Vinciguerria nimbaria (micronekton), environment and tuna: their relationships in the Eastern Tropical Atlantic

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Abstract – Micronekton is a major component of oceanic tuna diet. Within micronekton species, *Vinciguerria nimbaria*, was found to constitute the main forage fish for tuna in the [10–20° W, 0–5° N] area where a large seasonal tuna fishery occurs. The relationships linking the *Vinciguerria* abundance, its spatial distribution and behaviour to its dynamical or biological environment, were investigated as part of the Picolo program, devoted to the study of the mechanisms leading to the high seasonal tuna concentration in that area. During the Picolo 1 cruise, in January–February 1997, the 1° S–4° N transect was sailed nine times back and forth along 15° W. Micronekton and *Vinciguerria* were acoustically surveyed, hydrological conditions sampled, phytoplankton and zooplankton biomasses measured. South of 0° 30' N, a marked divergence (upwelling) was found, with high abundance of zooplankton and micronekton. From there to 4° N a stable situation occurred with a well mixed surface layer, a strong Deep Chlorophyll Maximum (DCM) but less zooplankton and micronekton. While most micronekton performed large diel vertical migrations, schools of *Vinciguerria* remained at the surface by day in the stable zone, therefore becoming vulnerable to tuna in contrast to the upwelling area. It is concluded that *Vinciguerria* fits its behaviour according to zooplankton abundance, having to spend more time in the surface layer for feeding in poor areas. More precisely, they remain during the day near the strong DCM where they find aggregated zooplankton, and they become available for tuna. This could explain why a rather poor area may hold and sustain a high biomass of tuna. © 2000 Ifremer/CNRS/IRD/Éditions scientifiques et médicales Elsevier SAS

micronekton / tuna / food / Atlantic ocean / acoustics

Résumé – Relations entre le *Vinciguerria nimbaria* (micronecton), son environnement et les thons, dans l'est de l'Atlantique tropical. Le micronecton est un constituant majeur de l'alimentation des thons et d'autres grands poissons pélagiques océaniques. Dans un secteur de l'Atlantique équatorial [10° W – 20° W, 0° – 5° N] où la pêche saisonnière est importante, c'est un poisson mésopélagique, *Vinciguerria nimbaria*, qui joue le rôle clé dans leur alimentation. Son abondance, sa distribution spatiale et son comportement, en relation avec son environnement physique et biologique, expliquent la concentration des thons : c'est l'objet d'étude du programme Picolo (Production Induite en zone de Convergence par les Ondes LOngues équatoriales). Au cours d'une campagne réalisée en janvier–février 1997, la radiale méridienne 15° W a été parcourue neuf fois entre 1° S et 4° N. Des observations acoustiques en continu ont permis d'étudier la répartition et l'abondance du micronecton et des

bancs de *Vinciguerria*. Les conditions physiques ainsi que le zooplancton et le phytoplancton ont été observés en stations. Les détections ont été identifiées par une série de traits de chalut pélagique. La situation hydrologique se caractérisait par une divergence équatoriale relativement marquée au sud de 0° 30' N et par une situation stable avec un maximum profond de chlorophylle entre 1° N et 4° N. Le micronecton montre une alternance classique entre la couche 350–500 m (limite de l'observation) de jour et la couche de surface de nuit. Cependant les *Vinciguerria* ne suivent ce schéma de migration nycthémérale que dans la zone de divergence. En situation stable, ils demeurent de jour dans les couches supérieures où ils forment des bancs. La répartition méridienne présente un maximum très net de zooplancton et de micronecton dans la zone de divergence. Dans la zone de stabilité, la situation hydrologique a évolué au cours de la campagne, avec une remontée de la thermocline et un renforcement du gradient thermique, particulièrement entre 1° N et 2° N. Le maximum profond de chlorophylle a également augmenté ainsi que la concentration des bancs de *Vinciguerria*. On émet l'hypothèse que la différence de comportement nycthéméral des *Vinciguerria* est de nature trophique : dans les zones riches en zooplancton, ils peuvent se nourrir rapidement en surface et plonger de jour alors que dans les zones relativement pauvres ils passent plus de temps à chercher leur nourriture et restent toute la journée près de la surface. Les bancs se concentrent là où le zooplancton est abondant, notamment en présence d'un fort maximum profond de chlorophylle, ce qui pourrait expliquer qu'une zone plutôt pauvre retienne et alimente une forte biomasse de thons. © 2000 Ifremer/CNRS/IRD/Éditions scientifiques et médicales Elsevier SAS

micronecton / thon / nourriture / acoustique / océan Atlantique

1. INTRODUCTION

The micronekton biomass plays a major role in the diet of oceanic tuna [2, 5]. Its spatial distribution and abundance are largely influenced by the thermal structure and the oceanic currents [12]. However, the availability of the micronekton for tuna feeding is controversial, since a large part of the organisms of the micronekton perform large diel vertical migrations. It is usually considered that most of them remain in the surface layers at night-time, while they are mostly found below 300 m or more during daytime. Consequently, they escape large predators like surface tuna which feed essentially upon organisms in the surface layer during the day. However in a restricted area of the equatorial Atlantic Ocean [10–20° W, 0–5° N], where a large seasonal tuna fishery has been developed [15] (*figure 1*), a mesopelagic fish of the micronekton, *Vinciguerria nimbaria*, has been observed in the surface layer during day time, forming schools on which tuna are feeding [13, 24]. Therefore, the concentration of tuna is probably related to the presence of *Vinciguerria*, itself depending on zooplankton and phytoplankton abundance and concentration, as well as its physical environment (e.g. currents, temperature). The program Picolo (*Production Induite en zone de Convergence par les Ondes LOngues équatoriales*) is mainly devoted to the study of these relationships [16].

Two fishing periods can be distinguished: from October to February, the fishery is concentrated in that area and catches skipjack (*Katsuwonus pelamis*) and juveniles of yellowfin (*Thunnus albacares*) and bigeye (*Thunnus obesus*); from March to May, the fishery extends its fishing ground and the catch mainly consists of large tuna. This area and the tropical Atlantic in general is characterized dynamically by two marked situations and a minor transitional one [11, 17]. The boreal summer (May to September) is characterized by a strong equatorial divergence, well developed current systems and the occurrence of tropical instability waves north of the equator [18]. The boreal winter, from about January to March, shows well stratified structures, a rather deep thermocline and a weak upwelling intensity [11]. Between them, the boreal fall presents a less but still active divergence [17].

