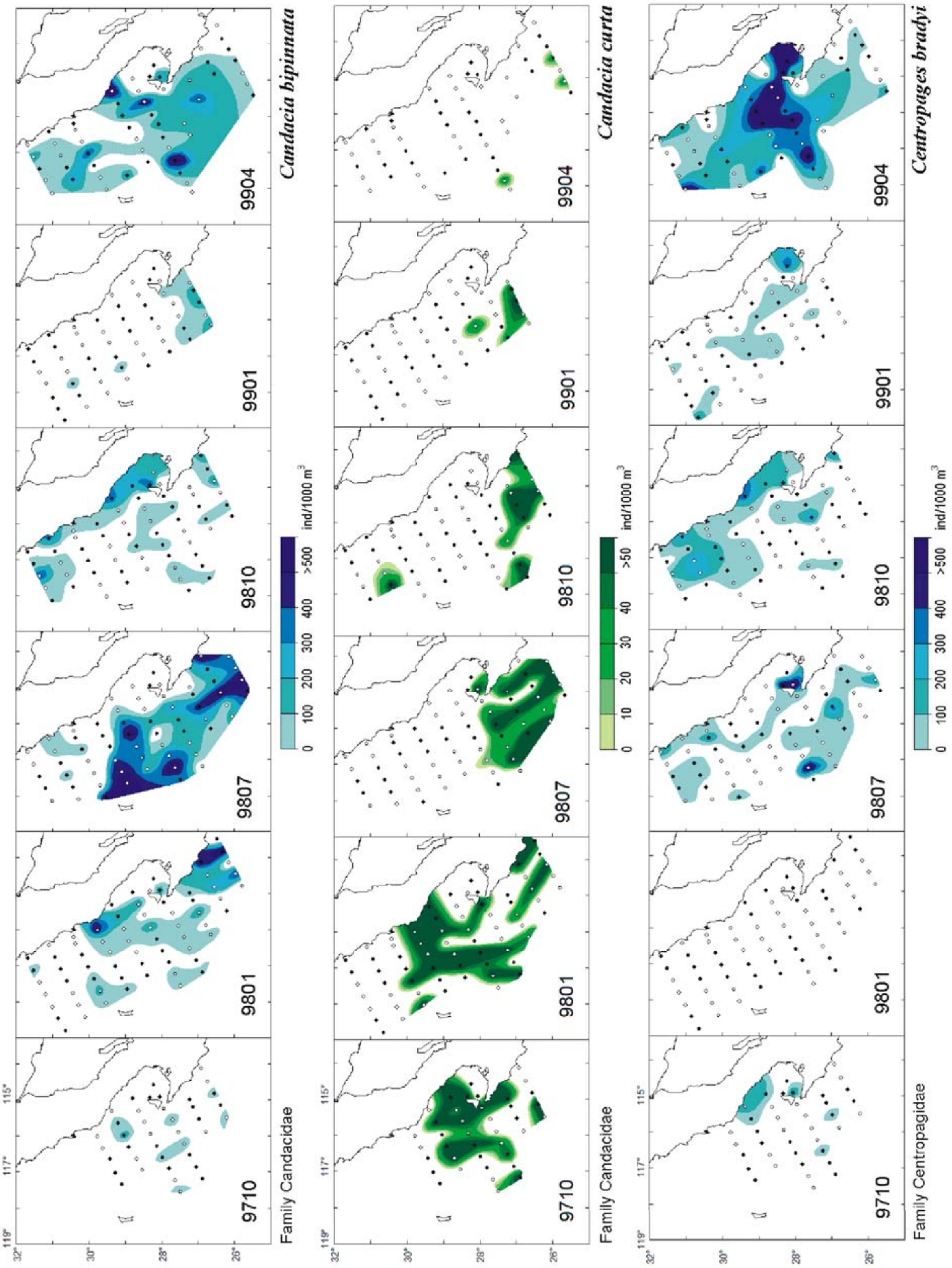
Lavaniegos, B.E. & L.C. Jiménez-Pérez. 2006. Biogeographic inferences of shifting copepod distribution during 1997-1999 El Niño and La Niña in the California Current. Pp. 113-158, *in*: M.E. Hendrickx (ed.). Contribuciones al Estudio de los Crustáceos del Pacífico Este 4 (1) [Contributions to the Study of East Pacific Crustaceans 4 (1)]. Instituto de Ciencias del Mar y Limnología, UNAM. 158 pp.

APPENDIX

Geographic atlas of copepods distributed in the Mexican sector of the California Current during October 1997 (9710), January, July and October 1998 (9801, 9807, and 9810, respectively), January and April 1999 (9901 and 9904 respectively). The species shown occurred in more than 27% of the samples in one or more cruises. The distributional charts are in alphabetic order. Colors used (red, blue, and green) are associated to abundance scales of 1000, 100 or 10 ind/1000 m^3 respectively. Closed circles indicate stations occupied during night and open circles during daylight hours.


Family Acartiidae
Acartia danae
Family Acartiidae
Acartia negligens
Family Aetideidae
Aetideus bradyi
9710
9801
9807
9810
9901
9904
ind/1000 m3
0
1000
2000
3000
4000
>5000
ind/1000 m3
0
100
200
300
400
>500
119°
117°
115°
32°
30°
28°
26°


Family Calanidae
Calanus pacificus
Family Calocalanidae
Calocalanus pavo
Family Candacidae
Candacia aethiopica
9710
9801
9807
9810
9901
9904
ind/1000 m^3
0
1000
2000
3000
4000
>5000
0
10
20
30
40
>50
0
100
200
300
400
>500
119°
117°
115°
32°
30°
28°
26°


Candacia bipinnata
Candacia curta
Centropages bradyi
Family Candacidae
Family Candacidae
Family Centropagidae
9710
9801
9807
9810
9901
9904
ind/1000 m³
0
100
200
300
400
>500
0
10
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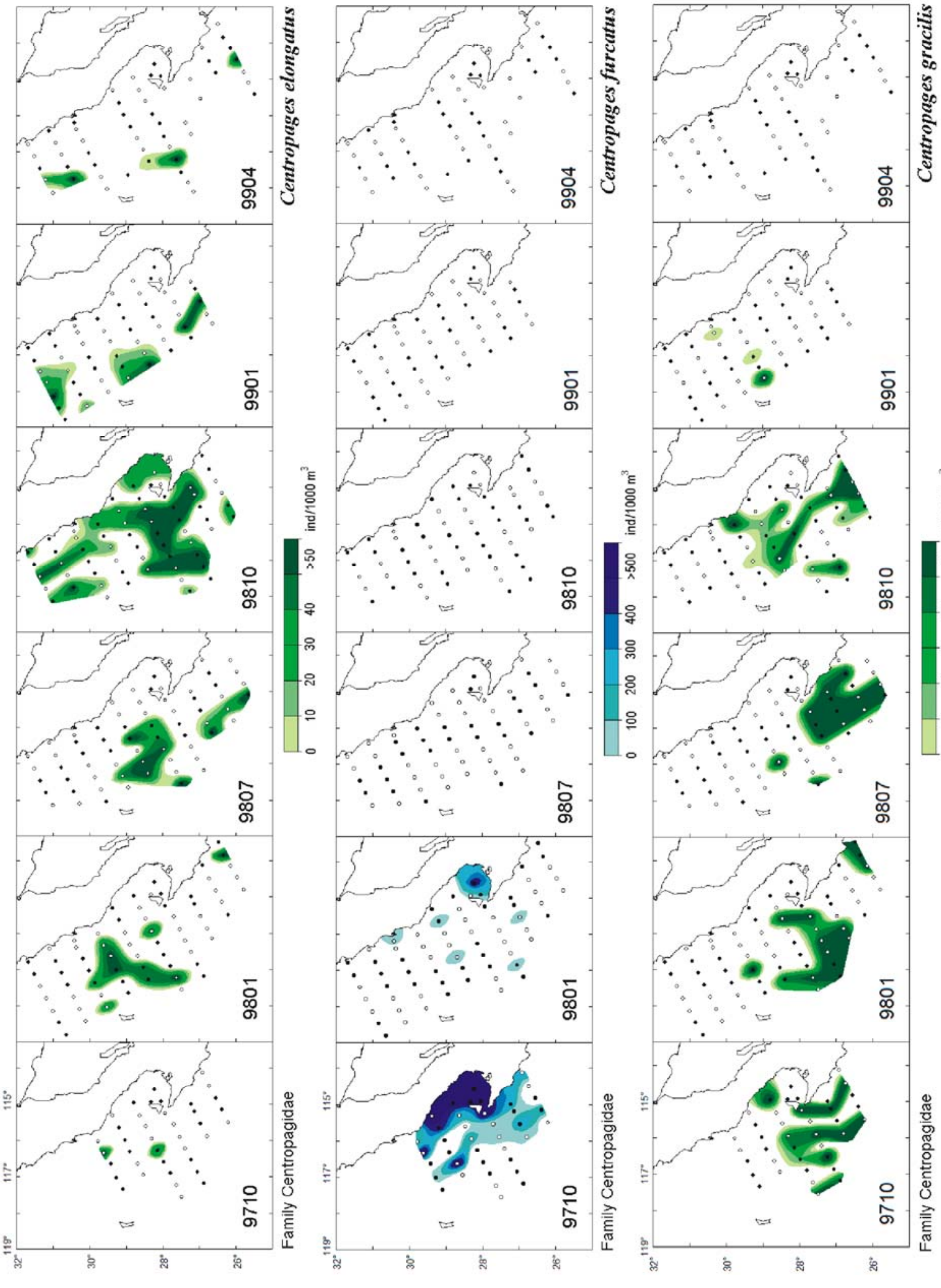
30
40
>50
119°
117°
115°
32°
30°
28°
26°


