Feeding behavior of adult *Vinciguerria nimbaria* (Phosichthyidae), in the tropical Atlantic (0°–4°N, 15°W)

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Abstract Adult *Vinciguerria nimbaria* are the main prey of tuna during the tuna fishing season (late autumn and winter) in the equatorial Atlantic (0–4°N, and ∼15°W). *V. nimbaria* trophic behavior in the fishing grounds was studied in relation to hydrobiological factors to determine its role in the trophic food web. Sampling stations spaced by 20 nautical miles were set up along a 15°W north–south transect from 4°N to 0°40S. At each station, the temperature and vertical fluorescence profiles were recorded. Nitrate and chlorophyll *a* analyses were performed on water sampled at different levels in the euphotic zone. Vertical plankton hauls were carried out at depths of 0–100 and 0–200 m using a standard WP2 net fitted with a 200-μm mesh gauze. *Vinciguerria nimbaria* adults were collected using a young-fish mid-water trawl net (10 × 15 m opening mouth, 10 mm cod end mesh). The weight of the stomach contents, the stomach fullness index, the number of prey, the frequency of occurrence and the prey preponderance were recorded for 20 fish from each haul. An oligotrophic typical tropical structure (TTS) was found between 1° and 4°N where small zooplankton was relatively abundant above or near the thermocline. In the TTS,

V. nimbaria behaved as an epipelagic fish, feeding on the dominant small prey during the daytime. In turn, it was a prey for tuna. In the equatorial zone, where zooplankton was more abundant than in the north equatorial zone, *V. nimbaria* behaved as a mesopelagic fish and as an opportunistic mesozooplankton feeder. It consumed a wide range of sizes of food, feeding on the most abundant species of zooplankton as well as the largest zooplankton species, possibly while migrating towards the surface in the late afternoon or in the deep layer.

Introduction

Vinciguerria nimbaria is a mesopelagic fish which is widely distributed in oceanic intertropical zones. This fish is small and therefore not of commercial interest but its abundance means that it plays an important role in the pelagic ecosystem. Adult *V. nimbaria* migrates vertically (Silas and George 1969; Clarke 1974, 1980; Gorbunova 1982; Menon et al. 1996), possibly for active feeding at night in the upper layers (Kalinina and Shevchenko 1984). However, *V. nimbaria* feeding in relation to its environment is poorly documented.

Studies have shown that *V. nimbaria* feeds on zooplankton in the Pacific (Legand et al. 1972; Ozawa et al. 1977; Clarke 1978, 1982; Kawamura and Hamoaka 1981) and the Indian Ocean (Kalinina and Shevchenko 1984; Menon et al. 1996). Little information is available about its trophic behavior in the Atlantic Ocean (Shevchenko 1986, 1996; N'Goran and Pagano 1999) but recent studies have shown that *V. nimbaria* is abundant off the African coast (Marchal and Lebourges 1996; Marchal et al. 1996; Lebourges-Dhaussy et al. 2000) and that adults are

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seasonally important as the main food for tuna, in particular *Thunnus albacares* and *Katsuwonus pelamis* (Roger and Marchal 1994; Ménard et al. 2000). In the main fishing area, around 0–5°N and 10–20°W, there is a seasonal variation in the distribution and migratory behavior of *V. nimbaria* (Marchal and Lebourges 1996) which may explain the seasonal abundance of tuna. Maximum tuna concentrations occur during autumn and early winter when the waters are stratified (Herbland and Voituriez 1979). During this period, adult *V. nimbaria* have an "atypical" behaviour as compared with other mesopelagic fish. Indeed, adults are found mainly in the upper 150 m during the day as well as at night and there is no significant vertical migration (Lebourges-Dhaussy et al. 2000), making it more vulnerable to tuna predation. Conversely, tuna are scarce during summer when tropical instability waves develop (Legeckis 1977; Morlière et al. 1994). During this period, adult *V. nimbaria* live in or around the deep scattering layer during the day and rise towards the surface at night fall, behaving as a "typically migrating" mesopelagic fish (Clarke 1974; Ozawa et al. 1977; Gorbunova 1982; Kalinina and Shevchenko 1984). Larval phase is always located in the surface layer (Stequert et al. 2003).

PICOLO (*Production Induite en zone de Convergence par les Ondes Longues Océaniques*) is a multidisciplinary program set up by the French IRD (*Institut de Recherche pour le Développement*) to give a better understanding of the reason for the high tuna concentrations in the oligotrophic Atlantic tuna fishing area.

To try to determine the origin of the atypical behaviour of *V. nimbaria* adults and to understand the role of this fish in the tuna food web, two hypothesis were put forward: one related to reproduction, the other related to feeding. To test this last hypothesis we studied the *V. nimbaria* trophic activity in the fishing grounds during the tuna fishing season. In this paper we present the variations in diet and feeding behavior of adult *V. nimbaria* in relation to hydrological conditions (temperature, salinity, nutrients) and biological factors [chlorophyll *a* (Chl *a*), zooplankton abundance and diel distribution].

Materials and methods

This study was carried out during the PICOLO 1 cruise (17 January–10 February 1997) aboard R/V ANTEA in the tuna fishing area in the tropical Atlantic off Africa (0°–4°N; 9°–15°W).

Hydrobiological sampling stations were set up at intervals of 20 nautical miles along a 15°W north–south transect from 4°N to 0°40S. Each sampling station was visited while traveling back and forth. Conductivity, temperature and fluorescence vertical profiles were recorded down to 250 m using a CTD probe (Seabird SBE 911) with a carousel. Nitrate and Chl *a* analyses were performed on water sampled at 12 depths in the euphotic zone (10, 20, 30, 40, 50, 60, 70, 80, 90, 100, 125, 150 m). The Chl *a* concentration was measured using a Sequoia Turner 112 fluorometer (Yentsch and Menzel 1963). The nitrate concentration was measured as described by Wood et al. (1967) but using an automatic Technicon analyzer.

Vertical plankton hauls were carried out at each station between 0 and 100 m (3 transects) and between 0 and 200 m (two transects) using a standard WP2 net fitted with a 200-μm mesh gauze (UNESCO 1968). On board, zooplankton samples were splitted into two parts using a Motoda box (Motoda 1959). One part (three quarters of the sample) was used to estimate the zooplankton biomass from freshly collected plankton sorted into <1,000 and >1,000 μm organisms through a sieve. Samples were dried at 60°C for 72 h and the biomass was calculated in mg dry weight m^{-3} (DW). The other part (a quarter of the sample) was preserved in 5% buffered formaldehyde to determine the taxonomic composition (individual m^{-3}) from aliquots whose size varied according to the sample size. The Shannon–Wiener diversity index (H') was calculated from the determined taxa (species, genus, family, or order, according to the determination level) using the formula:

$$H' = -\sum (N_i/N) \log_2(N_i/N)$$

where N_i and N are the individual numbers of the taxa i and the total individual numbers of taxa considered, respectively (Frontier and Pichod-Viale 1998).

During the cruise, the *V. nimbaria* distribution was monitored by continuous acoustic soundings (Lebourges-Dhaussy et al. 2000). Adult *V. nimbaria* were collected horizontally at selected depth horizons, for about 30 min, between 25 m and 135 m, using a young-fish pelagic midwater trawl (YFT, 10 × 15 m opening mouth, 10 mm cod end mesh). The trawl was equipped with a pressure sensor (Netsond Furuno) to determine the depth of the haul. The YFT was towed at a speed of approximately three knots. Eighteen hauls were made at 15°W between 0°20S and 3°N (0° two hauls, 1°N five hauls, 2°N eight hauls, 3°N three hauls) and two hauls were made at 9°W at 3°N. *V. nimbaria* were preserved in buffered formalin on board immediately after the catch. From each haul, 20 fish were withdrawn at random (draw lot, i.e., without any criterion of selectivity), measured to the nearest 0.1 mm (standard length, SL from the tip of snout to the distal end of the caudal peduncle) and weighed to the nearest 0.1 mg (W). The sex was determined. Only mature fish (>30.6 mm according to Stequert et al. 2003) were studied. The condition index of the fish ($K = W/SL^3$) (Fulton 1904) was calculated. The stomach was cut at the pylorus and

weighed with the stomach content. Then, the content was removed and the empty stomach was weighed. The difference gives the wet weight of the stomach content (SCW), calculated to the nearest 0.1 mg.