The Picolo 1 (P1) cruise, the first of a series of five, took place in January–February 1997 with the R.V. *Antea*, i.e. at the end of the first fishing period and at the beginning of the second main hydrological season (in fact, the season was probably late since an active divergence was still observed during the cruise). The

north–south transect along the meridian 15° W was repeated nine times in order to study the temporal variability. Observations included acoustics for micronekton abundance and spatial distribution, and trawl sampling. Zooplankton, in-situ chlorophyll and primary production, nutrients, salinity, temperature, currents and fluorescence were sampled concurrently. In this paper, we analyse the physical and biological environment of the Picolo area to identify the mechanisms that aggregate in surface a high biomass of *Vinciguerria* exploited by tuna.

2. MATERIAL AND METHODS

2.1. Acoustics

The R.V. *Antea* is equipped with a dual frequency (120 and 38 kHz) hull fixed transducers echo-sounder

(Ossian trade mark). Continuous records were made all along the cruise. In addition, a dual beam dual frequency (120 and 38 kHz) towed transducers echo-sounder (Biosonics, trade mark) was used occasionally for Target Strength (TS) determination. The onboard RDI 150 kHz Acoustic Doppler Current Profiler (ADCP) was used to estimate in-situ currents down to about 300 m with a resolution of 8 m [3].

Acoustic signal from Ossian Echo-sounder was first digitized and sub-sampled every 10 cm. Computed backscattering volume was averaged by integration cells, the vertical surface being divided into 10 depth stratum from 20 m to 500 m by one nautical mile. However, the raw data were saved and could be reproduced in any other configuration. Only 38 kHz data are presented here because high propagation loss at 120 kHz precludes the use of this frequency beyond a range of about 200 m. Data are referred to acoustic values rather than biomass conversions, except for *Vinciguerria*.
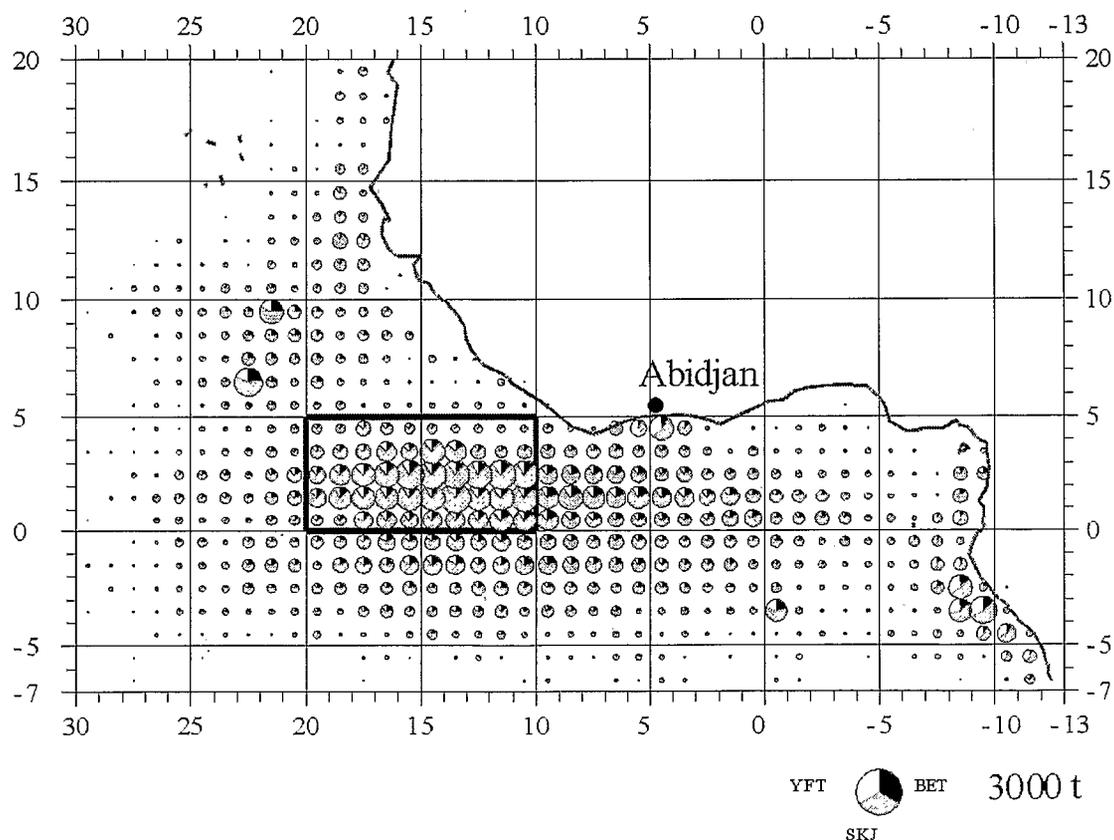
Figure 1. Averaged 1991–1996 purse-seine tuna catch by degree and species (YFT: Yellowfin, SKJ: Skipjack, BET: Bigeye). Catch under logs (almost all artificial). 'Picolo' area highlighted.

We use:

The *Mean Volume Backscattering Strength* (MVBS), more simply written S_v: it is the scattering strength, measured in the backward direction, produced by 1 m³ of water. This density is obtained from averaging the target strengths of the organisms present in the integration cells. S_v is expressed in dB, the linear measure s_v ($s_v = 10^{Sv/10}$) being called mean volume backscattering coefficient (in $m^2 \cdot m^{-3}$, or m^{-1}).

The *Area backscattering strength* $S_a = S_v + 10 \log(h)$: it corresponds to the integration of MVBS over a height h of water below 1 m². The linear expression or area backscattering coefficient is written $s_a = s_v * (h)$ (no units). We can define it as a perfectly reflecting surface producing the same backscattering energy as the water column below a surface unit. In the case of *Vinciguerria*, s_a was transformed in biomass ($g \cdot m^{-2}$) using average target strength and average weight of the fish. TS were obtained from dual-beam data on scattered fish in the near surface layer. A computed average TS of −56.7 dB corresponding to a 43 mm standard length (SL) fish weighing 0.60 g was used for the whole cruise. Details are reported elsewhere (Lebourges and Marchal, in preparation).