Centropages elongatus
Centropages furcatus
Centropages gracilis
Family Centropagidae
9710
9801
9807
9810
9901
9904
119°
117°
115°
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26°
ind/1000 m³
0
10
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>50
100
200
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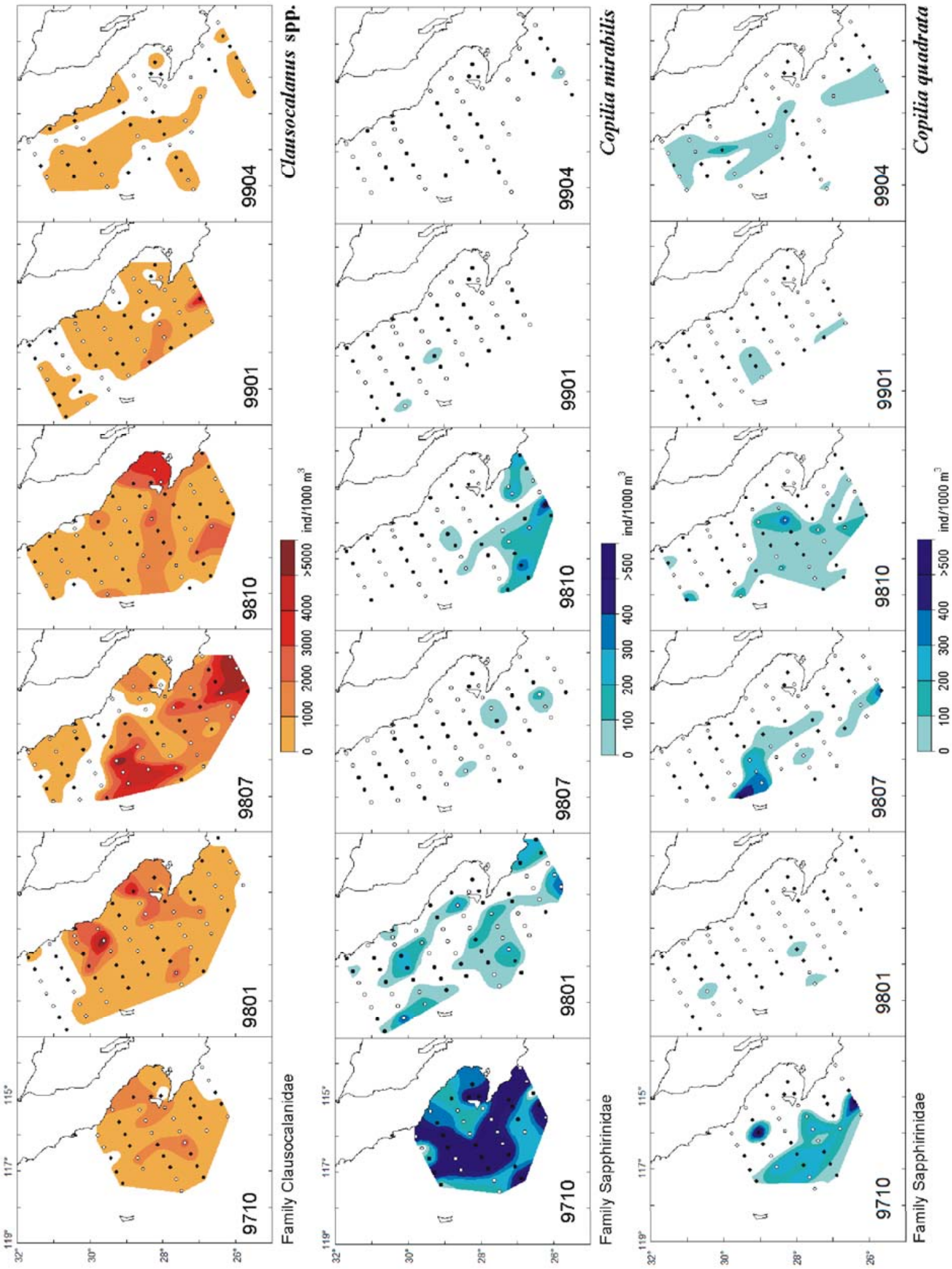
400
>500



9710
9801
9807
9810
9901
9904
Family Clausocalanidae
Clausocalanus spp.
Family Sapphirinidae
Copilia mirabilis
Copilia quadrata
0
1000
2000
3000
4000
>5000
ind/1000 m³
0
100
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300
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>500
ind/1000 m³
119°
117°
115°
32°
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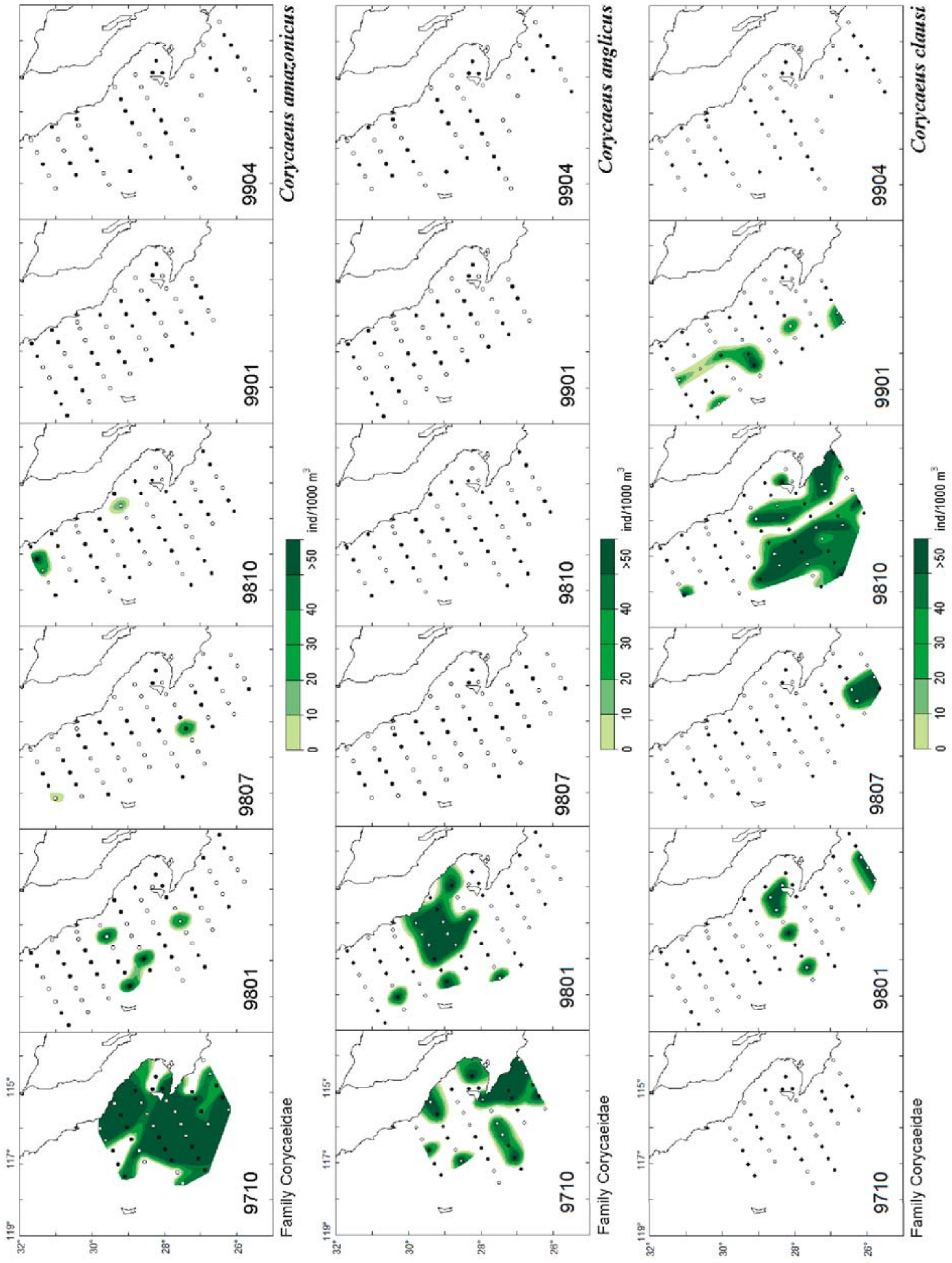
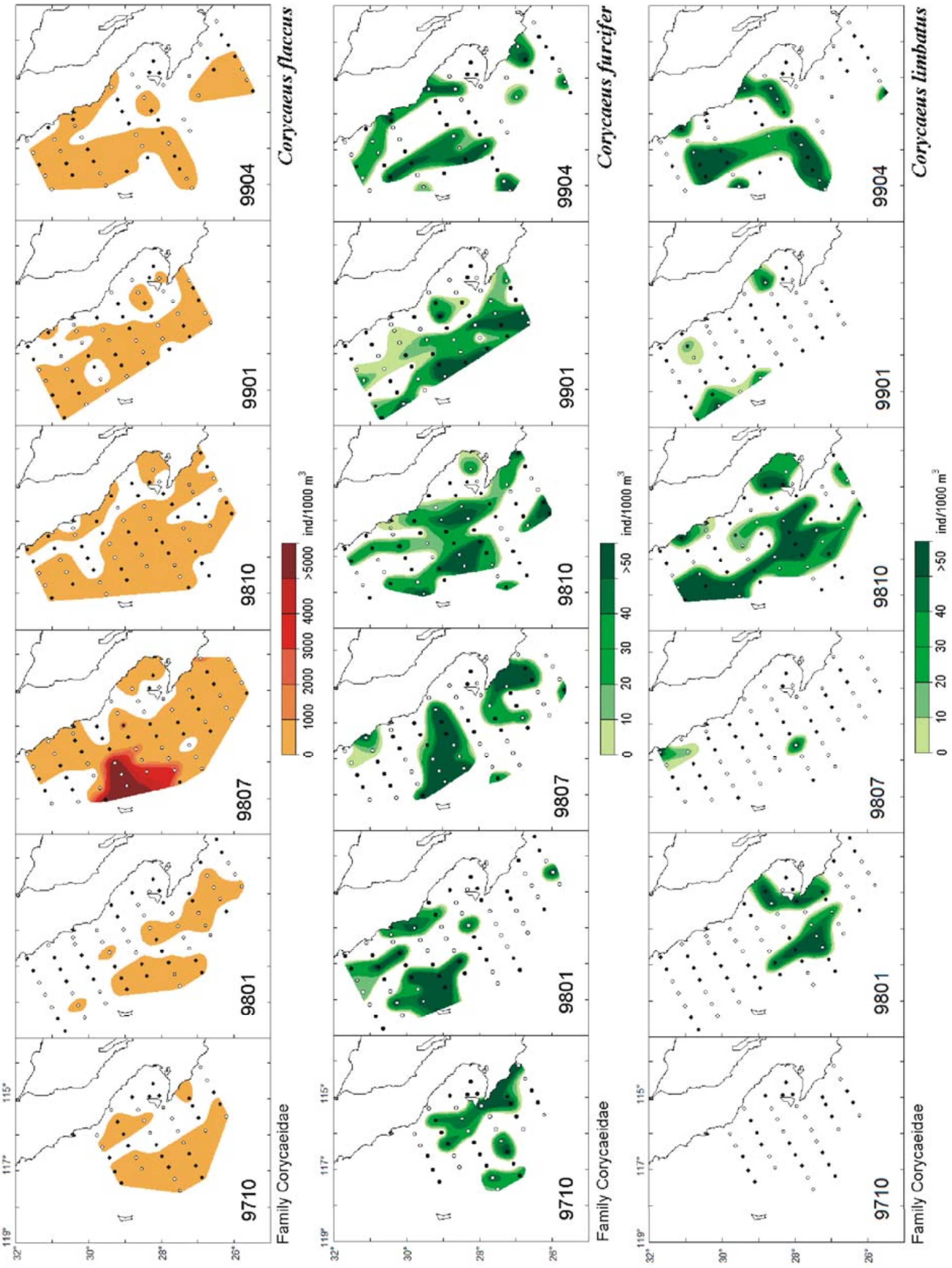
26°


Family Corycaeidae
9710
9801
9807
9810
9901
9904
Corycaeus amazonicus
Corycaeus anglicus
Corycaeus clausi
ind/1000 m3
0
10
20
30
40
>50
32°
30°
28°
26°
119°
117°
115°