The vacuity index (I_v) and stomach fullness index (FI) (Berg 1979) were calculated using the formulae:

$$I_v = (ES/TS) \times 100$$

where ES is the number of empty stomachs and TS the number of total stomachs studied; and

$$FI = (SCW/W) \times 100$$

To determine the diet of the *V. nimbaria*, identifiable prey were counted (number of prey PN). The frequency of occurrence (O_i) and the preponderance index of the prey (I_p, Marshall and Elliott 1997) were calculated using the formulae:

$$I_p = M_i \times O_i / \sum^{i=p} (M_i \times O_i)$$

where M_i is the ratio of the weight of the prey i to the total weight of the prey; and

$$O_i = p_i/N$$

where p_i is the number of stomachs containing the ith prey and N is the number of stomachs analyzed.

The individual weights of the different prey were taken from James (1987).

The mean day and night values of the hydrobiological parameters for the 0–100 and 0–200 m layers were calculated for the following zones: equatorial Zone (EZ) pooled samples taken between 0°40S and 0°. The "1°N" zone included samples from 0°20, 0°40 and 1°N, "2°N" included samples from 1°20, 1°40 and 2°N, "3°N" included samples from 2°20, 2°40 and 3°N and "4°N" included samples from 3°20, 3°40 and 4°N. No 0–200 m night samples were available at 0° and 4°N owing to technical problems. The zones from 0°20 to 4°N were called the

north equatorial zone (NEZ). The mean values of the *V. nimbaria* trophic parameters were calculated for two times of day (day and night), two depths (the homogenous surface layer, i.e., the upper 30 m at 0° and the upper 60 m in the NEZ; the deeper layer below 60 m) and four latitudes of sampling pooled as above (0°, 1°N, 2°N and 3°N).

ANOVAs and t tests were performed to analyze the effects of external factors (latitude, day–night and depth) on zooplankton biomass and abundance and on the *Vinciguerria* trophic parameters. The correlation between the hydrological and biological factors was examined by principal component analysis (PCA) using ADE-4 software (Thioulouse 1997).

Results

Temperature, salinity, nutrients and chlorophyll

The mean vertical profiles of temperature (Fig. 1a) showed that the homogenous layer was around 30 m at 0° and 1°N and around 50 m from 2°N to 4°N. The surface temperature increased from the divergence zone (26°C) northward (28°C at 4°N). Conversely, the mean salinity decreased from the EZ (35.7) to 4°N (35.0) (Fig. 1b). At the surface, mean values of fluorescence were highest at the equator (Fig. 1c). The deep fluorescence maximum (DFM) was greatest at 2°N around 65 m and lowest at 4°N around 70 m. At the DFM, the mean values of Chl a and nutrients (NO_3–N) were highest at 2°N (2.15 ± 1.3 µg l^{-1} and 7.2 ± 3.8 µM l^{-1} respectively) and lowest at 4°N (0.9 ± 0.5 3 µg l^{-1} and 4.1 ± 3.2 µM l^{-1}).

Taxonomic composition of in situ mesozooplankton

Table 1 gives the mean relative abundance of the different taxa identified in the 0–100 and the 0–200 m layers in the equatorial zone (EZ) and the NEZ.

Fig. 1 Mean vertical profiles of temperature (**a**), salinity (**b**), and fluorescence (**c**), at the different latitudes
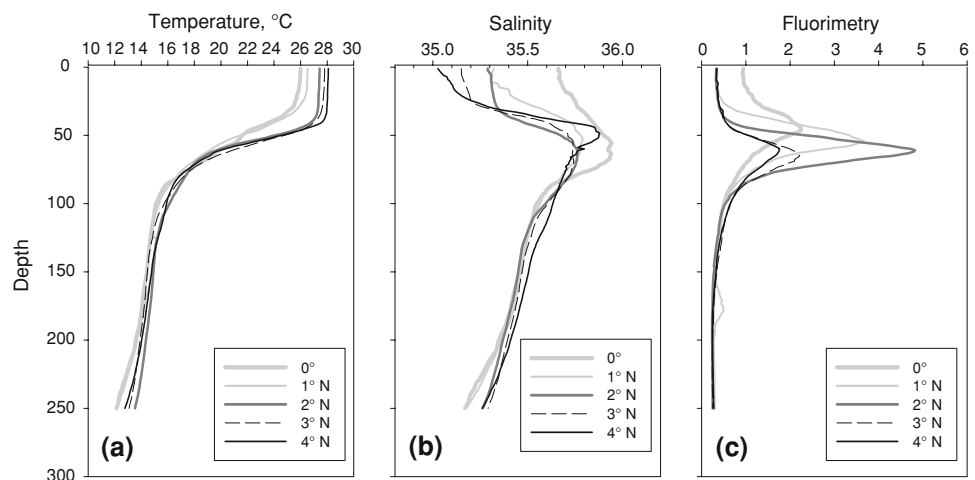
Table 1 Mean percentages of the mesozooplankton taxa and Shannon–Wiener diversity index between 0 and 100 m and between 0 and 200 m in the two main hydrological zone (equatorial zone EZ, north equatorial zone NEZ)

Taxa	EZ 0–100 (m)	NEZ 0–100 (m)	EZ 0–200 (m)	NEZ 0–200 (m)
Oithonidae				
Oithona spp.	8.9	11.2	13.5	13.8
Oncaeidae				
Oncaea spp.	13.2	16.6	26.0	17.8
Lubbockia sp.		0.02		0.01
Corycaeidae				
Corycaeus speciosus	0.09	0.04	0.12	0.05
Corycaeus flaccus	0.01	<0.01		<0.01
Urocorycaeus furcifer	0.01	<0.01		0.02
Onychocorycaeus giesbrechti	0.19	0.02		<0.01
Corycaeus latus	0.01			0.02
Corycaeus ovalis			0.36	0.01
Corycaeus spp.	11.3	14.2		10.9
Corycella carinata	0.06	<0.01	0.36	0.02
Corycella gracilis	0.63	0.11	16.38	1.22
Corycella rostrata	0.83	0.21		0.03
Clausocalanidae–Paracalanidae				
Clausocalanus sp.	20.1	20.3	22.3	19.9
Paracalanus sp.	2.51	1.75		3.72
Acrocalanus andersoni	0.47	0.96		0.58
Calocalanus pavo	2.26	2.61	0.72	2.09
Calanidae				
Calanus minor	3.7	1.1	2.9	0.2
Calanus gracilis	0.01		0.12	0.08
Calanus tenuicornis		0.02		
Calanus robustior		0.14		
Calanoides carinatus	0.09	0.08		0.37
Undinula vulgaris	1.80	3.59	0.36	2.43
Undinula darwini				<0.01
Calanus spp. juveniles	1.07	0.26		0.02
Eucalanidae				
Eucalanus mucronatus	0.67	0.09	0.90	0.14
Eucalanus subcrassus	4.73	3.28	0.84	4.31
Rhincalanus cornutus	0.18	0.32	2.53	2.05
Other copepods				
Lucicutia flavicornis	2.43	0.87		1.54
Lucicutia sp.	1.59	1.36	0.96	1.28
Mecynocera clausi	0.43	0.64		
Phaenna spinifera		0.02		
Temoropia mayumbaensis		0.01		
Scolecithrix danae	0.30	0.32	0.12	0.08
Pleuromamma abdominalis		0.05		1.24
Pleuromma xiphias	0.21	0.40		0.54
Pleuromma robusta	0.34	1.64		0.05
Temora stylifera	0.01	0.20	0.12	0.02
Augaptilus sp.		0.02		
Euaugaloptilus sp.		0.03		
Heterorhabdus sp.		0.22		
Euatideus giesbrechti		<0.01		0.02
Gaidius sp.	0.06			
Haloptilus longicornis	0.01	0.04		0.01
Haloptilus acutifrons				0.01
Arietellus plumifer		0.02		
Centropages violaceus	0.06	0.05	0.60	0.01
Euchierella intermedia				<0.01
Euchierella rostrata				<0.01
Scottocalanus persecans				<0.01
Labidocera sp.		0.03		
Pontellina plumata	0.52	0.10		0.28
Copepod spp (juveniles)	0.62	0.31	0.72	2.54
Ostracoda	1.2	1.8	0.5	1.3
Cladocera		0.6	0.1	