At 38 kHz, the main contribution to the echo is given by fish, since the other components of the micronekton like Euphausiids present a very weak response: for the same size, the TS of an euphausiid is about 30 dB less than a fish with a swimbladder like *Vinciguerria* [4]. In other words, 1000 euphausiids are necessary to give the same echo strength as a single fish. MVBS may be taken as an index representative of the heterogeneous biomass, assuming a constant composition of the micronekton [12]. In a comprehensive study of the micronekton between 3° N and 10° S in a contiguous area, Roger [23] found very stable proportions between fish, Crustacea, and other organisms. However two points have to be considered when calculating relative or absolute biomass at different depths:

− The threshold effect [1] can result in an underestimated biomass due to the loss of the signal with depth, the weakness of the target strength, or the "shadow effect" generated by very dense aggregations of organisms. As it is difficult to determine precisely the level of the bias, we did not apply corrective methods since we were more interested in the relative variations of the biomass than in its absolute value.

− The second point is related to the behaviour of the detected organisms which perform large vertical diel migrations. In theory, such vertical migrations are expected to produce large variations in the volume of the swimbladder of fish, and consequently in the TS which is strongly dependent on it. However, we did not observe any clear difference in the TS distribution according to the depth, probably because mesopelagic fishes, and particularly *Vinciguerria* [14], rapidly equilibrate their swimbladder. Similar conclusions have been presented by Koslow et al. [8] in a study on the pelagic biomass community structure off SE Australia. Therefore, the TS value measured in the upper layers was considered, at least for *Vinciguerria*, as representative of the TS value for any depth.

2.2. Micronekton sampling

Micronekton was sampled with a young-fish mid-water trawl, about 10 m height and 15 m width at the mouth, with 10 mm² meshes in the cod-end. All the hauls were horizontal, but the depth could vary during the haul, in relation with the fish distribution. The trawl was towed at about three knots, for a 30 min standard time; however this length was adjusted for catching a school. A total of 23 hauls were made, exclusively on aggregations (schools or dense layers). There is no opening-closure device on this type of trawl, so contamination could arise when the net is being brought up at the end of the haul, sometimes crossing other layers; however the problem is not very serious, since the crossing time is short in comparison to the towing time, except when high-density upper layers occur. The size of the meshes in the cod-end did not allow us to catch very small-sized fish. On the other hand, large or fast-swimming fish may escape the net. However, since we were interested in tuna prey organisms, this trawl was well-suited for sampling the mid-size organisms of the micronekton which are the potential prey of tuna.

2.3. Physical and biological environment

During the cruise, a total of 122 hydrological and productivity stations (CTD casts) were done, evenly spaced every 20 nautical miles along the transects.

Conductivity (salinity), temperature, fluorescence vertical profiles down to 250 m were recorded with a CTD probe (CTD Seabird SBE 911) equipped with a Sea Tech fluorometer. Nitrate, nitrite, phosphate and in-situ chlorophyll were also sampled concurrently at 12 depth levels. Nitrate and nitrite were analysed on board as described by Oudot and Montel [20]. In-situ measurements of chlorophyll were also analyzed on board using fluorometric method [25].

2.4. Zooplankton sampling

Zooplankton was sampled at each hydrological station with a WP2 vertical haul net, meshes 200 μm, from 100 m to the surface on the transects 1, 2 and 9, from 200 m to the surface for transects 5 and 6. A surface 'hyponeuston-net' was used on the other transects, the data are not analysed here. Averaged zooplankton biomass (in dry weight per cubic metre) was then computed. Sub-samples were stored for further species analyses. Also a number of on board incubations were done to measure grazing, breathing and nitrogen excretion of the mesozooplankton (not in this paper).

3. RESULTS

3.1. Currents, hydrology, nutrients and chlorophyll

A summary of these variables along the transect is presented on *figure 2*. This is an average situation for all the north–south transects. Variability to this mean is discussed later.

Two surface currents from 4° N to 1° S are crossed: from 4° N to 1° N, the North Equatorial Counter Current (NECC) is weakly eastward (about 20 cm·s^{-1}) and the South Equatorial Current (SEC) flowing westward south of 1° N with an average speed of 30 cm·s^{-1}. These currents are known to be relatively weak at the season of the cruise [21, 22]. At the equator the Equatorial Under Current (EUC) flows eastwards under the SEC at an average speed of 50 cm·s^{-1} and creates an equatorial divergence at and above its core that can be seen in the spreading of the thermocline and the shallowing of the nitracline.

Although the maximum of the equatorial divergence occurs in summer, when the trade-winds are strong, the data show that the divergence was still active at the time of the cruise, leading to a surface nutrient enrichment in the equatorial zone. This is in agreement with previous CZCS-satellite observations [10] showing an extension of the divergence in autumn and even at the beginning of the year, especially in the 10–20° W area. Although the core of the EUC was localised at the equator, the divergence maximum was slightly south of the equator, as is often the case. In the divergence area, the vertical distribution of chlorophyll *a* shows maximum values near the surface without subsurface maxima, typical of rich areas. However, integrated chlorophyll biomass within the euphotic layer (*table I*) is not particularly higher than similar values calculated in the 1–2° N sector where divergence is absent.

North of 1° N, we found the so-called 'Typical Tropical Structure' or TTS, as described by Herbland et al. [7], characterized by a two layer system: a mixed and nutrient depleted surface layer on top of a deep rich layer separated by a marked thermocline. Primary production and chlorophyll biomass present a deep maximum, called Deep Chlorophyll Maximum (DCM) at the nitracline (thermocline) level. Following the depth of this thermocline, the DCM is more or less rich [6] in relation to the available light at the thermocline level. During P1, observations show a very strong DCM especially between 1° N and 2° N where there does not seem to be any particular structure in the nitracline compared to further north, on the mean section (*figure 2*). This mean section hides the variability observed during the cruise. The situation pictured in *figure 2* evolved during the cruise as the nitracline and pycnocline rose by about 20 m (*figure 3*) with a reinforcement of the thermal vertical gradient in the 1–2° N sector (*figure 4*). The increasing vertical gradient of the thermocline in this area is an indication of a strengthening vertical stratification, i.e. a reduced mixing.