Corycaeus flaccus
Corycaeus furcifer
Corycaeus limbatus
Family Corycaeidae
9710
9801
9807
9810
9901
9904
0
1000
2000
3000
4000
>5000
ind/1000 m3
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ind/1000 m3
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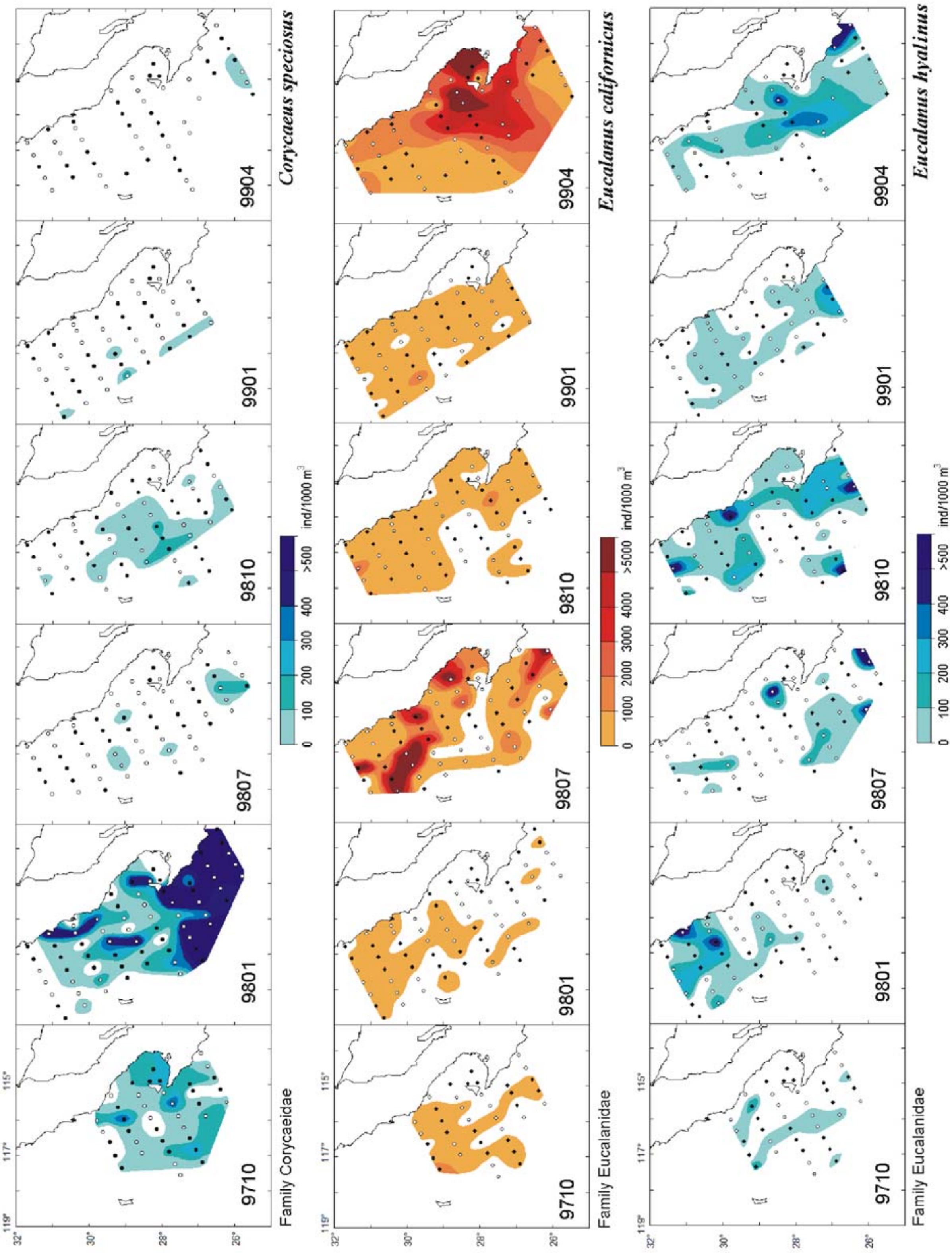
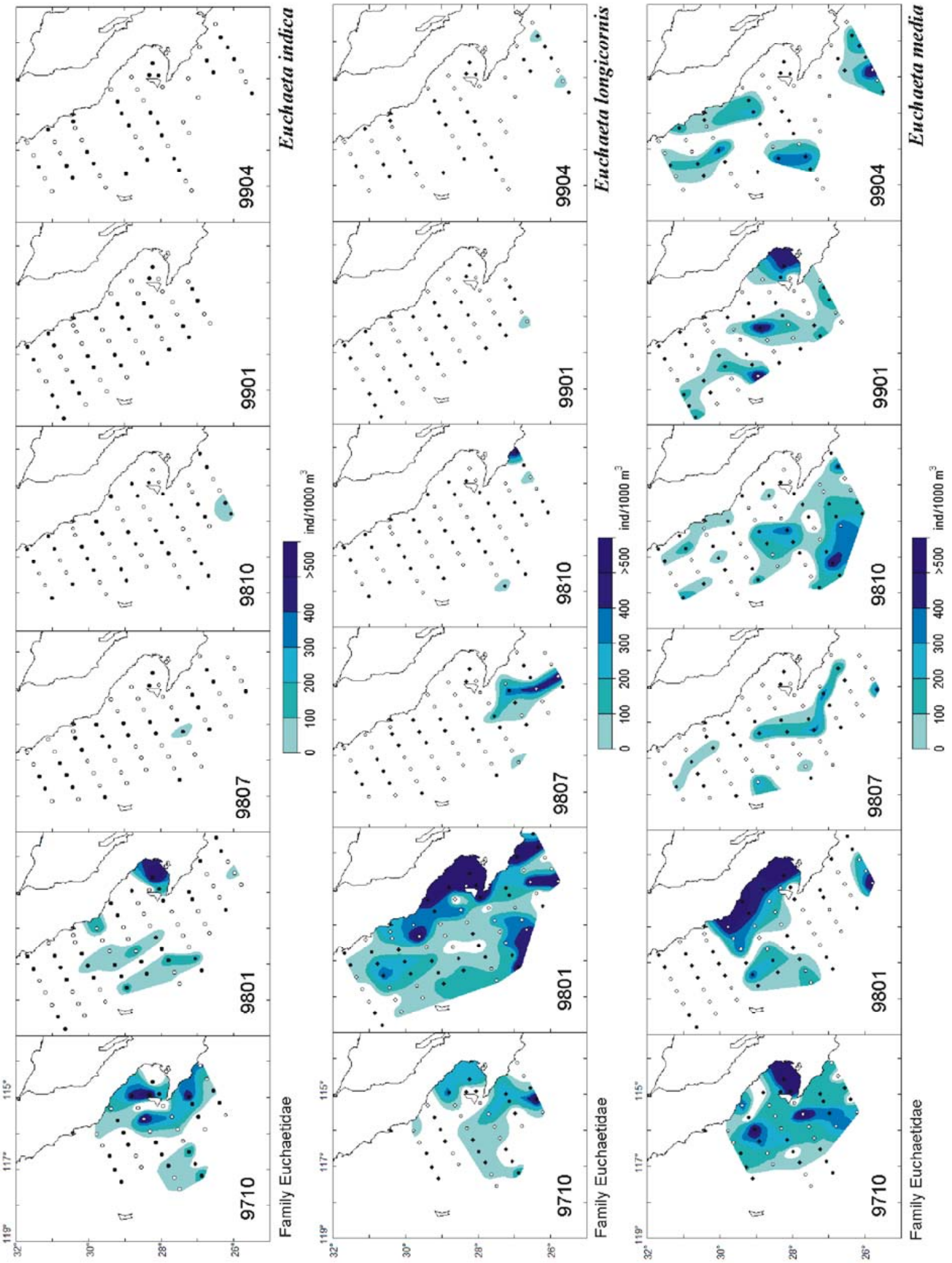

32°
30°
28°
26°
119°
117°
115°
9710
9801
9807
9810
9901
9904
Family Corycaeidae
Corycaeus speciosus
0
100
200
300
400
>500
ind/1000 m^3
Family Eucalanidae
Eucalanus californicus
0
1000
2000
3000
4000
>5000
ind/1000 m^3
Family Eucalanidae
Eucalanus hyalinus
0
100
200
300
400
>500
ind/1000 m^3