Table 1 continued

Taxon	EZ 0–100 (m)	NEZ 0–100 (m)	EZ 0–200 (m)	NEZ 0–200 (m)
Euchaetidae				
Euchaeta marina	0.70	0.39	0.36	0.18
Euchaeta hebes	0.01	0.07		0.01
Undeuchaeta major				<0.01
Acartiidae				
Acartia negligens		0.04		0.01
Acartia danae	0.44	0.11	0.60	0.13
Candaciidae				
Candacia pachydactyla	0.10	0.10		0.04
Candacia curta		0.13		
Candacia bipinnata		0.02		0.31
Candacia sp.	1.83	0.67		3.95
Harpacticoida				
Microsetella sp.		0.01		0.07
Macrosetella gracilis	0.01	0.15	0.24	0.36
Euterpina acutifrons		0.02		
Miracia minor	0.28	0.26		
Miracia efferata	0.36	0.39		0.23
Clytemnestra sp., *C. scutellata*		0.05		0.02
Sapphirinidae				
Sapphirina angusta	0.43	0.02		
Sapphirina ovatolanceolata	0.04		0.36	0.01
Copilia mirabilis		0.03		
Copilia denticulata	0.02	0.01		0.01

Taxon		EZ 0–100 (m)	NEZ 0–100 (m)	EZ 0–200 (m)	NEZ 0–200 (m)
Appendicularia		4.8	3.5	1.9	2.6
Chaetognata		4.9	3.3	2.5	1.9
Gelatinous organisms	Medusa	1.2	1.1		0.3
	Salpidae		0.1		0.01
	Doliolidae	0.2	0.04	0.1	0.1
	Siphonophora	0.03	0.01	0.8	0.1
	Pteropoda		0.2		
Other crustaceans	Euphausiacea	1.2	1.2	0.8	0.5
	Mysidacea			0.48	
	Amphipoda	0.24	0.33		0.27
	Lucifer sp	0.1	0.1	0.4	0.02
Meroplankton	Penaeid larvaeae		0.01		0
	Brachyoura larvae	0.9	0.3		0.7
	Decapod larvae	0.9	0.3	0.4	0.7
	Gasteropod larvae	0.2	0.4		0.1
	Fish larvae	0.3	0.1		0.2
	Fish eggs		0.3		0.07
	Echinoderm larvae	0.2	0.2		0.2
	Polychaet larvae	0.2	0.3	0.6	0.2
	Total copepods	83.6	85.8	91.5	90.6
	Other groups	16.4	14.2	8.5	9.4
	Diversity index (H')	3.7	3.6	3.2	3.3

In the upper 100 m, copepods always represented more than 83% of total mesozooplankton with the lowest mean value (83.7%) in the EZ, and the highest (89.5%) at 4°N (Table 2). Clausocalanidae and Paracalanidae clearly dominated during the day and at night (23.8 to >30% of total individuals). Together with Coryceaeidae, Oncaeidae and Oithonidae, they constituted between ~60 and 73% of total mesozooplankton. Smaller numbers of Calanidae (~5%) and Eucalanidae (~4%) were found (Table 2). Of other taxa, appendicularians and chaetognaths prevailed, representing ~5% each at 0°.

Clausocalanidae, Paracalanidae and Oithonidae dominated in the 0–200 m layer. With Oncaeidae and Corycaeidae they accounted for between 71 and 84% of the total mesozooplankton. Eucalanidae and Calanidae were the most numerous of other copepods. Appendicularians and chaetognaths were the other main taxa (Table 2).

Mesozooplankton dry weight and abundance

Between 0 and 100 m, the mean mesozooplankton abundances and biomass (DW) were greatest at 0° and lowest at 4°N (Fig. 2a). Abundance decreased more or less regularly while the DW did not vary greatly between 1° and 3°N. Between 0 and 200 m, latitudinal variations of zooplankton DW and individuals were less significant than in the upper 100 m, in particular abundance variations (Fig. 2b). DW tended to decrease north to 3°N.

Day–night variations

In the 0–100 m layer, night/day ratios (N/D) for most taxa were much higher in the EZ than further north (Table 2). However, the N/D ratio of gelatinous organisms, chaetognaths and ostracods were higher at 4°N. At night, the proportion of medium and large size copepods (Candaciidae and Euchaetidae) tended to increase at the different latitudes, particularly in and around the EZ. N/D of >1,000 μm zooplankton were between 1.4 and 2.2 but N/D ratios of the <1,000 μm organisms were much lower (Table 2). N/D ratios of copepods and other taxa were much higher in the EZ than in the NEZ.

Two way ANOVAs carried out on abundances and DW indicated that latitude and day–night variations had a significant effect on total DW (Table 3). Latitude had a significant effect on organisms <1,000 μm but day–night variations were not significant. Inversely, in organisms >1,000 μm day–night variations were significant and latitude had no significant effect. There was no significant interaction between latitude and day–night variations for DW, <1,000 and >1,000 μm organisms. Latitude and day–night variations had a significant effect on total abundance,

copepod numbers and other taxa abundance. Interactions between factors were also significant (Table 3).

Between 0 and 200 m, there was little day–night variation at 3°N where individual numbers were lowest. The highest N/D ratios of DW were found in organisms >1,000 μm at 1° and 2°N (Table 2). A two way ANOVA indicated that latitude and day–night had a significant effect on total mesozooplankton abundance and copepod numbers. Day–night variation had a significant effect on total mesozooplankton DW, organisms >1,000 μm, but had no significant effect on organisms <1,000 μm and on numbers of other taxa (Table 3). There was no significant interaction between latitude and day–night variation.

Mesozooplankton specific diversity

On the whole, a two way ANOVA showed that the depth ($P < 0.001$) and the time of day ($P = 0.027$) had a significant effect on the Shannon–Wiener indexes (H'). The interaction between day–night and depth was not significant ($P = 0.259$). Latitude was not significant ($P = 0.167$).

In the 100 m layer, H' varied between 2.95 and 4.0. Day values (3.46 ± 0.3) were lower than night values (3.73 ± 0.19). In the 0–200 m layer, H' varied between 2.7 and 3.8 (mean day values 3.2 ± 0.3; mean night values 3.32 ± 0.11).

Principal component analysis

A PCA was carried out using the mean values for day and night zooplankton abundance, biomass and diversity in the 0–100 m layer, the Chl a and nutrients at the DFM, and the surface temperature and salinity at the five latitudes (Fig. 3). Axis 1 provided most of the information (69.9% of the variance). On this axis, high temperature (left) were opposed to high salinity, high abundance, biomass and day diversity (right). Axis 2 explained 25% of the variance. The plot of the latitudes showed the association of the sampling areas (latitudes) with the hydrological structures. The EZ was well individualized and corresponded to high biomass, high nocturnal abundance and low surface temperatures. It was opposed to 4°N and 3°N characterized by high temperatures. 2°N plots had the highest Chl a values at the DFM.