Concurrently, the DCM increases dramatically in this area, by the conjunction of the general shallowing of the thermocline (more light is then available) and the reduced mixing leading to a more stable situation which is more favourable to the development of the phytoplankton cells than further north.
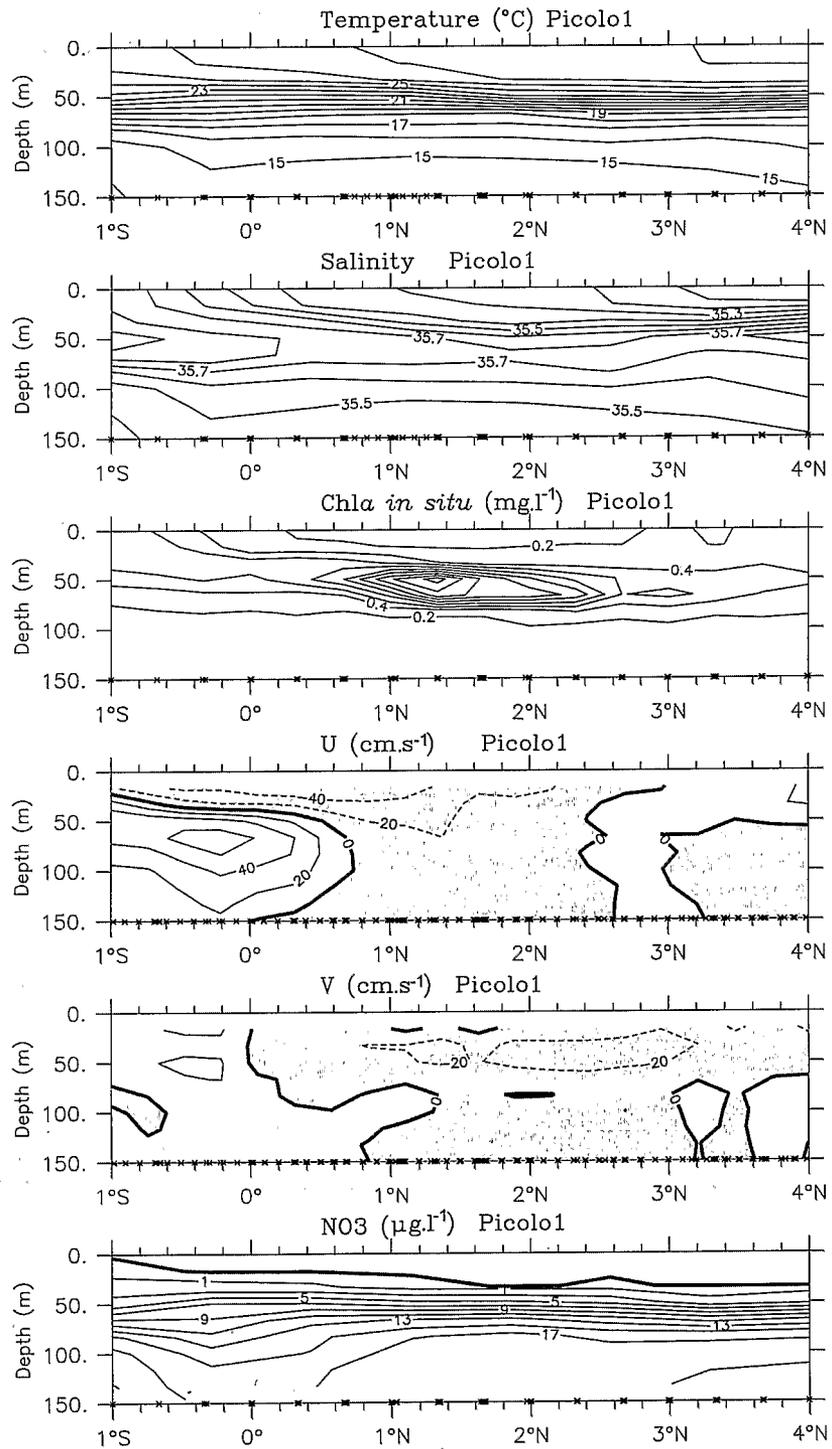
Figure 2. Mean depth profiles over all the transects for temperature, salinity, chlorophyll *a* in situ, zonal and meridional currents components and nitrates.
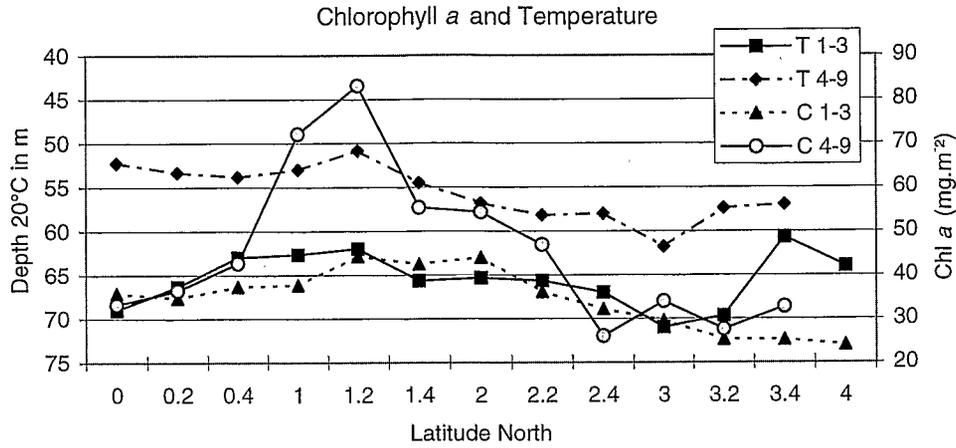
Chlorophyll *a* and Temperature

Figure 3. Integrated chlorophyll *a* and depth of the isotherm 20 °C by third of latitude degree averaged for the first three transects and for the last six. T: isotherm 20 °C; C: chlorophyll *a*.
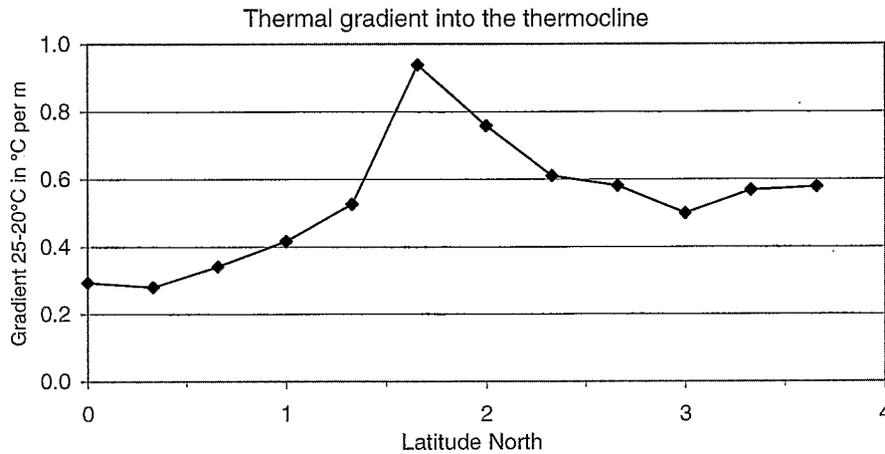
Thermal gradient into the thermocline

Figure 4. Thermal gradient into the thermocline (25 °C–20 °C) by third of latitude degree, averaged for the last six transects, in $°C·m^{-1}$.