Euchaeta indica
Euchaeta longicornis
Euchaeta media
Family Euchaetidae
9710
9801
9807
9810
9901
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0
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ind/1000 m3
119°
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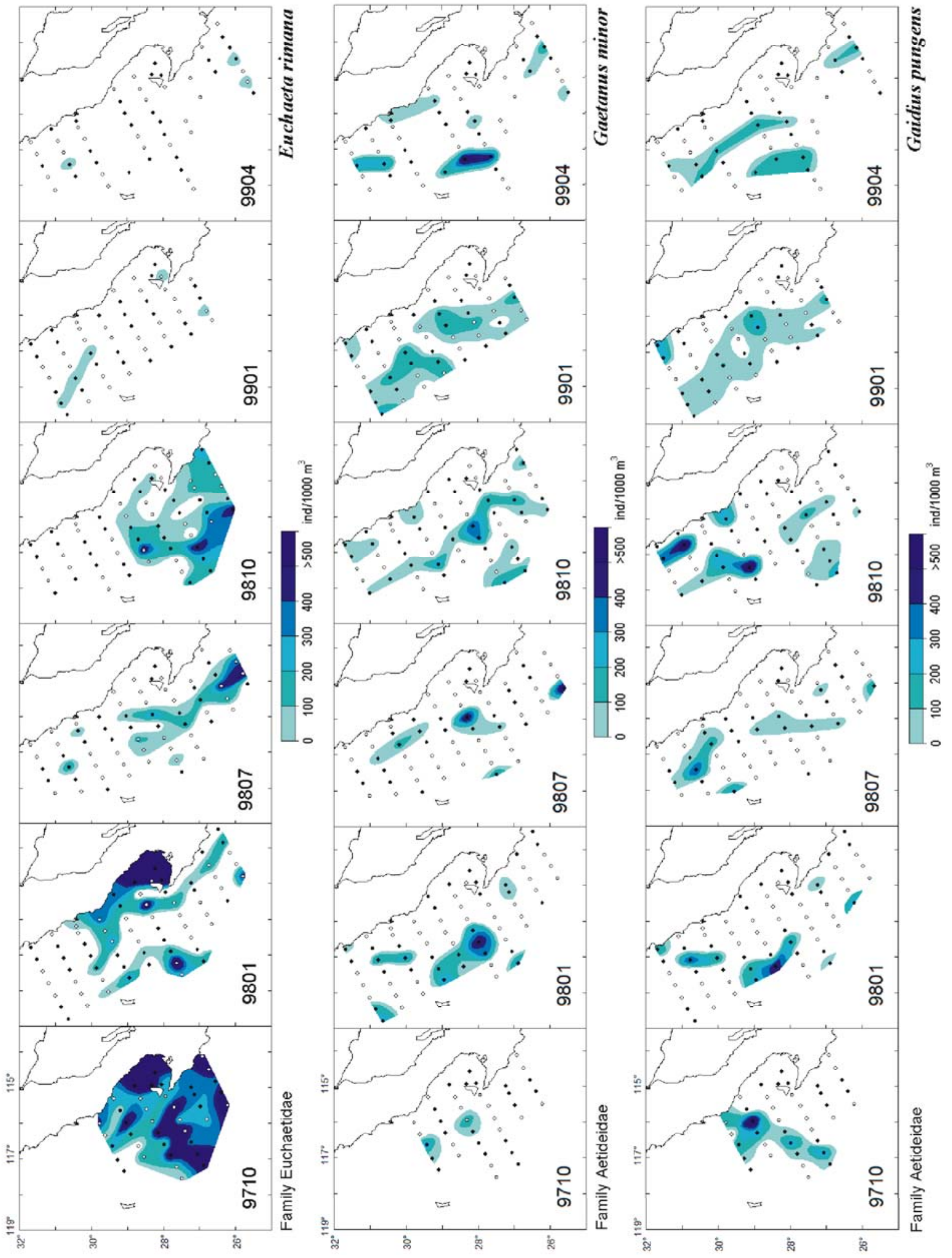
9710
9801
9807
9810
9901
9904
Euchaeta rimana
Family Euchaetidae
Gaetanus minor
Family Aetideidae
Gaidius pungens
Family Aetideidae
ind/1000 m^3
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32°
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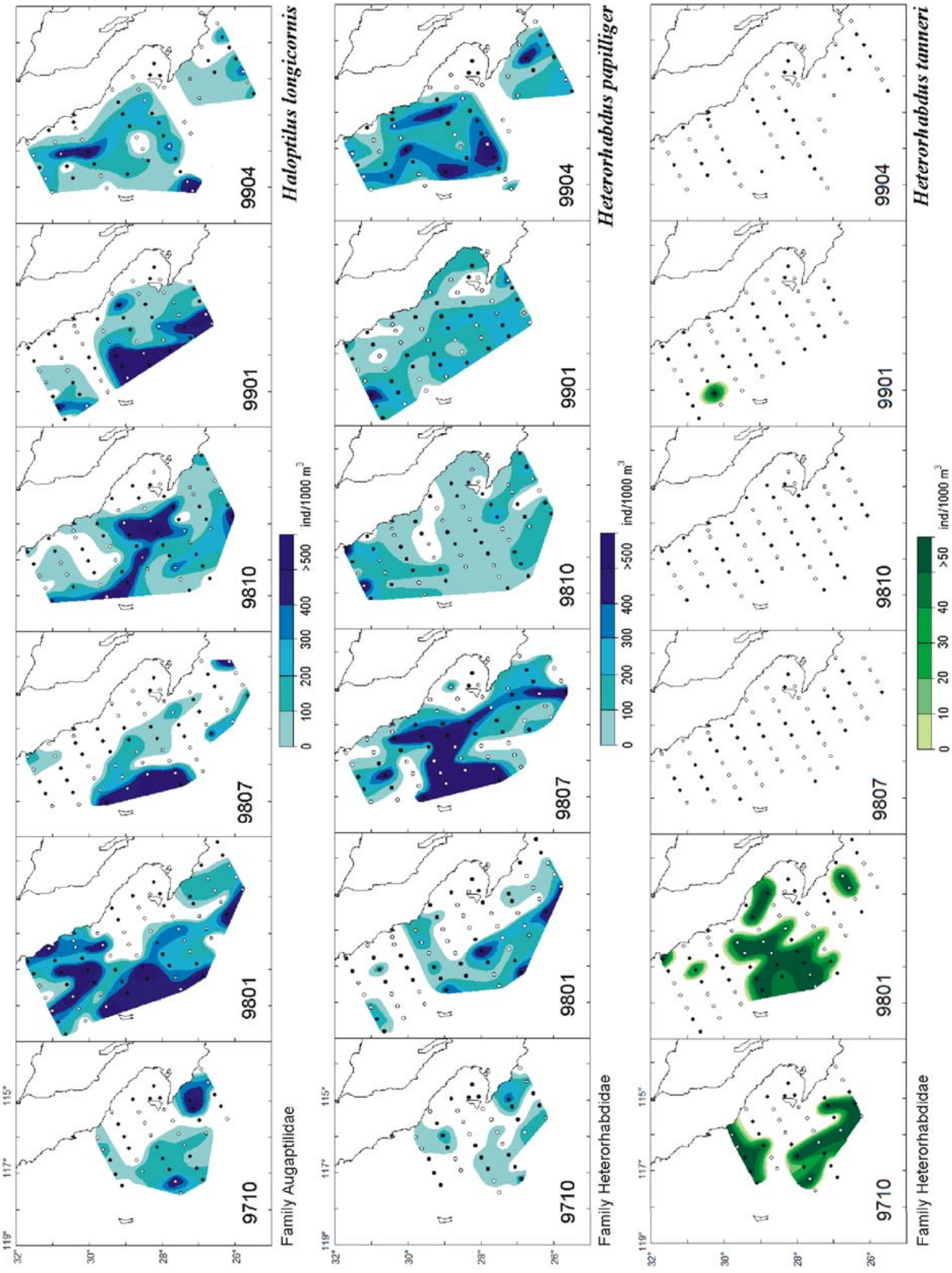
9710
9801
9807
9810