Vinciguerria nimbaria trophic activity

Four hundred thirteen adult fish were analyzed. The mean standard length was 41.6 ± 3 mm with a mean weight of 464.3 ± 99.4 mg. As there was no significant difference in the stomach content weight (SCW) of males and females for several trawls, male and female fish were pooled. At 3°N, no significant effect of longitude was shown for FI, PN, SCW and K ($P = 0.11$, $P = 0.48$, $P = 0.6$, $P = 0.1$,

Table 2 Mean relative abundance (%) and night-day ratios (N/D) of the mesozooplankton dominant taxa, the <1,000 μm organisms and the >1,000 μm organisms at the different latitudes between 0 and 100 m and between 0 and 200 m

0–100 m	% 0°	% 1°	% 2°	% 3°	% 4°	N/D 0°	N/D 1°	N/D 2°	N/D 3°	N/D 4°
Oithonidae	8.8	9.5	12.0	11.0	14.7	12.6	0.7	1.0	1.2	1.1
Oncaeidae	13.1	16.2	16.9	16.2	17.1	3.4	1.2	1.3	0.9	2.6
Corycaeidae	13.5	16.3	13.3	15.9	10.9	2.3	1.7	1.0	0.8	1.7
Clausocalanidae–Paracalanidae	25.2	23.8	26.8	24.3	30.3	5.0	0.6	1.0	1.1	1.4
Acartiidae	0.4	0.3	0.1	0.1	0.1					
Calanidae	6.6	7.9	2.8	5.7	3.0	4.6	2.1	1.6	0.8	2.9
Eucalanidae	5.6	4.8	3.4	4.0	0.4	2.2	2.6	0.9	1.0	0.6
Euchaetidae	0.7	0.6	0.5	0.3	0.3	9.0	1.3	5.0	0.6	2.8
Candaciidae	1.9	1.0	1.1	0.6	0.7	7.4	3.0	5.2	1.4	7.2
Harpacticoida	0.7	0.3	0.4	0.8	4.1	0.0	1.8	1.1	1.8	2.8
Other copepods	7.1	5.3	6.8	7.5	7.8	4.7	2.3	3.3	1.2	8.6
Ostracoda	1.2	1.6	2.2	1.6	2.0	4.4	2.1	1.6	1.1	20.8
Cladocera	0.0	1.3	0.02	0.3	0.3		59.5		0.1	2.5
Appendicularia	4.8	3.7	3.7	3.8	2.5	5.0	0.7	0.8	1.2	3.3
Chaetognatha	4.9	3.1	3.6	3.9	2.1	1.5	1.1	1.2	1.2	13.9
Gelatinous organisms	1.4	1.7	1.4	1.4	1.0	3.9	4.5	1.3	5.4	6.5
Other crustaceans	1.5	1.1	2.2	1.3	1.3	4.7	9.3	4.4	2.3	6.6
Meroplankton	2.7	1.6	2.7	1.4	1.3	2.5	1.3	0.6	2.1	1.2
Total copepods	83.7	86.0	84.1	86.3	89.5					
<1,000 μm organisms	54.6	51.9	46.8	49.6	46.0	1.3	1.0	1.2	0.9	1.0
>1,000 μm organisms	45.4	48.1	53.2	50.4	54.0	1.9	1.8	1.8	2.2	1.4

| 0–200 m	% 0°	% 1°	% 2°	% 3°	% 4°	N/D 1°	N/D 2°	N/D 3°
Oithonidae	13.5	10.6	23.9	23.4	11.1	0.7	3.2	1.4
Oncaeidae	26.0	17.9	13.4	14.1	16.7	0.8	3.4	1.2
Corycaeidae	17.2	11.9	13.1	8.6	12.2	0.6	3.7	0.5
Clausocalanidae–Paracalanidae	23.0	24.5	24.5	29.2	41.1	0.6	0.9	1.2
Acartiidae	0.6	0.0	0.2	1.1	0.5			0.8
Calanidae	3.4	2.9	5.2	1.7	1.5	0.5	38.7	1.0
Eucalanidae	4.3	7.4	3.0	1.6	0.3	0.7	1.4	3.0
Euchaetidae	0.4	0.1	0.2	0.6	0.6	2.7	6.3	0.9
Candaciidae	0.0	7.0	0.3	0.1	0.1	3.8	5.3	
Harpacticoida	0.2	0.2	0.5	3.5	7.1	0.3	3.9	0.6
Other copepods	2.9	8.2	6.8	8.5	2.0	0.8	3.5	1.6
Ostracoda	0.5	1.3	1.5	1.4	0.5	0.5	4.3	2.3
Cladocera	0	0.05	0.1	0	0	0.03		
Appendicularia	1.9	2.7	2.2	0.8	1.9	0.6	2.9	0.6
Chaetognatha	2.5	1.8	1.6	2.1	2.3	0.7	0.4	0.8
Gelatinous organisms	1.0	0.4	1.0	1.2	0.6	0.3	12.9	0.6
Other crustacea	1.7	0.8	0.5	1.3	0.5	0.6	1.3	0.5
Meroplankton	1.0	2.3	1.6	0.8	0.9	0.9	8.1	1.3
Total copepods	91.5	90.7	91.3	92.4	93.2			
<1,000 μm	62.8	43.2	47.2	40.9	56.4	2.0	1.8	0.9
>1,000 μm	37.2	56.8	52.9	59.1	43.6	2.9	2.8	1.1
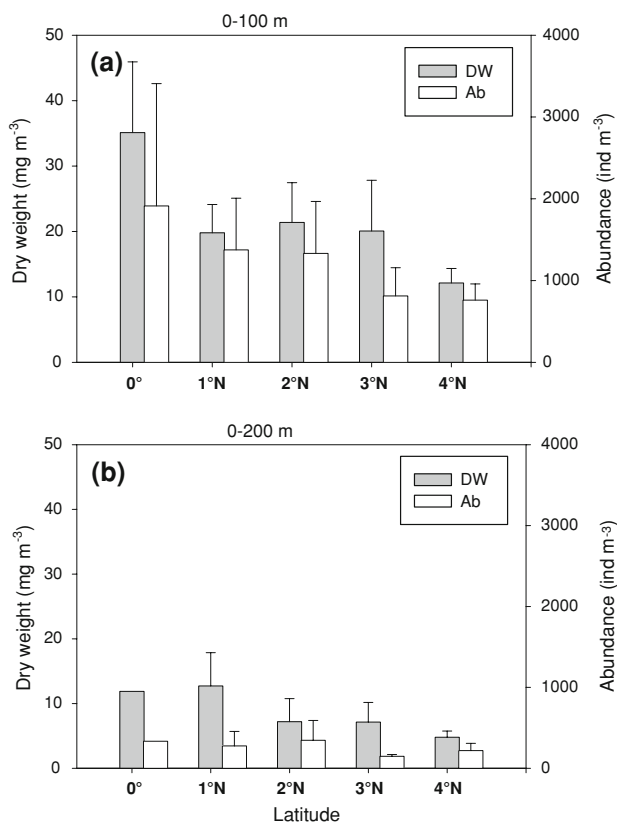
Fig. 2 Mean values (and standard errors) of zooplankton dry weights and abundance at the different latitudes in the 0–100 m (**a**), and the 0–200 m (**b**), layers

respectively). Therefore, values were pooled. The stomachs of fish sampled late at night (4 and 5 am) never contained entire prey.

The mean vacuity index (I_v) for all fish sampled in the EZ was zero. For fish sampled in the NEZ, I_v was 18.1 ± 31.7.

Two way ANOVAs were performed on normalized FI, PN, SCW and K data (log +1) to test the effect of depth, latitude and time of day (Table 4). Latitude and depth were found to have a significant effect on FI, PN and SCW. In both

areas, the effect of day–night variation was significant. Latitude had a significant effect on K but depth had no effect.

The trophic parameters at two depths and different times in the EZ and the NEZ were studied. Overall, trophic activity was higher above the thermocline than below. Trophic activity (FI, PN, SCW) tended to increase from early morning to the afternoon and started to decrease in early night (Fig. 4).

Vinciguerria nimbaria diet

Table 5 gives the number of stomachs with food versus the number of stomach analyzed at the different depths and sampling hours and the relative abundance of prey in fishes caught in the EZ and the NEZ at different times of the day. Fifty-six taxa were identified in the stomach contents, copepods being dominant (45 genus or species) and accounting for over 89% of the whole prey. Small copepods such as Oncaeidae, Corycaeidae, Clausocalanidae and Paracalanidae accounted for over 79% of the *Vinciguerria* prey, except in fish collected in the EZ at night. The highest numbers of larger copepods such as Calanidae, Eucalanidae, Candaciidae and Euchaetidae were found in the EZ at night. Unidentified digested copepods accounted for around 1–5% of the stomach contents. There was little latitudinal and day–night variation in the specific composition of the stomach contents in the NEZ but Clausocalanidae and Paracalanidae were more numerous during the day than at night. The greatest prey diversity indexes (Table 5) were found in fishes caught in the EZ at night (3.7) and during the day (2.8). In the NEZ, the prey diversity index varied between 1.1 and 2.5.