This evolution during the cruise explains the high standard deviation associated with the chlorophyll mean biomass in this sector (*table I*).

3.2. Zooplankton

As mentioned before, zooplankton was sampled from 100 m to the surface for the two first transects (and the last one) and from 200 m to the surface for the transects 5 and 6 in the middle of the cruise. The overall ratio (0–100 m)/(0–200 m), was 2.9 for day-time volumic densities of biomass and 2.1 for night-time. A density ratio of 2 meant that the averaged

integrated biomass for the column was the same, assuming that all the zooplankton was concentrated in the first 100 m. It was probably the case during night, therefore the averaged night biomass for the two sets of transects was comparable. Now, considering the day-time ratio of nearly 3, it is likely that a larger part of the zooplankters dive deeper by day to the 5th and 6th transects than to the upper ones. This is also clear from the night/day ratio for the same set of transects: 1.22 for transects 1–2 and 1.74 for transects 5–6 whereas the depth is double in the late transects. Finally the assumption that the overall biomass was rather constant during the survey is reasonable. Then we averaged the data by degree of

Table I. Upper layer means and standard deviations by degree of latitude, of: Area backscattering coefficient 'sa' of the column 20–200 m, regarded as a micronekton biomass index. Zooplankton dry weight biomass of the column 0–100 m or 0–200 m (see text). Potential Tuna Forage (PTF) biomass, quite exclusively schools of Vinciguerria north of 0°30′ N, observed during day-time from 20 m to 200 m. Integrated chlorophyll a from surface to 100 m.

|	Night acoustic integration s_a*1e−05		Zooplankton biomass (g.m^{-2})		PTF biomass (g.m^{-2})		Integrated chl a (mg.m^{-2})	
	Mean	Standard deviation	Mean	Standard deviation	Mean	Standard deviation	Mean	Standard deviation
3°–4°N	2.62	1.90	1.27	0.55	1.34	1.56	28.91	6.15
2°–3°N	3.97	2.62	1.71	0.72	3.02	2.29	40.55	15.93
1°–2°N	4.30	2.74	1.72	0.76	4.18	4.77	59.31	21.48
0°–1°N	4.34	3.56	2.56	1.07	1.28	2.55	37.30	7.04
1°S–0°	7.36	1.39	3.97	0.40	1.48	1.46	41.36	2.87

latitude, as biomass integrated per square metre of the column, regardless of the sampling range and time. In this way, the averaged values are likely to be a little under-estimated, especially for daytime, but for the purpose of spatial comparison, the bias is small with regard to the increased sampling.

From south to north there was a clear maximum of zooplankton biomass south of the equator (*table I*) with nearly 4 g·m^{-2} dry weight and a low standard error (but only one transect was sampled there, the last one). North of the equator to 1° N, the averaged biomass was still high (2.5 g·m^{-2}) with a higher standard error. From 1° N to 3° N the averaged biomass was stable at 1.7 g·m^{-2} and fell to 1.3 g·m^{-2} in the northern sector. There was no clear

trend during the cruise. Concerning the variability, the coefficient of variation (standard error/mean) was nearly the same from the equator to 4° N, between 42 and 44 %.

3.3. Trawl catch composition

Vinciguerria nimbaria represented nearly 100 % of the catches made during the daytime on schools or layers within the 0–200 m layer (*figure 5*). It is worth noting that no *Vinciguerria* was caught in this depth stratum south of 0° 30' N, and very few north of 3° N. Night hauls performed in the upper layer along 15° W, provided a majority of *Vinciguerria* among fish (63 % on average). Other components of the night hauls