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9904
Family Augaptilidae
Haloptilus longicornis
0
100
200
300
400
>500
ind/1000 m3
Family Heterorhabdidae
Heterorhabdus papilliger
Family Heterorhabdidae
Heterorhabdus tanneri
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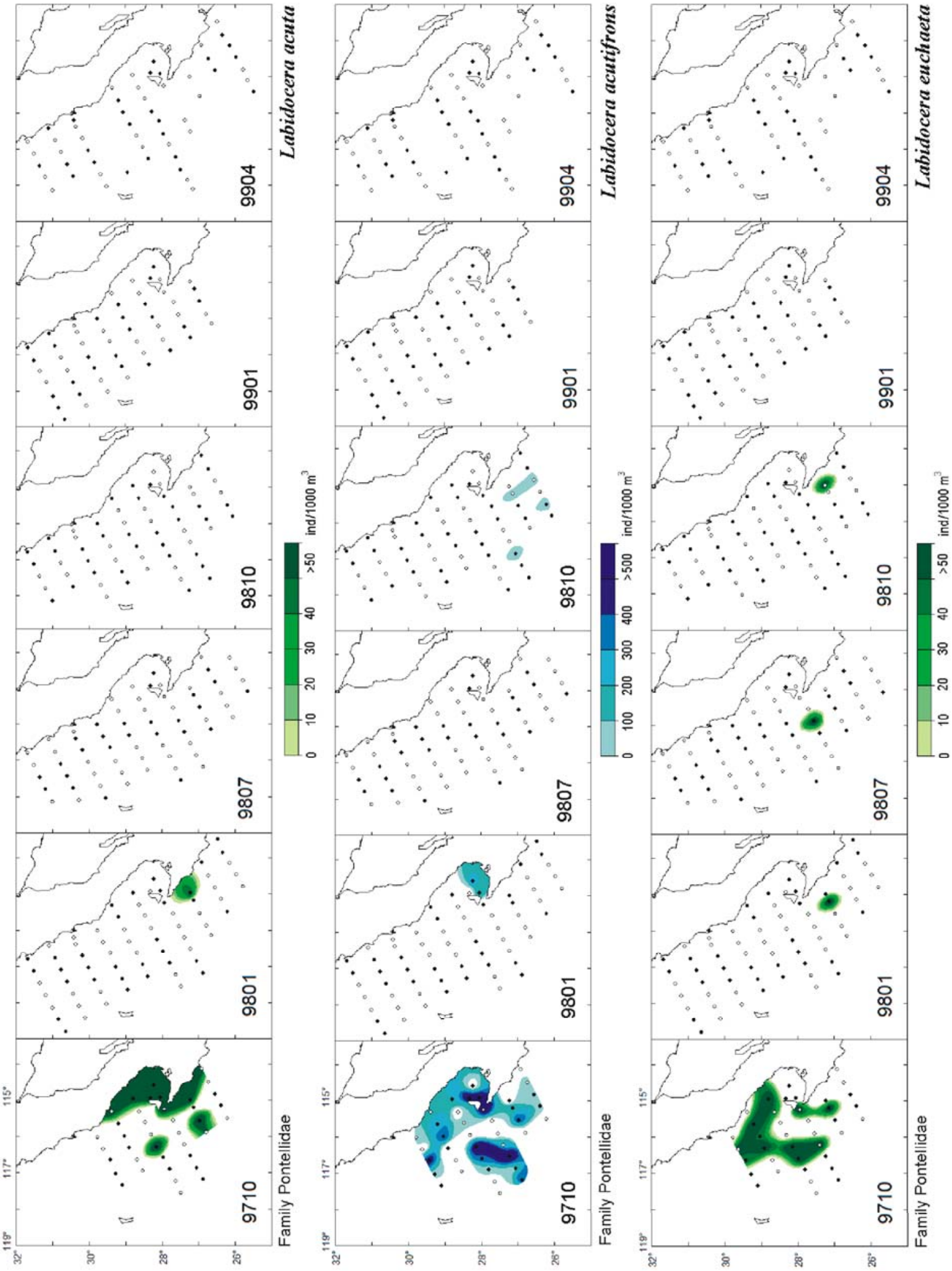
9710
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9810
9901
9904
Family Pontellidae
Labidocera acuta
Labidocera acutifrons
Labidocera euchaeta
ind/1000 m3
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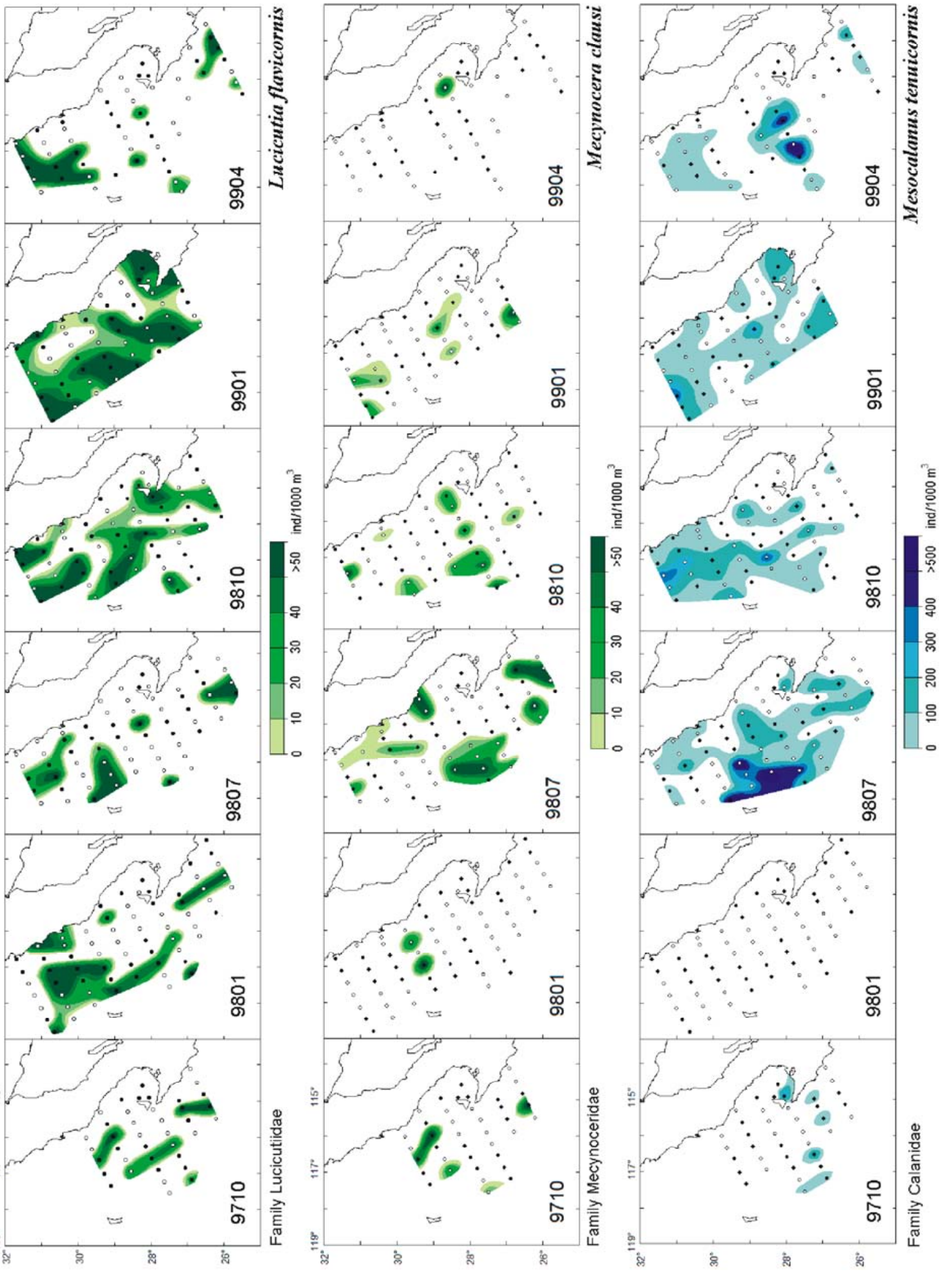
Family Lucicutiidae
Lucicutia flavicornis
Family Mecynoceridae
Mecynocera clausi
Family Calanidae