The preponderance index varied with latitude and time of day (Fig. 5). In the EZ (Fig. 5a), there was significant day–night variation. During the day, small copepods (Clausocalanidae and Paracalanidae, Oncaeidae, Corycaeidae) and Eucalanidae had the highest indexes. At night, the highest index was for various larger copepods (Calanidae, Euchaetidae, Candaciidae principally). The frequency

Table 3 Two way ANOVAs to test the effects of latitude, day–night, and interactions on dry weights, abundances, <1,000 µm organisms, >1,000 µm organisms, copepods and other taxa of zooplankton sampled between 0 and 100 m and between 0 and 200 m

| Dependent variable	0–100 m source of variation			0–200 m source of variation		
	Latitude	Day–night	Interactions	Latitude	Day–night	Interactions
Dry weights	**<0.001**	**0.005**	0.34	0.17	**0.016**	0.123
Abundances	**<0.001**	**0.002**	**0.01**	**0.019**	**0.047**	0.09
<1,000 µm organisms	**<0.001**	0.833	0.66	0.179	0.174	0.241
>1,000 µm organisms	0.115	**0.015**	0.88	0.268	**0.005**	0.112
Copepods	**<0.001**	**0.004**	**0.01**	**0.023**	**0.05**	0.118
Other taxa	**<0.001**	**<0.001**	**0.03**	0.195	0.488	0.097

Significant values are in bold
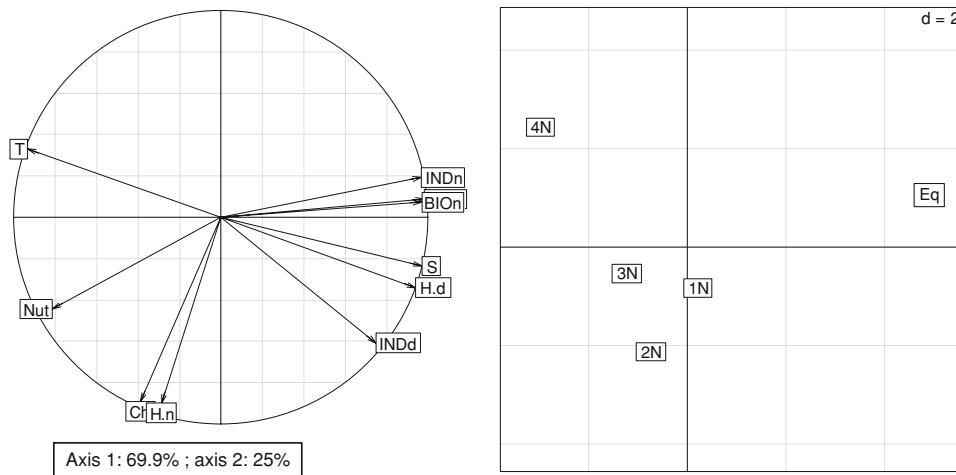
Fig. 3 Principal component analysis for the hydrobiological parameters; plots of the variables and the samples at the five areas on the planes 1, 2. *T* surface temperature, *S* surface salinity, *Chl* chlorophyll *a* at the deep fluorescence maximum (DFM), *Nut* nutrients at the DFM, *INDd* daytime individual numbers, *INDn* night individual numbers, *BIOd* daytime biomass, *BIOn* night biomass, *H.d*, *H.n* day and night Shannon–Wiener diversity indexes, *Eq* equatorial zone, *1N* 0.2–1°N, *2N* 1.2–2°N, *3N* 2.2–3°N, *4N* 3.2–4°N. BIOn and BIOd samples are superimposed

Table 4 Two way ANOVAs to test the effects of depth, latitude, day–night and interactions on fullness index (FI), prey numbers (PN), stomach content weights (SCW) and condition index (*K*) of *Vinciguerria nimbaria*

Source of variation	DF	Log FI	Log PN	SCW	Log *K*
Depth	1	**<0.001**	**<0.001**	**<0.001**	0.576
Latitude	3	**<0.001**	**<0.001**	**<0.001**	**0.002**
Depth × latitude	3	**0.016**	**<0.001**	**<0.001**	0.099
Day–night	1	**0.041**	**<0.001**	**0.041**	**<0.001**
Latitude	3	**<0.001**	**<0.001**	**<0.001**	**0.024**
Day–night × latitude	3	**<0.001**	**<0.001**	**<0.001**	**<0.001**

Significant values of *P* (*P* < 0.01) are in bold

of occurrence of these taxa was also high (Fig. 5c). Conversely, there was less day–night variation in the NEZ. A high preponderance index (Fig. 5b) was only observed for a few taxa, mainly small copepods (Oncaeidae, Corycaeidae, Clausocalanidae and Paracalanidae) and there was a high occurrence of a more limited number of taxa than in the EZ (Fig. 5d).

Comparison of stomach contents and in situ mesozooplankton composition

In the EZ, *Vinciguerria* preyed upon Oncaeidae and Corycaeidae that were abundant in the area (Fig. 6), and on a few larger, less abundant, organisms (Candaciidae, Euchaetidae, Scolecithrichidae, Sapphirinidae, chaetognaths, amphipods, euphausids) and on some ostracods.
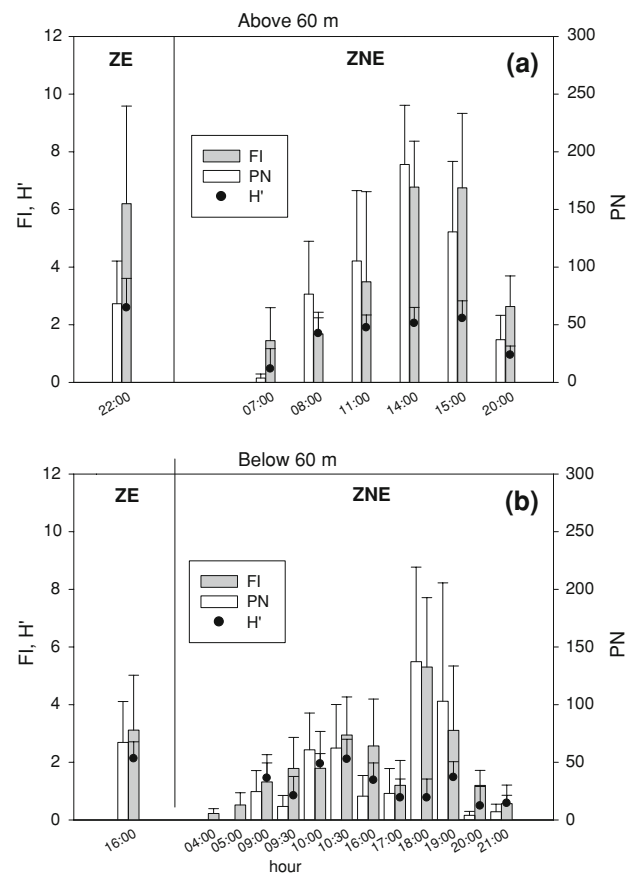

Fig. 4 Diel variations of prey numbers (*PN*), fullness indexes (*FI*), and diversity indexes (*H′*) of the prey items of *Vinciguerria nimbaria* sampled above and below 60 m in the equatorial zone (*EZ*) and in the north equatorial zone (*NEZ*)

Table 5 *Vinciguerria nimbaria* diet composition: mean relative abundance of prey and diversity index (H') for fishes caught in the equatorial zone (EZ) and the north equatorial zone (NEZ) at different time of the day. In early night, all stomachs were empty