Trawls components over the whole cruise
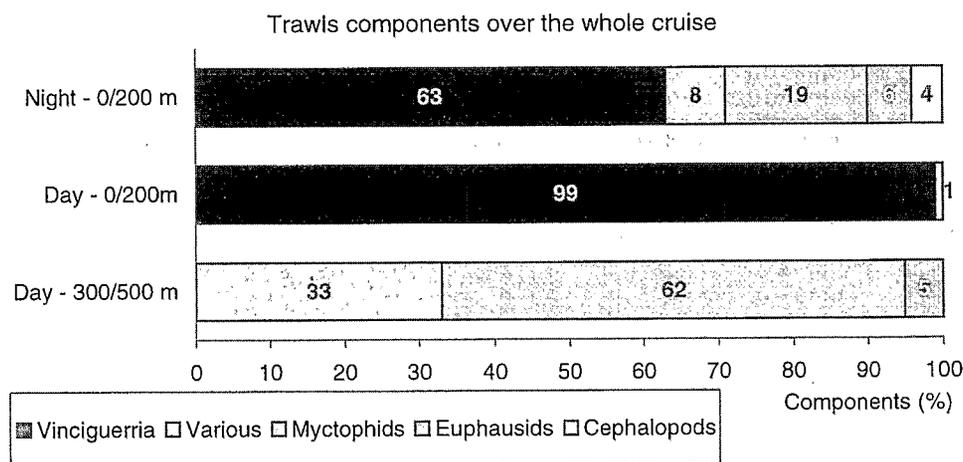
Figure 5. Averaged trawl composition by large groups and *Vinciguerria nimbaria*; hauls during day-time in the upper layer were made exclusively on schools.
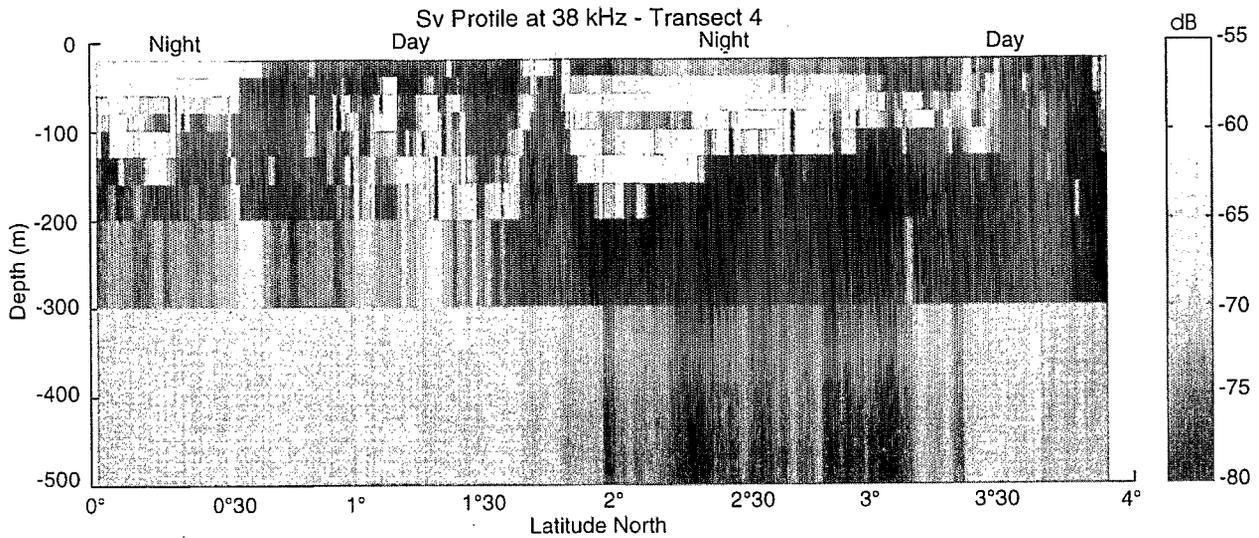
Figure 6. Transect 4, Mean volume backscattering strength (S$_v$) profiles along 15° W, from 0° to 4° N.
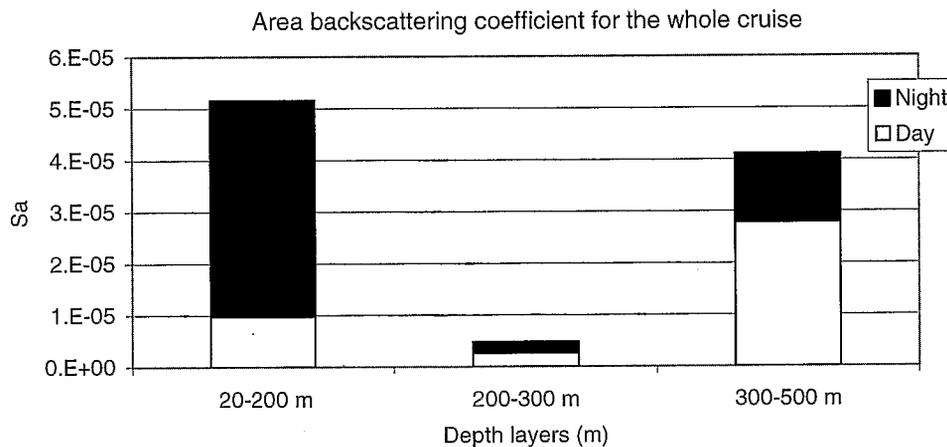

Figure 7. Night and day area backscattering coefficient s$_a$ by depth layer for the whole cruise (units as in *table II*).

were dominated by several species of Myctophids and other fish coming from deeper layers; euphausiids and other Crustacea varied from 1 to 17 % and cephalopods 0 to 6 %. Gelatinous organisms were sometimes very abundant. Three hauls were made during the daytime in the layer 350–450 m, in the convergence as well as in the divergence area: most of the catch was composed of Myctophids and other bathypelagic fish (*Argyropelecus* sp. was the most important among them); only a few *Vinciguerria* were caught. Sometimes, schools were detected at the top

of this depth layer, but we were not able to sample them at this depth. However hauls made later in the afternoon at intermediate depth and when these schools were ascending to the upper layers provided mainly *Vinciguerria*, supporting the idea that the deep schools were also *Vinciguerria*. Surprisingly, there was very few *Cyclothone* spp. in the catch, although it is known to be a major component of the deep pelagic fauna. This fish is probably too slim to be kept in by the mesh of the trawl since two Bongo hauls (meshes 300 and 1000 μm) made in this deep

layer during day-time provided significant amounts of *Cyclothone* spp.

3.4. Micronekton biomass index

3.4.1. Overall night–day MVBS variations

The data were recorded throughout the cruise, night and day. To compare the night–day situation, averaged s_v were computed separately. Using a standard two-sample t-test, the null hypothesis (means are the same) is rejected at the 0.0001 level. The s_v night mean is largely higher than the day one with an overall ratio close to 1.4. The analysis of the MVBS depth distribution along a transect (see for example transect number 4, *figure 6*) suggests that there is a transfer of the MVBS strength between depth strata from night to day. To identify this phenomenon, we merged the data into only three layers: 20–200 m, 200–300 m, 300–500 m. Over the whole cruise, most of the biomass is within the deepest stratum during daytime and rises up to the uppermost stratum during night-time (*figure 7*). Even if the height of the medium stratum is only half of the others, the data show that very little of the biomass inhabits it, whether it be night or day.

3.4.2. MVBS spatial variations

In order to study the diel variations of the distribution along the north–south transects, we also aver-

aged the area backscattering coefficient s_a by degree of latitude. Regardless of the distribution in the layers, the night/day ratio of the total s_a is always higher than unity at any latitude. It highlights the vertical ascension at night of organisms inhabiting deeper than 500 m during the day, the biomass of which can be deduced from the difference between night and day total values (*table II*). The lowest vertical transfer of biomass at night is found between 1° N and 2° N in the stable area. The total values (20–500 m) that can be considered as a measure of the total micronekton biomass, show an overall decrease from south to north. In particular, for the night-time values the ratio is more than 2 between the south and the north, and even more when considering the upper layer only. This variation is clearly associated with three distinct areas: south of 0° (more precisely south of 0° 30' N) the equatorial divergence with very high values; northerly to 2° N, the stable situation with high DCM and medium values; 2° N to 4° N, the stable situation again but without strong DCM, and with the lowest values.