Mesocalanus tenuicornis
9710
9801
9807
9810
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9904
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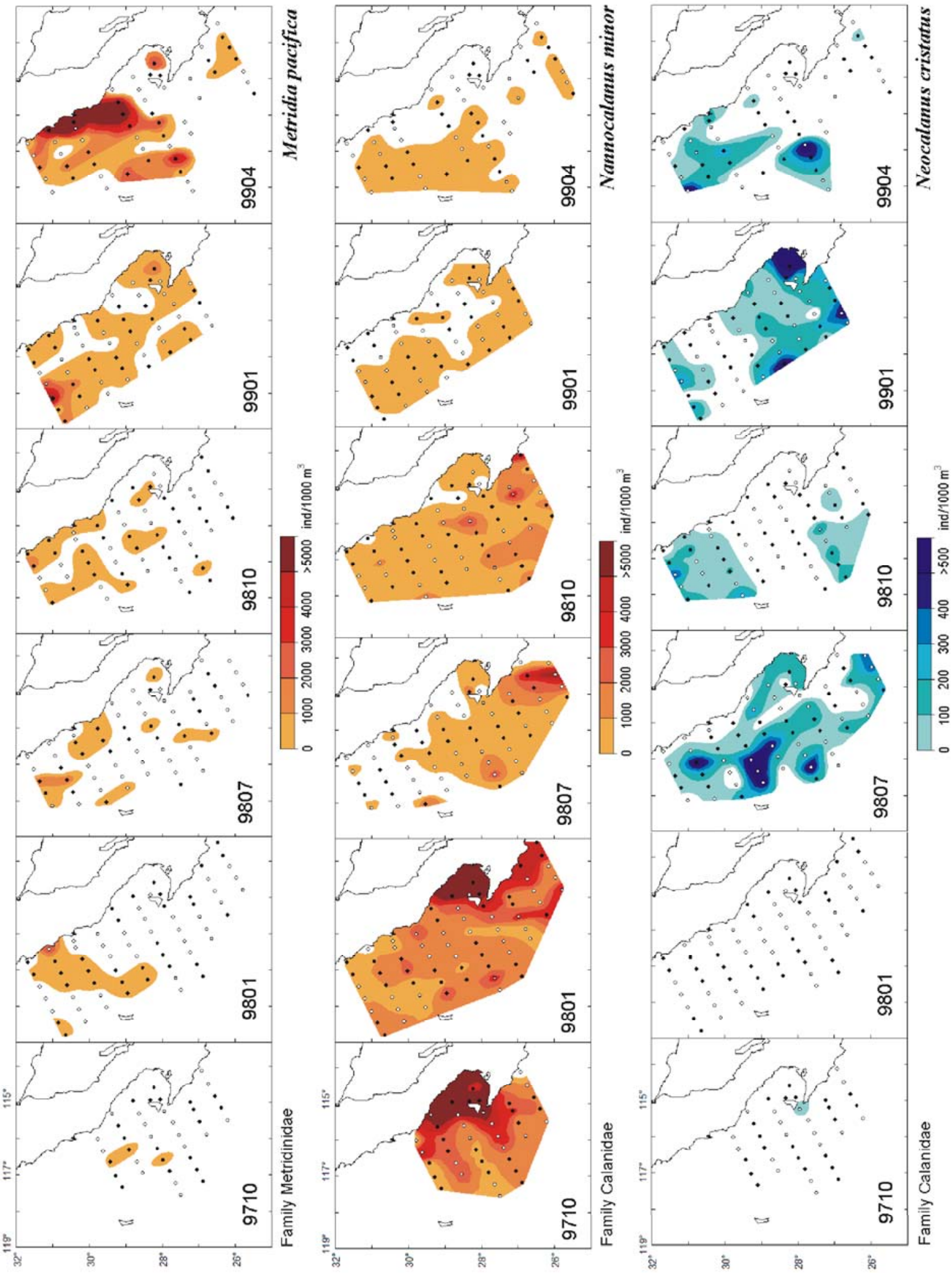
Family Metridinidae
Metridia pacifica
Family Calanidae
Nannocalanus minor
Family Calanidae
Neocalanus cristatus
9710
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ind/1000 m^3
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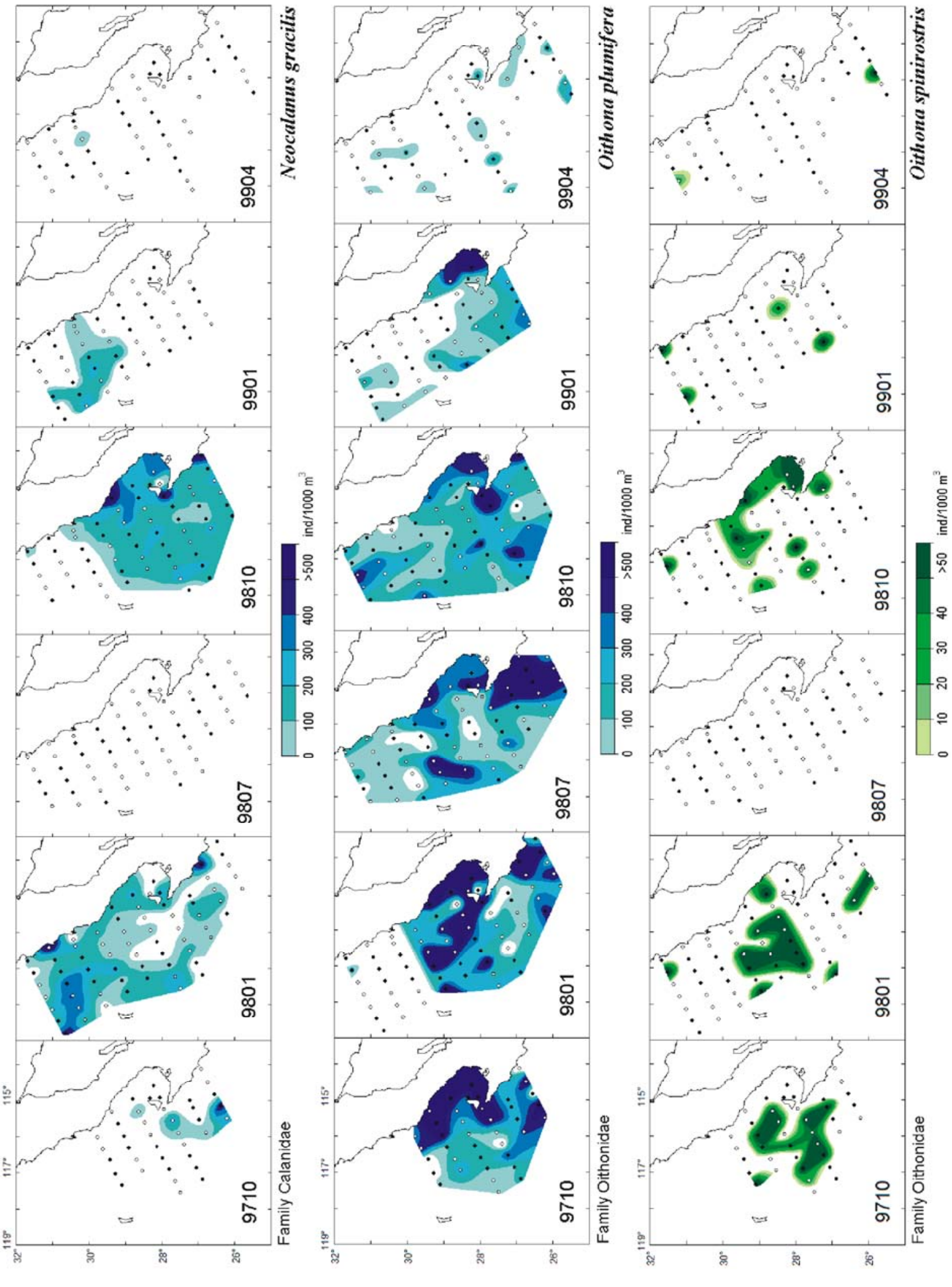
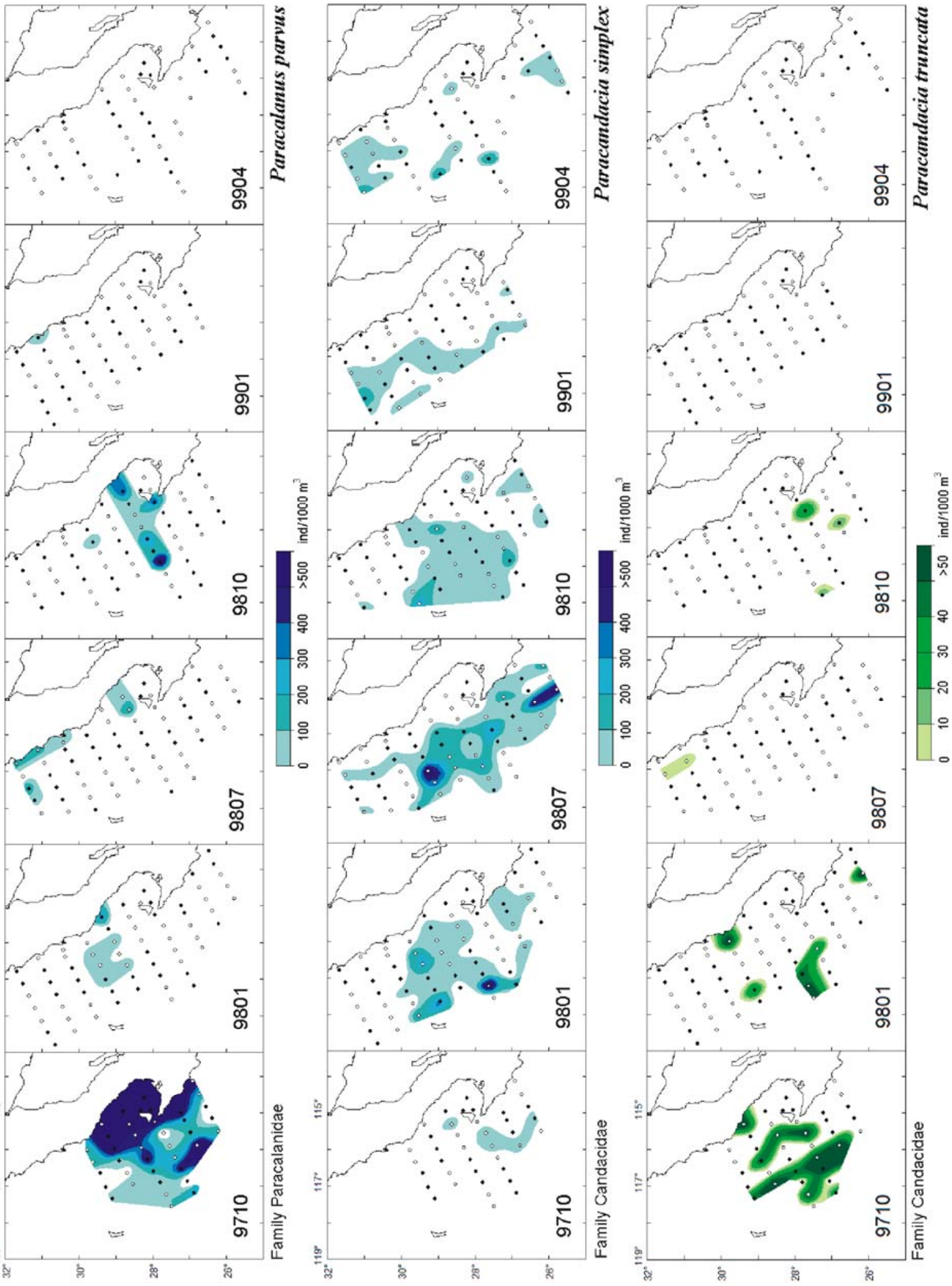
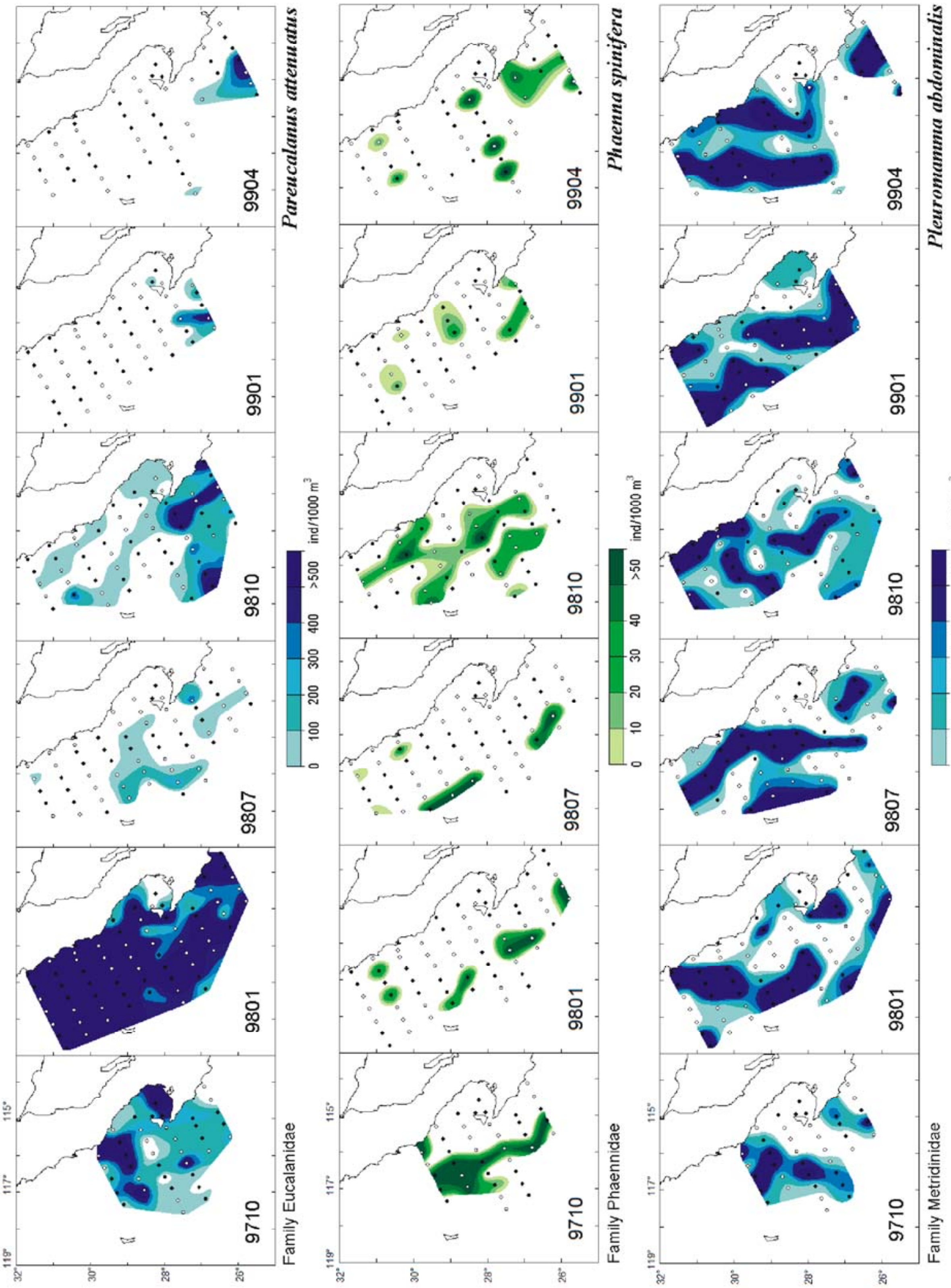
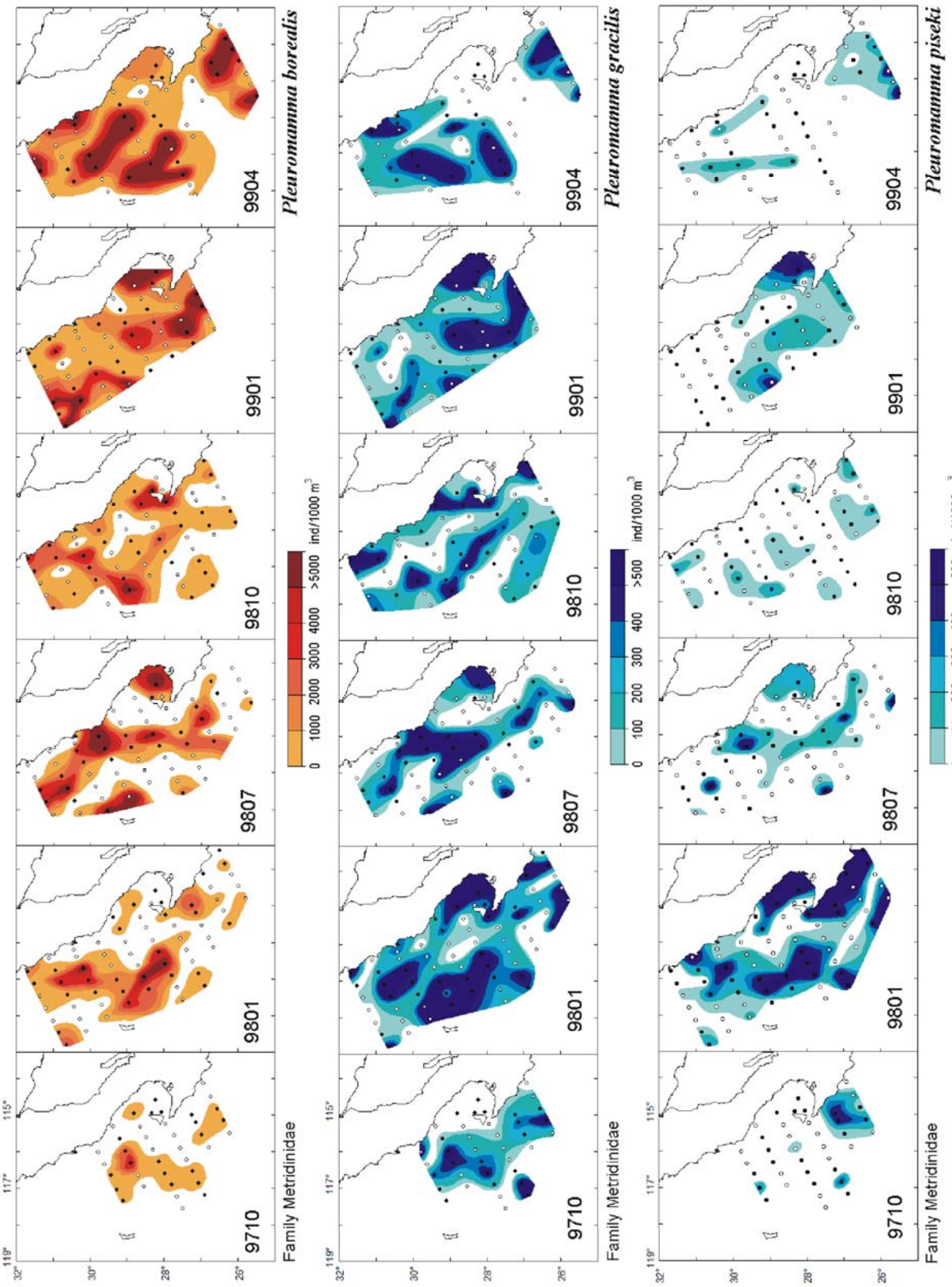
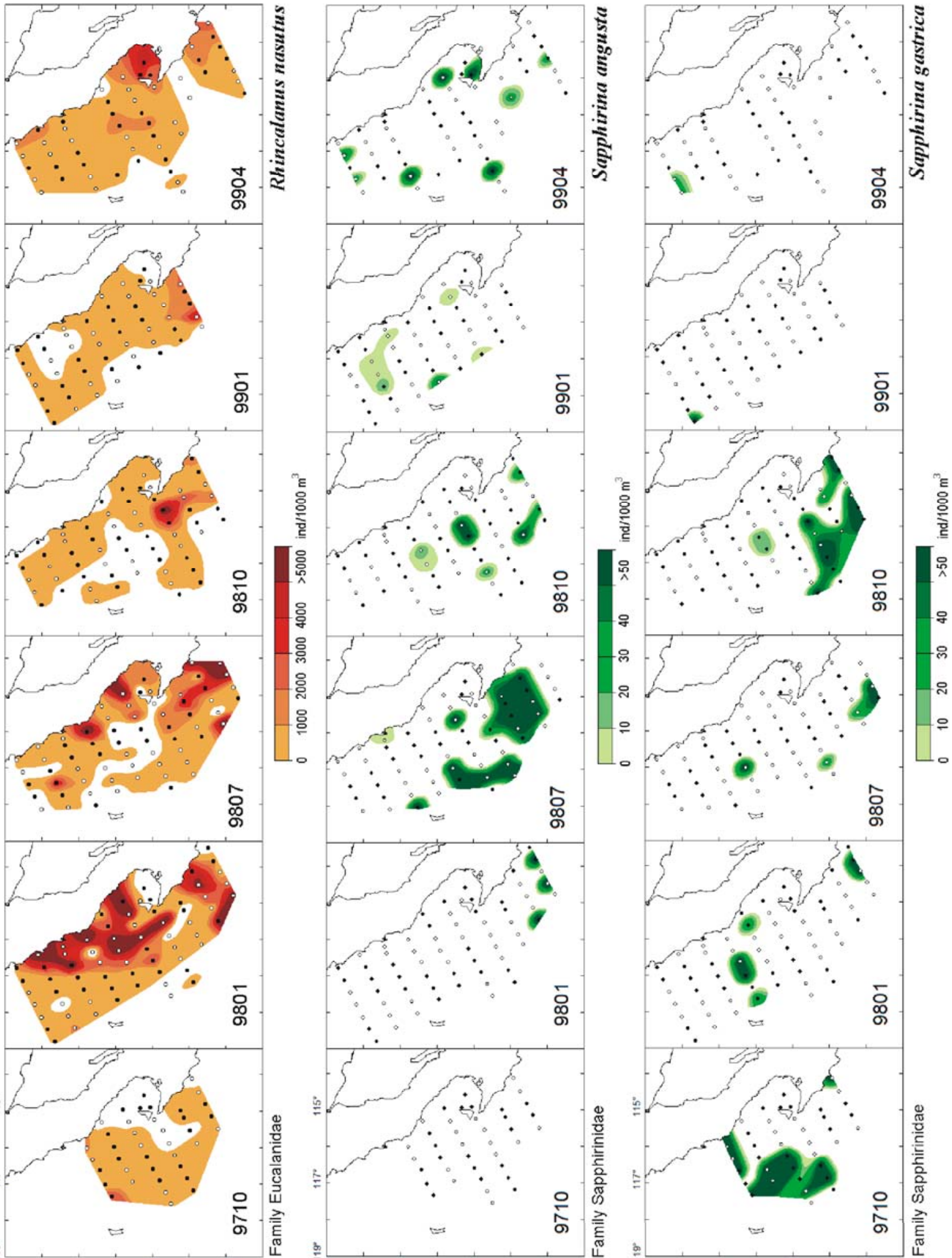
115°
32°
30°
28°
26°