	Zone	EZ	EZ	NEZ	NEZ	NEZ
	Time of day	Afternoon	Night	Morning	Afternoon	Early night
	Number of stomach with food	20	30	129	97	76
	Number of stomach without food	0	0	4	3	4
	Number of fishes examined	20	30	133	80	100
Small size copepods						
Clausocalanidae–Paracalanidae	*Paracalanus parvus, Paracalanus* sp.	1.58	0.49	1.66	1.58	0.37
	Clausocalanus furcatus, Clausocalanus spp.	4.47	1.53	12.49	13.88	1.92
	Calocalanus sp.		0.18	1.56	1.56	1.07
	Acrocalanus sp.		0.06	0.20	0.13	0.05
Oithonidae	*Oncaea* sp.	46.33	4.84	35.52	52.83	53.70
	Lubbockia sp.	1.06		0.20	1.32	0.02
Corycaeidae	*Onychocoryceus* sp.	23.73	4.72	34.33	16.19	36.30
	Corycella sp.	0.00	7.90	0.14		0.32
	Coryceus spp.	1.59	3.55	0.86	1.00	1.09
Oithonidae	*Oithona plumifera*	0.83		1.72	0.07	0.35
	Oithona sp.	0.00	0.06	0.53	0.33	0.18
Harpacticoïda	*Clymenestra* sp.	0.15		0.05		
	Microsetella sp.			0.02	0.01	
	Euterpina sp.				0.01	
Copepod nauplii				0.02	0.06	
Total small size copepods		79.8	23.3	89.3	88.0	95.4
Medium–large size copepods						
Calanidae	*Calanus minor*	0.08	1.90	0.05	0.15	0.05
	Calanus tenuicornis		0.24		0.07	
	Calanus spp. (juveniles)	0.15	3.61	0.20	0.17	0.02
	Undinula sp.	0.45	3.67	0.20	0.54	0.02
	Undinula darwini				0.03	0.00
	Calanus gracilis	0.23		0.02	0.08	0.00
Temoridae	*Temora* sp.	0.23	0.31	0.08	1.78	0.05
Acartiidae	*Acartia danae*	0.08		0.05	0.04	0.05
Lucicutiidae	*Lucicutia* sp.	0.91		0.53	0.54	
Centropagidae	*Centropages* sp.					0.02
Euchaetidae	*Euchaeta* sp.	0.08	7.65			
	Euchaeta marina			0.02		
	Paraeuchaeta sp.			0.00	0.01	
Candaciidae	*Candacia* sp.	0.23	26.76	0.06	0.26	0.04
Scolecithrichidae	*Scolecithrix* sp.	1.06	1.90	0.36	1.11	0.07
Metridiidae	*Pleuromamma* sp.				0.15	
Eucalanidae	*Rhincalanus* sp.	1.29	0.06	1.50	1.35	0.12
	Eucalanus sp.	0.08	0.24	0.42	0.08	
	Eucalanus elongatus	1.21	0.06	0.02	0.29	
Aetideidae	*Euatideus* sp.			0.02	0.06	
	Gaetanus sp.	0.15	0.12	0.06	0.11	0.04
	Aetideus armatus	0.38	0.06	0.05		0.02
Sapphirinidae	*Sapphirina* sp.	0.91	2.51	0.05	0.14	
	Copilia sp.	0.00	0.43		0.01	
Heterorhabdidae	*Heterorhabdus* sp.	0.08				
Aegisthidae	*Aegisthus micronatus*	0.38		0.02		0.07

Table 5 continued

	Zone	EZ	EZ	NEZ	NEZ	NEZ
	Time of day	Afternoon	Night	Morning	Afternoon	Early night
	Number of stomach with food	20	30	129	97	76
	Number of stomach without food	0	0	4	3	4
	Number of fishes examined	20	30	133	80	100
Phaennidae	*Phaenna* sp.				0.10	
Euaugaptilidae	*Euaugaptilus* sp.		0.12			0.02
	Undetermined copepods	4.85	16.23	2.78	1.22	1.07
Total medium–large size copepods		12.8	65.9	6.4	8.3	1.7
Total copepods		92.6	89.2	95.7	96.3	97.0
Other groups	Ostracoda	2.65	1.53	0.56	0.68	0.33
	Chetognatha	2.35	6.06	0.86	1.67	0.62
	Polycheta				0.03	
	Amphipoda	0.68	1.10	0.11	0.19	0.04
	Euphausiacea	0.53	0.31	0.14	0.22	0.11
	Appendicularia	0.83	1.41	0.71	0.61	0.30
	Pteropoda	0.15	0.31	0.20	0.07	0.16
	Doliolidea	0.08		0.03		
	Salpidae	0.15				0.04
	Cladocera	0.00	0.06	1.69	0.24	1.39
Total other groups		7.4	10.8	4.3	3.7	3.0
Diversity index (H')		2.8	3.7	2.15	1.8	1.8

Fig. 5 Mean day and night preponderance index and frequency of occurrence of *Vinciguerria nimbaria* prey in the two main hydrological areas (*EZ* and *NEZ*)
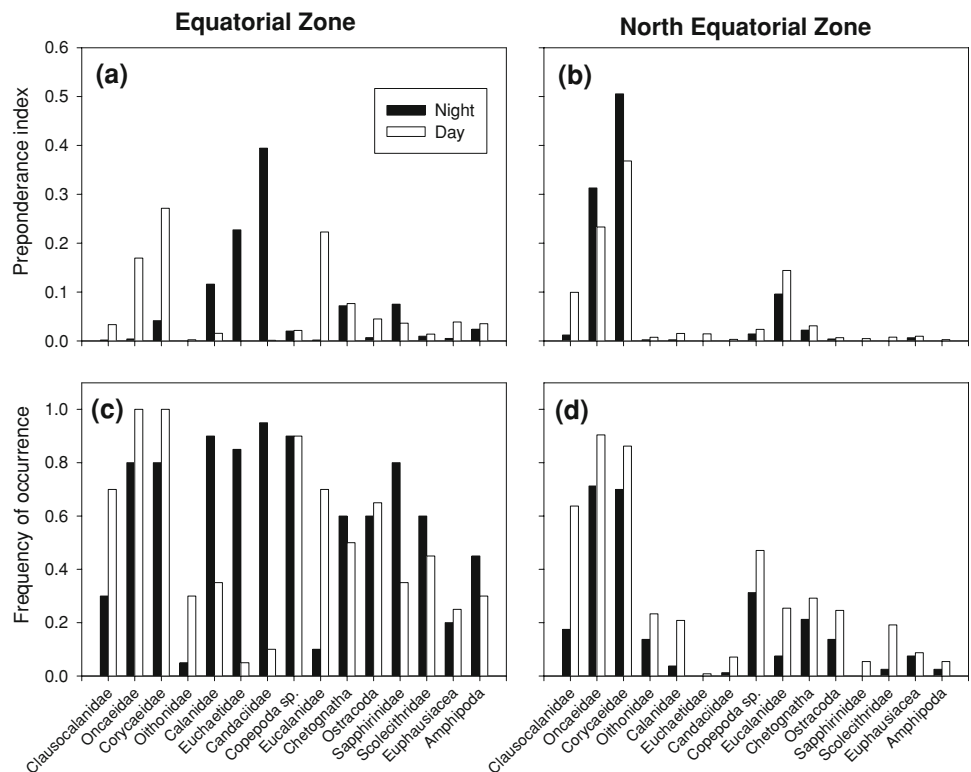
In the NEZ, both during the day and at night, Oncaeidae and Coryceidae (∼15% of the zooplankton) were the main prey of *V. nimbaria*. Clausocalanidae and Paracalanidae (17–37% of the total zooplankton in the area) and Oithonidae (often 10–20% of the total zooplankton) were not very abundant in the stomachs (Fig. 6). No Acartiidae