The analysis by depth strata shows large variations in the percentages of integrated biomass according to the meridian distribution (*table II*). The most striking feature appears during the daytime: from 1° S to 1° N, more than 80 % of the total day biomass is concentrated into the 300–500 m layer, this percentage falls to about 60 % between 1° N and 3° N and rises again to 80 % between 3° N and 4° N. On the
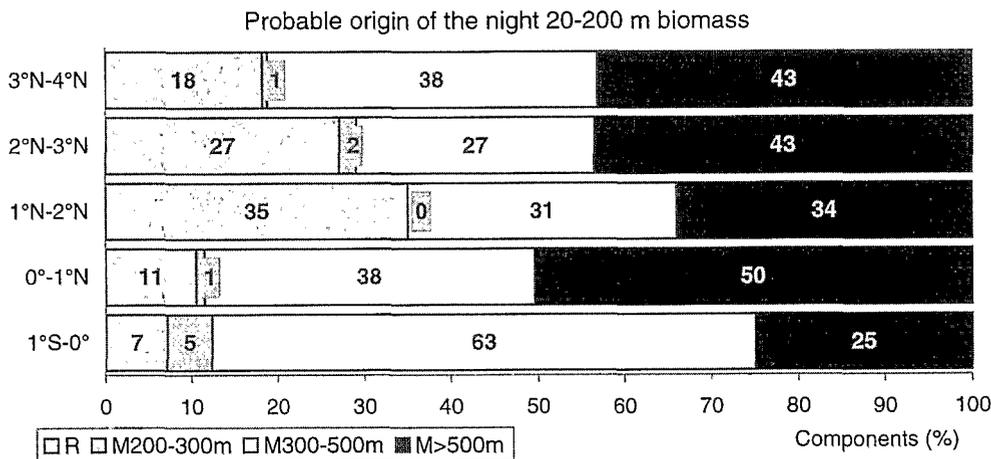

Figure 8. Probable origin of the night biomass in the 0–200 m layer by degree of latitude. Residents (R): day-biomass of the layer; Migrants (M): biomass coming up at night from different day-layers.

Table 2. Average area backscattering coefficient 'sa' of the column integrated by layer; the line 'Night–Day' means the difference between night and day. 'sa' is dimensionless, see text.

| Night s_a (*1e−05)	1°S–0°		0°–1°N		1°N–2°N		2°N–3°N		3°N–4°N	
	Val.	%	Val.	%	Val.	%	Val.	%	Val.	%
20–200 m	7.4	80	4.3	67	4.3	73	4.0	83	2.6	63
200–300 m	0.2	2	0.3	4	0.4	7	0.0	1	0.1	2
300–500 m	1.6	18	1.9	29	1.2	20	0.8	16	1.5	35
Total 20–500 m	9.2	100	6.5	100	5.9	100	4.8	100	4.2	100
Day s_a (*1e−05)	Val.	%	Val.	%	Val.	%	Val.	%	Val.	%
20–200 m	0.5	7	0.5	11	1.5	34	1.1	35	0.5	16
200–300 m	0.5	8	0.3	8	0.4	9	0.1	4	0.1	4
300–500 m	6.2	85	3.5	82	2.5	58	1.9	61	2.5	81
Total 20–500 m	7.3	100	4.3	100	4.4	100	3.1	100	3.0	100
NIGHT–DAY	1.8		2.2		1.5		1.7		1.1	

other hand, the 20–200 m layer biomass is much higher in the area 1° N to 3° N in comparison with the other latitudes. It is worth pointing out that this layer is inhabited by schools of *Vinciguerria*. During the night, most of the biomass is concentrated in the uppermost layer (20–200 m) whatever the meridional location is.

3.4.3. Upper layer

Special attention has been paid to the upper layer 20–200 m where almost all the primary production is found and the main part of the secondary production remains, particularly at night. In addition, tuna feed in this depth stratum. The micronekton biomass in this upper layer is made up of two categories (*figure 8*): the day-biomass, or 'residents' and the migrating biomass, or 'migrants'. For the latter we assume that the biomass from a given layer corresponds to the difference between day and night biomasses within this layer. Finally, since there is always a surplus in the night biomass, we compensate for it by the migrating night biomass from a layer deeper than 500 m.

The resident population of the upper layer represents a potential prey biomass for medium and large pelagic visual-hunters fish like surface tuna, and may be
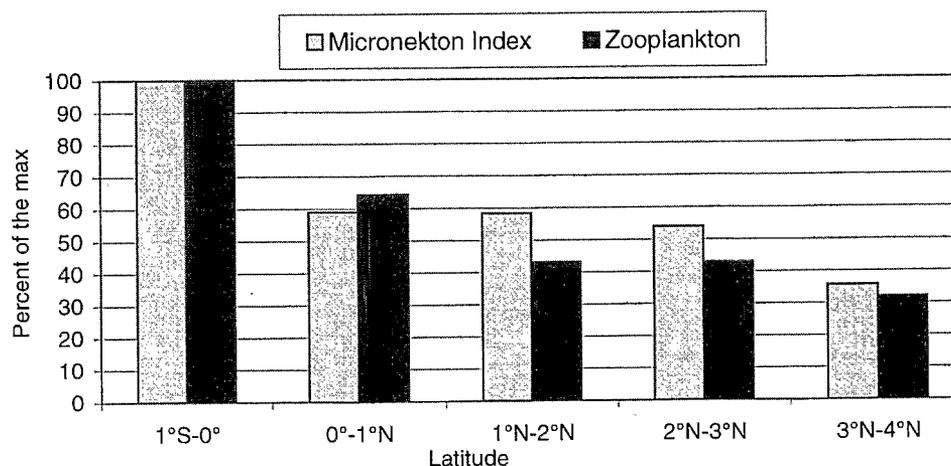
Figure 9. Averaged values by degree of latitude, as a percentage of the maximum, of night micronekton index of biomass, given by the integration of s_a upon 20–200 m and zooplankton dry biomass integrated on 0–100 m or 0–200 m (day and night).

characterized as 'Potential Tuna Forage, or PTF'. This is a major component of the total biomass from 1° N to 3° N (table II). Considering that most of this PTF is made of *Vinciguerria nimbaria* — as strongly suggested by trawl-sampling data (figure 5) — we computed its biomass using the TS of *Vinciguerria*, averaged by degree of latitude (table I). Obviously, it is not strictly correct to apply the TS of *Vinciguerria* to assess all the PTF biomass, especially in the southern sector where no schools were observed. But this species is by far the main species found in the hauls, other similar small fish have a similar TS, hence the assumption that the total biomass of small fish estimated by our acoustic survey are potential prey for tuna is realistic. In the southernmost area, the biomass was very low (figure 10). There is a remarkable maximum between 1° N and 2° N, associated with a high coefficient of variation (table I), partly due to a very contagious distribution of the schools but also to a temporal evolution, with a marked increase from the fourth track. Northerly the biomass decreases, with very low values between 3 and 4° N, comparable to those of the 1° S–1° N area.