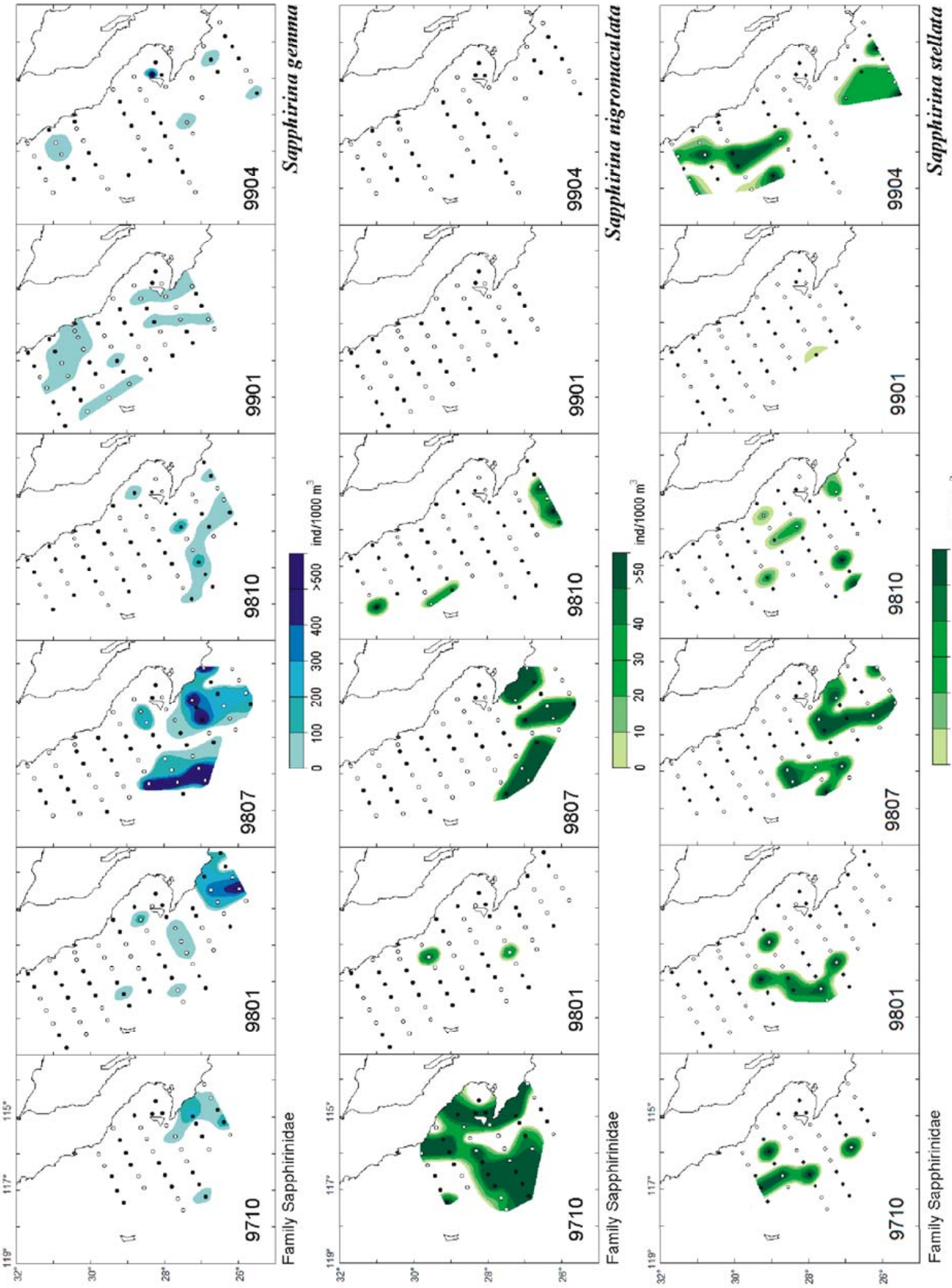

119°
117°
115°
32°
30°
28°
26°
9710
9801
9807
9810
9901
9904
Family Calanidae
Neocalanus gracilis
Family Oithonidae
Oithona plumifera
Family Oithonidae
Oithona spinirostris
ind/1000 m3
0
100
200
300
400
>500
0
10
20
30
40
>50

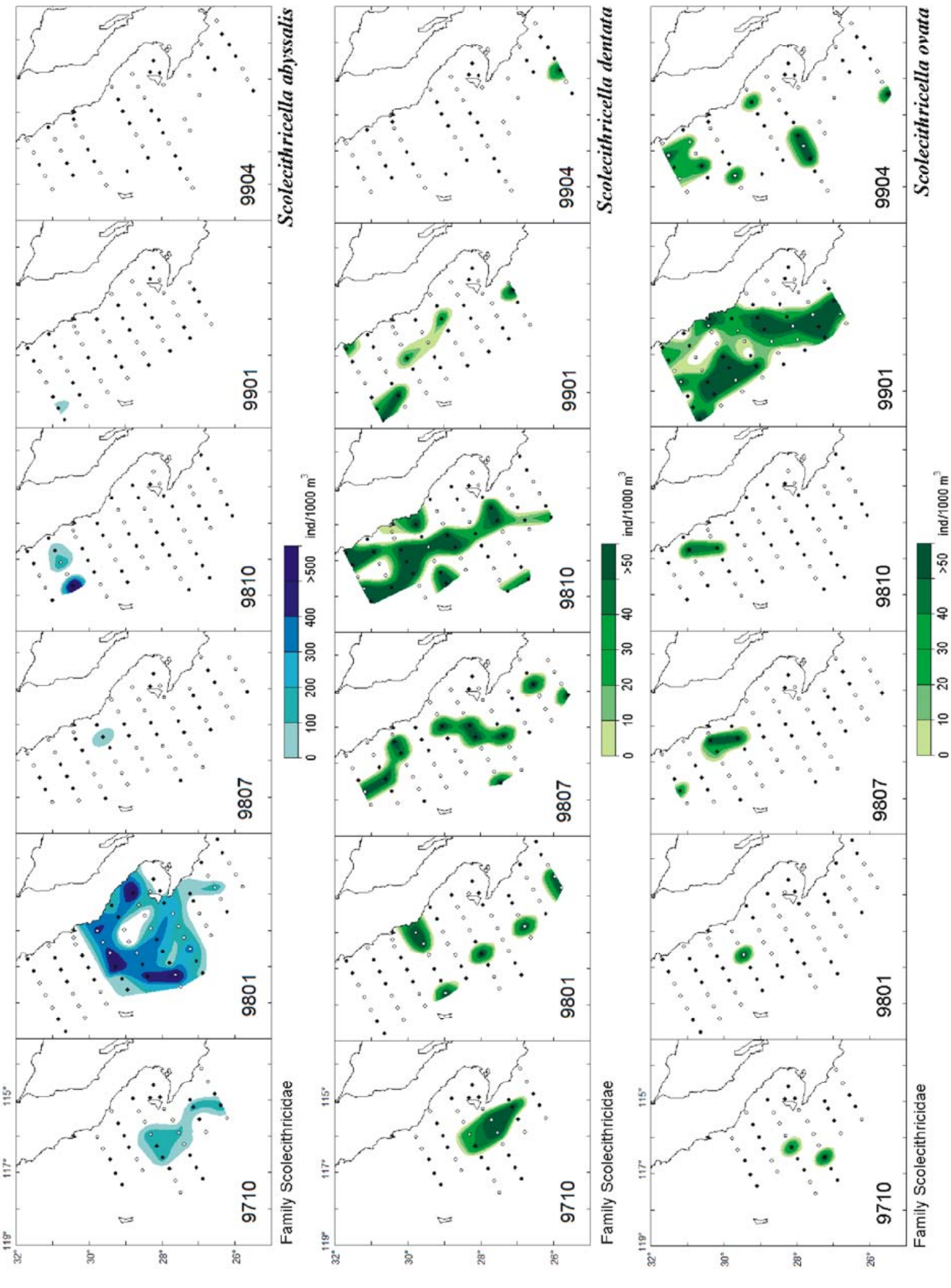

Family Paracalanidae
Paracalanus parvus
Family Candacidae
Paracandacia simplex
Family Candacidae
Paracandacia truncata
9710
9801
9807
9810
9901
9904
119°
117°
115°
32°
30°
28°
26°
ind/1000 m³
0
100
200
300
400
>500
0
10
20
30
40
>50

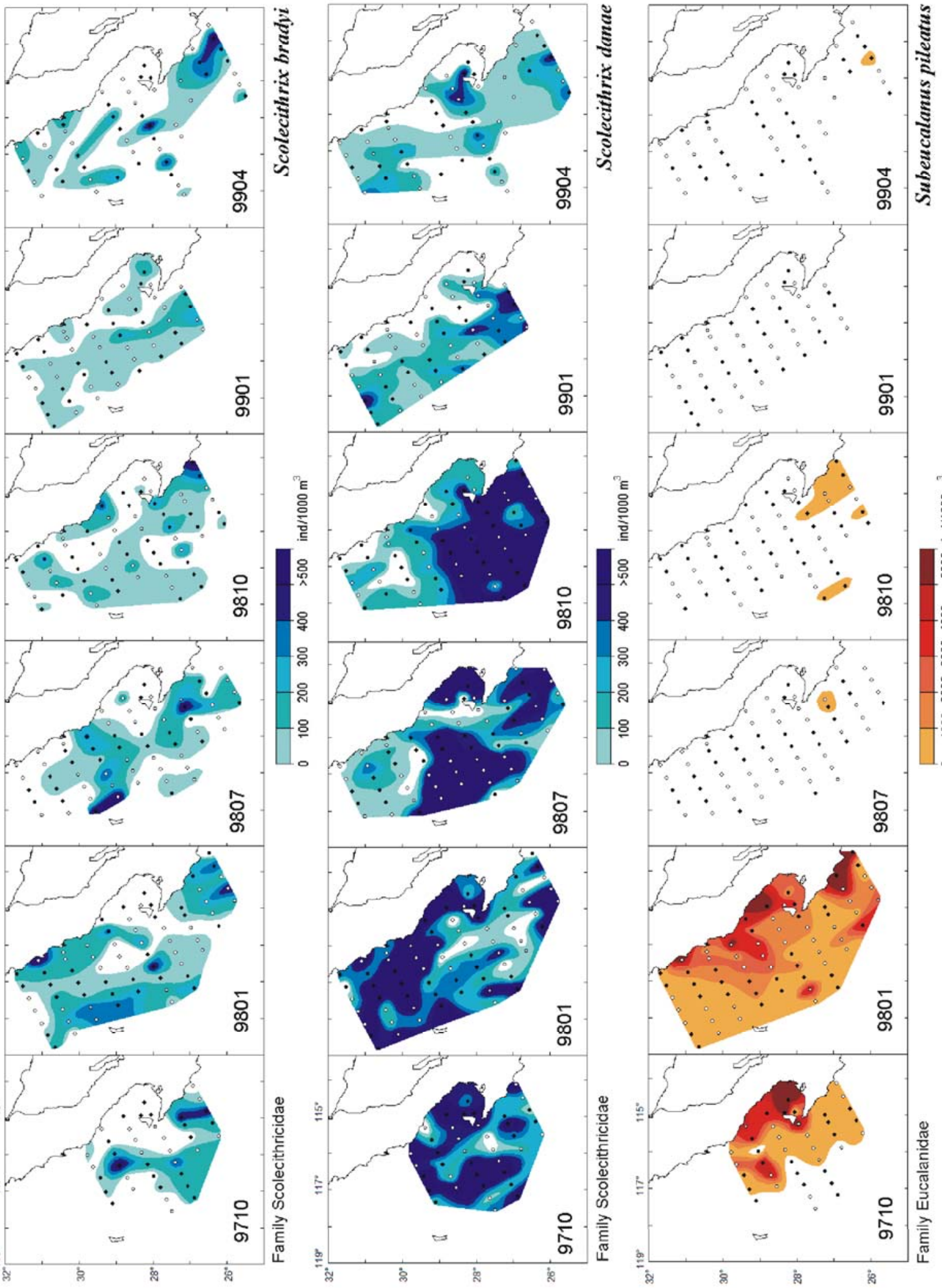

119°
117°
115°
32°
30°
28°
26°
9710
9801
9807
9810
9901
9904
Family Eucalanidae
Pareucalanus attenuatus
0
100
200
300
400
>500
ind/1000 m^3
Family Phaennidae
Phaenna spinifera
0
10
20
30
40
>50
ind/1000 m^3
Family Metridinidae
Pleuromamma abdominalis
0
100
200
300
400
>500
ind/1000 m^3