Fig. 6 Percentages of the main prey in the stomach contents (*SC*) of *Vinciguerria nimbaria* and in situ
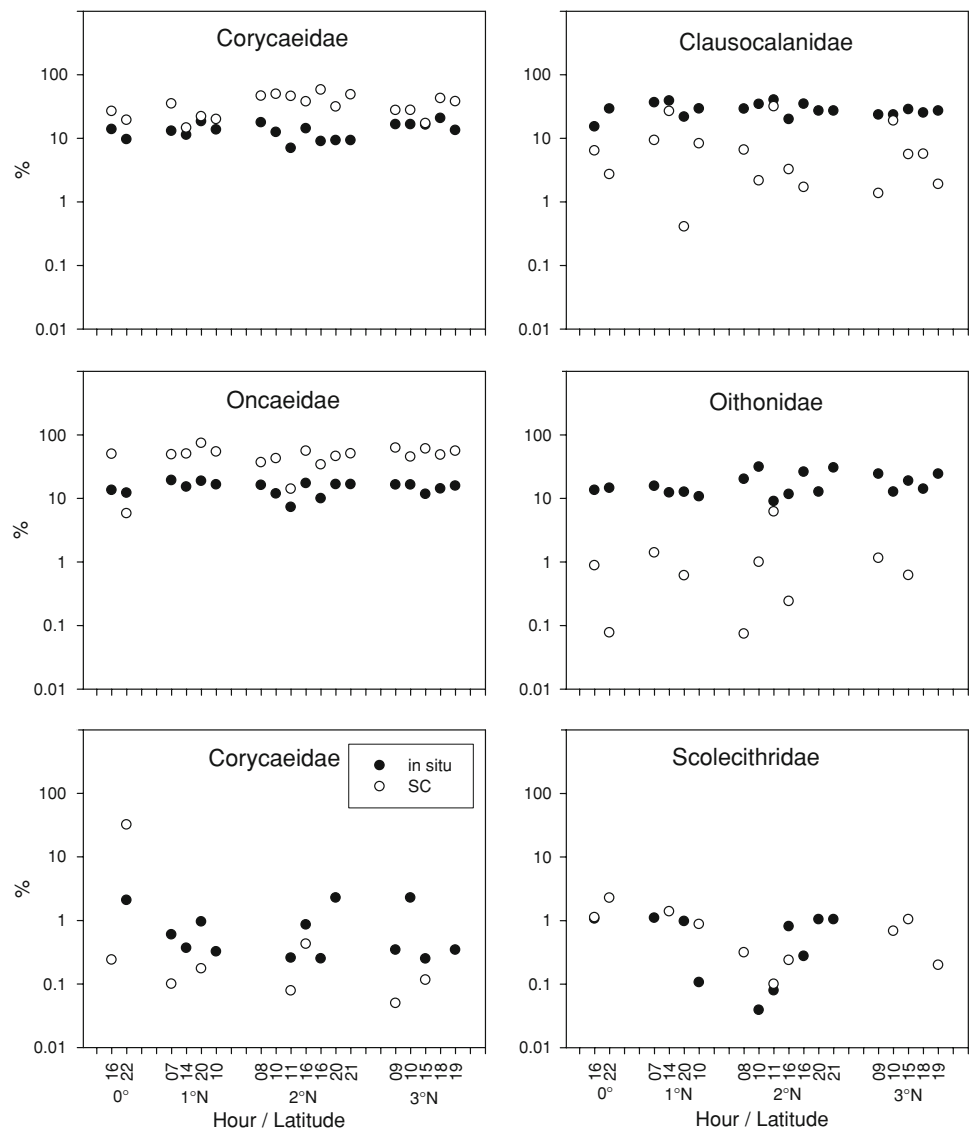
were found. A few larger or more colored organisms (Eucalanidae, Calanidae, Scolecithrichidae Lucicucidae and ostracoda), rather scarce in the area, were occasional prey.

Discussion

Vinciguerria nimbaria environment

This study showed two main hydrobiological zones in the tuna fishing area. The equatorial zone (EZ) located in the South equatorial current was characterized by weak upwelling with low surface temperatures, high surface salinity and fluorescence (Fig. 1). The EZ was clearly different from the NEZ with the highest zooplankton biomass and abundances in the upper 100 m (up to 50 mg m^{-3}, 4,450 ind. m^{-3}) suggesting a continuous enrichment

supporting high biological production (Herbland et al. 1983; Le Borgne et al. 1983; Champalbert and Pagano 2002; Menkes et al. 2002; Champalbert et al. 2005).

The NEZ located in the north equatorial counter current, characterized by a warm homogeneous surface layer, a strong thermocline and low surface chlorophyll concentrations (~ 0.25 µg l^{-1}), corresponded to a typical tropical structure (Herbland et al. 1983; Lebourges-Dhaussy et al. 2000). The area located at 4°N was the most oligotrophic, as already noted during other seasons and cruises in the tuna fishing zone (Menkes et al. 2002; Champalbert and Pagano 2002; Champalbert et al. 2005). In the upper 100 m of the NEZ, abundances (between 380 and 2,570 ind. m^{-3}) and biomass (between 7 mg m^{-3} and 28 mg DW m^{-3}) were within the range of those found in the tropical Atlantic (Greze et al. 1969; Binet 1993; Postel et al. 1995; Lebedeva et al. 1997; Champalbert et al. 2005). The small

differences observed may be due to the differences in the sampling methods (Piontkovski and Williams 1995), temporal variability as observed in the Atlantic upwelling (Voituriez et al. 1982; Le Borgne et al. 1983) or areas of enhanced water dynamic activity (Piontkovski et al. 2003). Mean mesozooplankton biomass (m^{-3}) in the upper 0–100 m was about twice that of the 0–200 m layer showing a "superficial" vertical distribution already described in the Atlantic (Finenko et al. 2003; Champalbert et al. 2005). As suggested by Longhurst and Harrison (1989) this distribution is probably related to the increased surface productivity of oligotrophic areas (Le Borgne and Rodier 1997).

Zooplankton communities were fairly homogeneous and relatively diverse (indexes between 2.5 and 3.8) but with greater diversity in the more permanently productive EZ area than in the NEZ area. As in the Gulf of Guinea (Le Borgne and Roger 1983; Le Borgne et al. 1983) and the south equatorial current (Piontkovski and Landry 2003), copepods formed the bulk of the zooplankton communities (>83% of total individuals in the upper 100 and 200 m). At all latitudes, small copepods were dominant, representing between 2/3 and 3/4 of total zooplankton, with Clausocalanidae and Paracalanidae counting for approximately a third. The percentages of the medium and large organisms were higher in the EZ than in the NEZ as observed during the summer when there was a higher proportion of large organisms near the equator and in enriched zones than in the stratified waters (Champalbert et al. 2005).

This study showed typical diel vertical migration for zooplankton (Roe 1974; Forward 1988; Hays 2003) that was more pronounced in the EZ than in the NEZ and in organisms >1,000 μm than in <1,000 μm, confirming the relationship between diel vertical migration and hydrological structures in the divergence and enriched areas during instability wave period (Champalbert et al. 2005).

Vinciguerria nimbaria regime

Studies on the trophic position, competition and migratory behaviour of mesopelagic fishes with attempts to investigate the diel periodicity in feeding suggest a relation between feeding purposes and migrations or mechanisms of predator avoidance (Baird et al. 1975; Hopkins and Baird 1977; Clarke 1978; Hopkins and Sutton 1998). Furthermore, studies by Hopkins and Baird (1975) and Clarke (1978) showed a minimal feeding in the net for most mesopelagic fishes. In the present study, feeding in the cod end or in the net which could bias the analyses seems improbable as *V. nimbaria* mainly feeds on small-sized copepods, unlikely retained by the mesh size of the net.

Literature on *V. nimbaria* indicates that this species is zooplanktophagous (Clarke 1974; Ozawa et al. 1977;

Shevchenko 1986, 1996; Menon et al. 1996; N'Goran and Pagano 1999). This study showed that, during the tuna fishing season, *V. nimbaria* mainly fed on copepods which constituted 87 to >97% of its food in number and 78.5% in weight. These values are close to those found by Shevchenko (1986) in the tropical Atlantic where copepods represented 91.8% of the *Vinciguerria* food by numbers and 78.2% by weight and to those of Kalinina and Shevchenko (1984) in the Indian Ocean where copepods represented 84% in number and 71% in weight of the *Vinciguerria* food.

This study showed that the main prey of *V. nimbaria* were Oncaeidae (up to 100% of total prey in some stomachs) and Corycaeidae (>70% of total prey in some stomachs), i.e., small copepods. Other taxa such as Calanidae, Candaciidae, Euchaetidae, Scolecithrichidae, small euphausids, amphipods and ostracods accounting for less than 4% of total zooplankton in situ, were occasionally preyed upon. In other intertropical zones, *V. nimbaria* fed on the same copepod species (Ozawa et al. 1977; Clarke 1978; Kalinina and Shevchenko 1984; Menon et al. 1996) but the numbers and the percentages of the prey differed from area to areas, probably owing to the hydrobiological characteristics and to the *Vinciguerria* migrating behaviour.

Vinciguerria nimbaria feeding variations

This study revealed considerable variation in *V. nimbaria* feeding in the two main hydrological zones. The major differences concern the intensity of feeding, the prey composition and the feeding behaviour. They are related to (1) the hydrobiological conditions, (2) the prey behaviour, (3) the *Vinciguerria* migratory behaviour and (4) the interaction between factors.