The night upper-layer micronekton biomass is the part of micronekton which is directly concerned with the surface production. A strong maximum occurred in the southernmost sector (figure 9), then it was evenly distributed in the other sectors, except at the very northern one. Concerning its composition, migrants from 300–500 m were largely dominant in the southernmost sector (south of 0°). The deepest migrants coming from below 500 m, which represent a variable but substantial part of the night biomass in the upper layers, enter at a minimum level in the 1° S–0° (25 %) and at a maximum (50 %) in the contiguous 0–1° N area. Throughout the cruise, the biomass was stable south of 1° N, decreased in the 1° N to 3° N sector, and increased in the northernmost sector.

4. DISCUSSION

From the results, the overall averaged situation allows us to define two spatial zones, with regard to physical and biological environment, from south to north:
1- the divergence zone (or equatorial upwelling zone) within [1° S–1° N], marked by the presence of the EUC, the spreading of the thermocline and of the nitracline, and a surface maximum of chlorophyll. In 1997, the winter season was late with a relatively strong EUC, pronounced divergence and relatively rich surface waters in terms of primary production.
2- the stratified zone within [1° N–4° N], or TTS, with two layers separated by a strong thermocline/nutricline system. In that region, the upper layer is depleted in nutrients and the primary production, and especially the chlorophyll biomass is concentrated in a DCM at the nutricline (thermocline) level.
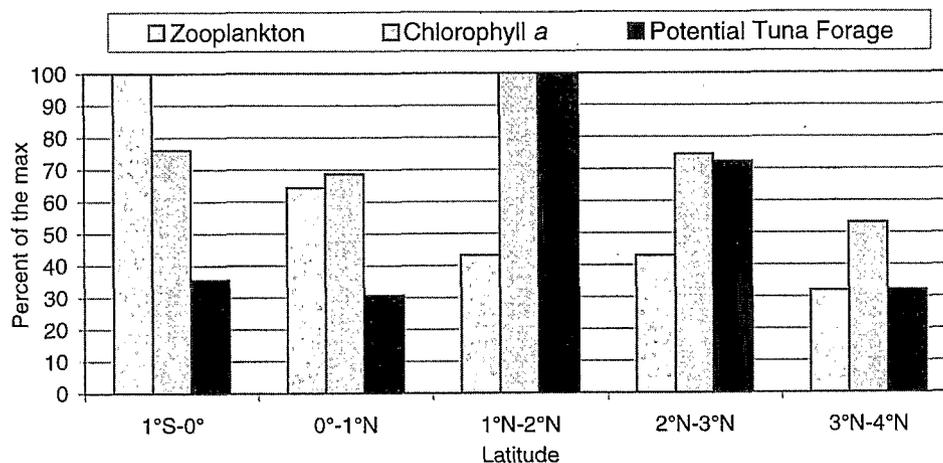

Figure 10. Averaged values by degree of latitude, as a percentage of the maximum, of zooplankton dry biomass as in figure 9, chlorophyll a integrated on 0–100 m (day and night), and PTF (potential tuna forage) biomass (*Vinciguerria* schools north of 0° 30' N) integrated on 20–200 m layer.

As far as the upper trophic levels are concerned, these two zones are also very different: zone 1 is rich in zooplankton and micronekton (*figure 9*) including *Vinciguerria* (60 % of the catch of the night-hauls). However, *Vinciguerria* is poor in day-schools. In that region, *Vinciguerria* behaves as the other components of the micronekton, diving to 300–500 m during the daytime.

It is likely that the high level of zooplankton and micronekton abundance is related to the stable up-welling. In contrast, zone 2 is relatively poor in zooplankton and in micronekton and this feature is accentuated northward. Here a remarkable and un-usual feature of the *Vinciguerria* is its high biomass in day-schools, particularly in the region [1° N–2° N] where the chlorophyll is high although vertically inte-grated zooplankton biomass is not particularly im-portant (*figure 10*).

It is a key issue here to understand the change in *Vinciguerria* behaviour from zone 1 to 2. The expla-nation may be found in its feeding activity.

First of all, this fish feeds essentially during daytime on copepods and occasionally on other zooplankton components [19, 24] found in the upper layers. In the 'rich' zone (zone 1), where the food is abundant, *Vinciguerria* probably finds the opportunity to fill its stomach quickly at night fall and dawn when it crosses the upper layers during its diel migration. In a rather poor zone (zone 2), it is obliged to spend more time for feeding, and in fact it changes its diel behaviour and stays in the upper layers all day (the question of schooling is not considered in this paper).

The correlation between the high day-school biomass of *Vinciguerria* and the presence of the marked DCM in the 1°–2° N region, without maximum of zooplankton integrated biomass, is puzzling. First, as *Vinciguerria* does not eat any phytoplankton, we must suspect an indirect correlation between them. The link may come from the fact that the presence of the marked DCM, which is related to the increasing of the stabilisation of the vertical density structure (*figure 4*), can lead to a zooplankton aggregation. As we only had access to vertically integrated zooplank-ton biomass during the cruise, we do not have proof of this. However, as stated by Leborgne [9] "the correlation between D.W. (Dry Weight of zooplank-

ton) and chl *a* is the result of the animal aggregating vertically on the algae".

We know that the concentration of the prey is a favourable factor for the predators. Therefore, the aggregation of the zooplankton could be the key factor in the unusual behaviour and the concentra-tion of the schools of *Vinciguerria* in the upper layers during the day.

Vinciguerria being concentrated during the day in this area, they become accessible to surface tuna (skip-jack, young tuna) which are seeking schools of prey and are thus likely to be looking for such thermal structures. Hence, we suggest that the seasonal tuna concentration in this zone, off the equator is certainly the result of an unusual availability and an increased vulnerability of the mesopelagic fish *Vinciguerria nim-baria*, in relation to the distribution of phyto- and zooplankton which is in turn related to the particular thermal structures found within [1–3° N].

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