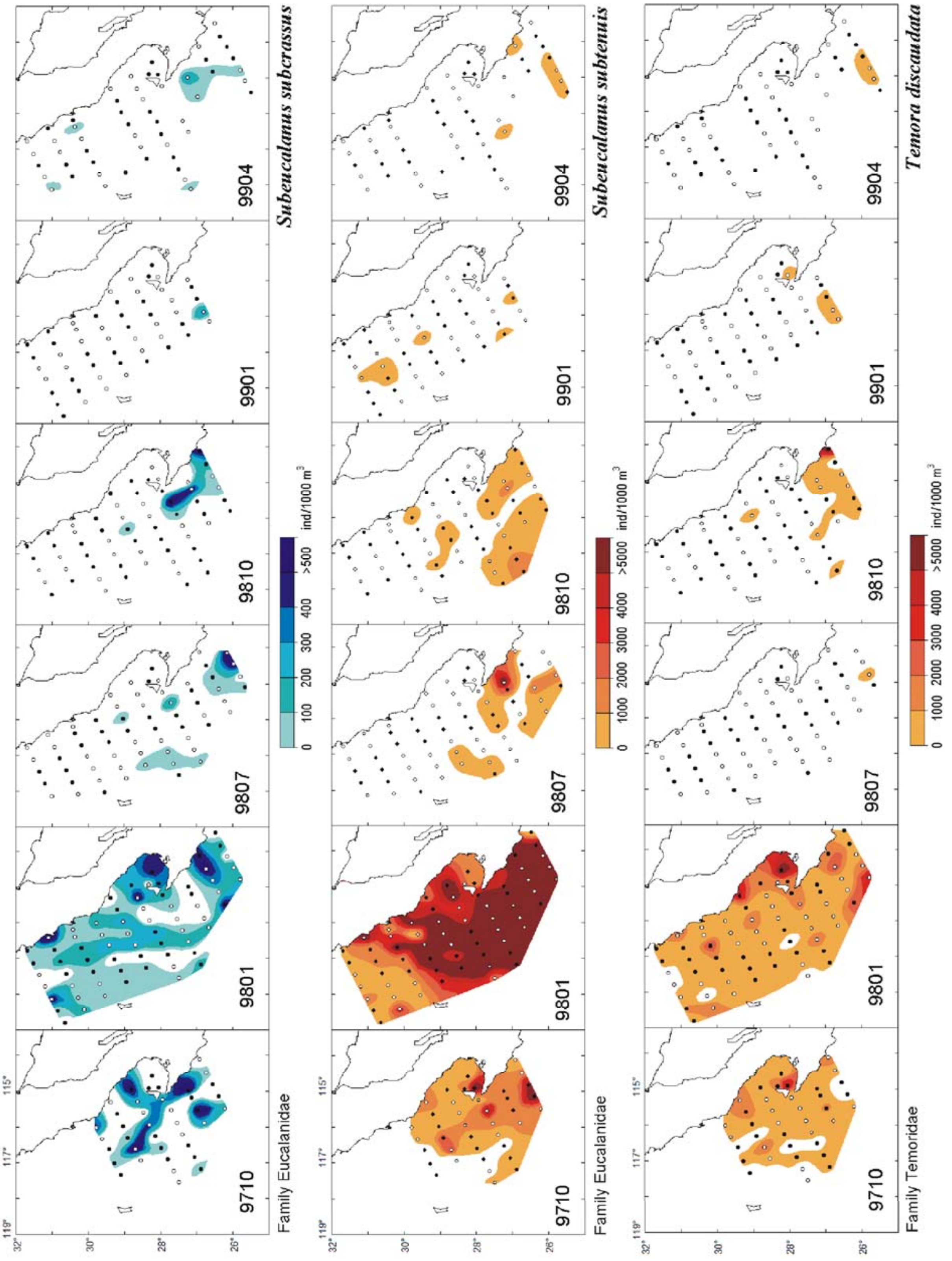

Family Metridinidae
Pleuromamma borealis
Pleuromamma gracilis
Pleuromamma piseki
9710
9801
9807
9810
9901
9904
119°
117°
115°
32°
30°
28°
26°
0
1000
2000
3000
4000
>5000
ind/1000 m³
0
100
200
300
400
>500
ind/1000 m³

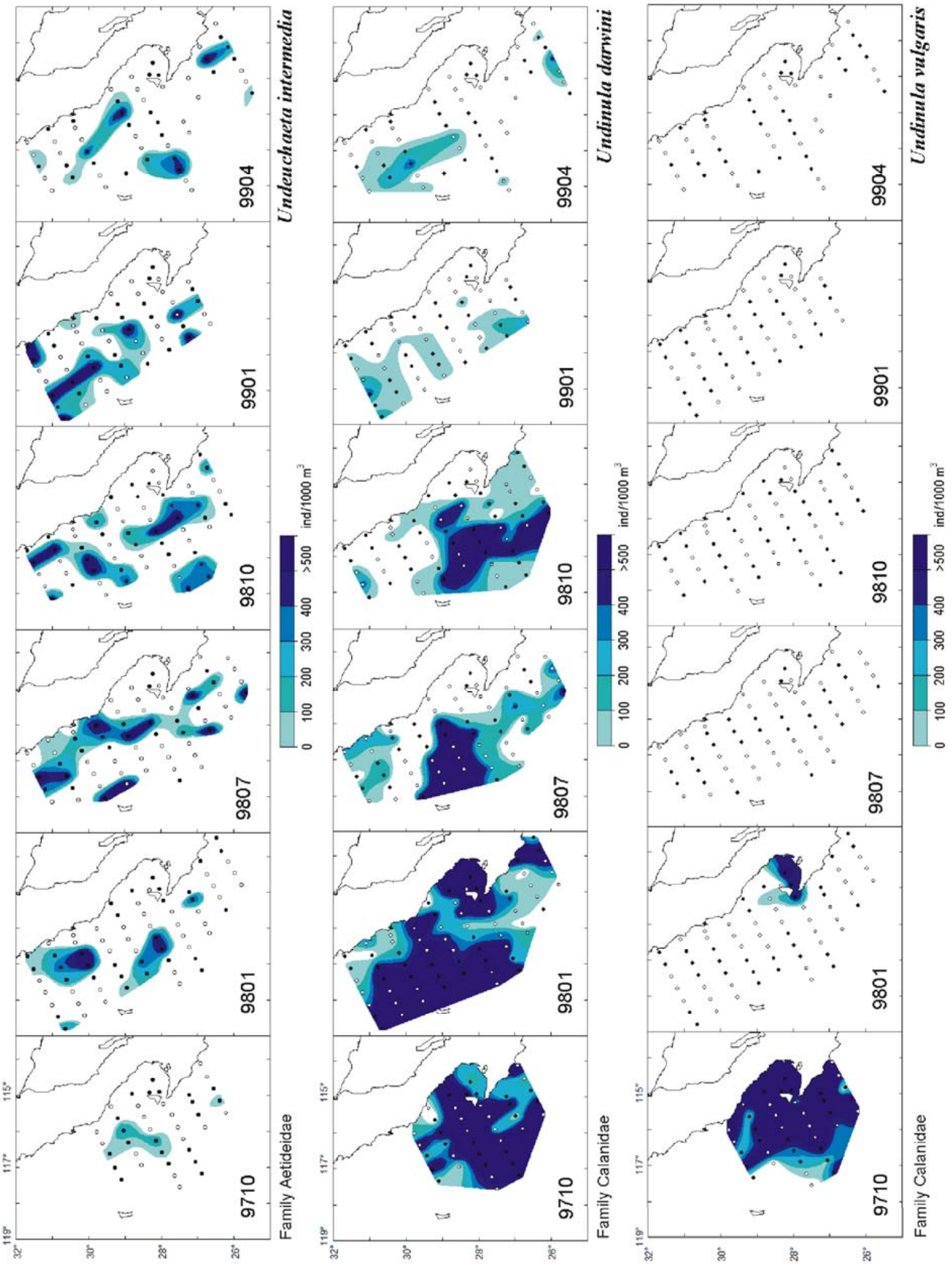

119°
117°
115°
32°
30°
28°
26°
9710
9801
9807
9810
9901
9904
Family Eucalanidae
Rhincalanus nasutus
0
1000
2000
3000
4000
>5000
ind/1000 m^3
Family Sapphirinidae
Sapphirina angusta
0
10
20
30
40
>50
ind/1000 m^3
Family Sapphirinidae
Sapphirina gastrica
0
10
20
30
40
>50
ind/1000 m^3


Family Sapphirinidae
Sapphirina gemma
Sapphirina nigromaculata
Sapphirina stellata
9710
9801
9807
9810
9901
9904
ind/1000 m3
0
100
200
300
400
>500
0
10
20
30
40
>50
119°
117°
115°
32°
30°
28°
26°


Scolecithricella abyssalis
Scolecithricella dentata
Scolecithricella ovata
Family Scolecithricidae
9710
9801
9807
9810
9901
9904
ind/1000 m^3
0
100
200
300
400
>500
0
10
20
30
40
>50
32°
30°
28°
26°
119°
117°
115°


119°
117°
115°
32°
30°
28°
26°
9710
9801
9807
9810
9901
9904
Family Scolecithricidae
Scolecithrix bradyi
0
100
200
300
400
>500
ind/1000 m^3
Family Scolecithricidae
Scolecithrix danae
0
100
200
300
400
>500
ind/1000 m^3
Family Eucalanidae
Subeucalanus pileatus
0
1000
2000
3000
4000
>5000
ind/1000 m^3


Family Eucalanidae
Subeucalanus subcrassus
9710
9801
9807
9810
9901
9904
0 100 200 300 400 >500 ind/1000 m3
Family Eucalanidae
Subeucalanus subtenuis
9710
9801
9807
9810
9901
9904
0 1000 2000 3000 4000 >5000 ind/1000 m3
Family Temoridae
Temora discaudata
9710
9801
9807
9810
9901
9904
0 1000 2000 3000 4000 >5000 ind/1000 m3
119°
117°
115°
32°
30°
28°
26°


Undeuchaeta intermedia
Undinula darwini
Undinula vulgaris
Family Aetideidae
Family Calanidae
Family Calanidae
9710
9801
9807
9810
9901
9904
ind/1000 m^3
0
100
200
300
400
>500
119°
117°
115°
32°
30°
28°
26°