Feeding variations in relation to hydrobiological conditions

This study demonstrated that *V. nimbaria* feeding intensity was different in the EZ and the NEZ. Differences in PN and composition found in the hydrobiological zones caused variations in SCWs and FIs. In particular, the SCWs of fish sampled in the equatorial zone, which is a permanently enriched area (Herbland et al. 1983; Le Borgne et al. 1983; Champalbert et al. 2005), was higher than the SCWs of fish sampled in the NEZ, suggesting a relationship between high trophic activity and high productive area. These results agree with observations by Shevchenko (1986) showing that *V. nimbaria* trophic activity was higher in upwelling and frontal zones than in oligotrophic zones. Supporting the relationship between the richness of the area and the feeding intensity, this study showed that, for all latitudes studied, the trophic parameters were higher in

fish collected above the thermocline where mesozooplankton biomass was high than in fish collected deeper where biomass was lower.

Prey composition and behaviour

There were higher PN and diversity in the stomachs of fish caught in the EZ than in the NEZ. The frequency of occurrence of the small prey found in the stomachs (Oncaeidae, Corycaeidae in particular and to a lesser extent Clausocalanidae and Paracalanidae) was high in the whole area studied but the frequency of occurrence and the preponderance index of medium and larger prey (Calanidae, Scolecithrichidae, Candaciidae, Euchaetidae, Chaetognatha) was much higher in the EZ than in the NEZ.

In the NEZ in particular, Corycaeidae and Oncaeidae were by far the major food items found in the *V. nimbaria* guts, but in the field these copepods were less abundant than Clausocalanidae and Paracalanidae or Oithonidae which were rarely eaten, suggesting that *V. nimbaria* was a selective feeder. Interestingly, anchovy behave similarly and did not feed selectively on Clausocalanidae, Paracalanidae and Oithonidae (Plounevez and Champalbert 1999). These results suggest a relation to prey color and behavior for these two visual predators. Indeed, food selection by a visual predator depends on the size, abundance, edibility and the ease with which the prey is caught (James 1987; James and Findlay 1989; Batty et al. 1990; Gibson and Ezzi 1990). It also depends on color. Translucent prey is less readily eaten than dark prey (Hobaek and Wolf 1991) and Clausocalanidae and Paracalanidae are light in color. Inversely, Oncaeidae are densely pigmented copepods (Clarke 1980). In the area studied, *Oithona plumifera* was the most frequent of Oithonidae species. Its large feathery antenna and jerky swimming probably make it an uneasy prey.

Diel variations of Vinciguerria nimbaria feeding

Diel patterns of mesopelagic fish feeding have shown a great variability in responses (Paxton 1967). For most mesopelagic fishes, the diel vertical migration is associated with a surface feeding as supported by the intact epipelagic prey items observed in samples taken at night (Dalpadado and Gjøsæter 1988; Hopkins and Baird 1985). Studies on feeding chronology of *V. nimbaria* (Ozawa et al. 1977; Menon et al. 1996) are rather conflicting. However, most observations have shown a daytime pattern of activity which peaks in the morning and the afternoon with occasional increased activity in early morning and in late afternoon or early night (Clarke 1978; Shevchenko 1986, 1996; Legand et al. 1972; Ozawa et al. 1977) and a reduced activity late at night (Menon et al. 1996).

In the tuna fishing zone, this study showed a clear diel activity rhythm in *V. nimbaria* feeding, similar to that observed by Clarke (1978). All prey found in stomachs of *V.nimbaria* sampled in the morning and the afternoon were in a good condition, indicating diurnal feeding usually with a main peak in early afternoon. Several factors suggested that feeding activity ceased after night fall and started again after dawn: the decreasing values of the FIs and PN found in the stomachs in the early part of the night; the higher numbers of unidentified more or less digested prey in fish caught in early night than in fish caught during the day; the absence of prey in the stomachs late at night and finally, the slowly increasing values of the indexes from early to late morning.

As well as diel variations in feeding intensity, the observations showed diel variations in diet composition and prey selection. During the day, over the whole area, *V. nimbaria* fed on two of the most abundant small copepods that were more colored and had short antenna (Oncaeidae, Corycaeidae). Although Clausocalanidae and Paracalanidae were not the main prey, some were ingested during the day but very few at night, demonstrating the importance of the prey color in the visual predation by *V. nimbaria*. In the tuna fishing area, the more marked day–night variation of zooplankton abundance and composition and the higher diversity in the EZ than in the NEZ could partly explain the marked differences in *V. nimbaria* prey composition between the two zones.

Coupling between Vinciguerria nimbaria diel feeding variations and diel vertical migrations

In the divergence zone, during the study period (winter), most of the *V. nimbaria* biomass was at a depth of between 20 and 200 m at night and 300 and 500 m during the day, (Lebourges-Dhaussy et al. 2000). Contrarily, in the stratified area, the bulk of the *V. nimbaria* population remained in the upper 80 m night and day. There were little *V. nimbaria* in the mid layer (200–300 m). Some differences in diet composition observed between *V. nimbaria* collected in the EZ and in the NEZ may be related to the diel vertical migrations (DVM) of zooplankton and *V. nimbaria* observed in the EZ. Because some prey was partly digested in the fish sampled at 22:00 at the surface in the EZ, it may be assumed that feeding started while *Vinciguerria* and zooplankton prey were ascending. This would partly explain the presence of larger, darker, less easily digested migratory prey (such as Candaciidae and Scolecithrichidae) (Ozawa et al. 1977) in the stomachs of *V. nimbaria* collected in the EZ than in fish collected in the NEZ. The *V. nimbaria* behavior observed in the EZ can be compared with the *V. nimbaria* behavior observed by Kawamura and Hamoaka (1981) in the south western north Pacific and by

Menon et al. ([1996](#)) in the Indian Ocean. Indeed, in the south western north Pacific *Vinciguerria* performed vertical migrations and fed mainly on the same relatively large copepods (Calanidae, Candaciidae and Euchaetidae). Similarly, in the Indian Ocean, *Vinciguerria* feeds selectively on copepods forming a small fraction of the DSL plankton while it ascends the water column along with the vertically migrating zooplankton during the evening.

Conclusions

This study supports the hypothesis that zooplankton plays a major role in the feeding ecology and the trophic web of tuna within which *V. nimbaria* plays a key role. The vertical distribution of zooplankton and *V. nimbaria* and the feeding behaviour of *V. nimbaria* differed in the two areas. In the NEZ, zooplankton food was relatively abundant above or near the thermocline and most prey was small. Most *Vinciguerria* behaved as epipelagic fish and remained near the surface day and night, feeding on the dominant small prey whose color and behaviour favour an easy catch. Consequently, *Vinciguerria* became more vulnerable to predation by tunas. Forming dense school by *V. nimbaria* might contribute to reduce visual predation by tuna in the epipelagic layer during the daytime. It is quite difficult to assess the balance between benefit (more food) and loss (tuna predation), but the continuous presence and the abundance of *V. nimbaria* in this area (Roger and Marchal [1994](#)) proves the advantage of this behaviour for the species. In the EZ zooplankton was abundant and *V. nimbaria* behaved as a mesopelagic fish. In deeper layers or during its vertical migration towards the warm epipelagic zone in late afternoon/early night, it can find zooplankton patches and a wider size range of prey than fishes remaining at the surface. Indeed, stomach contents showed that *V. nimbaria* feeds not only on the abundant small prey but also captures the large, dark organisms which may be a useful source of food. This study also evidenced that in the tuna fishing zone *V. nimbaria* displays a clear diel feeding rhythm independent on migration. Finally, it is interesting to note that whatever the season, small or large amplitude vertical migration of adult *V. nimbaria* towards the very surface seems clearly related to spawning (Stequert et al. [2003](#)). Typical females which dive at dawn and stay in deep layers during the day, ascend to the surface at dusk where they spawn at the surface (thus with full stomachs). Atypical females which form schools in the upper layer during the day and stay around the thermocline during night, move rapidly to the very surface at dawn where they spawn (thus with empty stomachs).

Thus, in addition to a similar study at a different season, which is in progress, it would be interesting to carry out simultaneous studies on reproduction and feeding and to estimate the daily ration and predation impact of *V. nimbaria* to plankton production at the two main hydrological seasons. It would also be interesting to observe whether competition between species influences prey selection.

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