On the relationship between scattering layer, thermal structure and tuna abundance in the Eastern Atlantic equatorial current system

Scattering layers
Equatorial dynamics
Tuna fisheries

Couches réfléchissantes
Dynamique équatoriale
Pêcheries de thon

Emile MARCHAL [a], François GERLOTTO [b], Bernard STEQUERT [c]

[a] Institut Français de Recherche pour le développement en coopération (ORSTOM), Institut Océanographique, 195 rue Saint Jacques, 75005 Paris, France.

[b] ORSTOM, B.P. 5045, 34032 Montpellier Cedex 1, France.

[c] ORSTOM, Centre de Brest, B.P. 70, 29280 Plouzané, France.

Received 19/11/92, in revised form 11/03/93, accepted 7/04/93.

ABSTRACT

A migrating Sound Scattering Layer (SSL) was observed in the Eastern Atlantic equatorial system during warm and cool seasons. Averaged column scattering strength was nearly the same during daytime at 350-400 m depth and during night-time close to the surface. The depth of the nocturnal SSL was correlated with the depth of the thermocline. In the warm stable season, the maximum column scattering strength was found south of the equator in a dome shaped structure. In the cool season, the maximum was found at the northern convergence where the thermocline was well-marked, whereas upwelled waters were acoustically poor. For the warm season, this pattern is consistent with the distribution of chlorophyll, zooplankton and micronekton. For the cool season, it fits also rather well, except for the net-sampled micronekton : this discrepancy could be related to the poor efficiency of the net in sampling adequately a thin layer. Finally, SSL strength coincides well with tuna catch distribution in this area, suggesting a trophic relationship.

Oceanologica Acta, 1993. **16**, 3, 261-272

RÉSUMÉ

Couche réfléchissante, structure thermique et abondance des thons dans le système de courants équatoriaux de l'Atlantique oriental

L'étude porte sur la variabilité d'une couche diffusante acoustique (SSL) observée au cours des saisons hydrologiques chaude et froide dans le système équatorial de l'Atlantique oriental. En moyenne, la réverbération de volume intégrée de la SSL ne présentait pas de différence entre le jour et la nuit : cependant la SSL, qui se trouve à 350-400 m de jour, remonte de nuit au niveau de la thermocline à quelques dizaines de mètres de la surface. En saison chaude stable, les valeurs les plus élevées de réverbération de volume ont été observées au sud de l'équateur dans une structure thermique en dôme. En saison froide, caractérisée par l'upwelling équatorial et une zone de convergence située quelques degrés plus au nord, c'est dans celle-ci que les plus fortes valeurs ont été rencontrées. On remarque qu'en saison chaude, ce maximum correspond à ceux de l'abondance de la chlorophylle, du zooplancton et du micronecton. Pendant la saison froide, le schéma de répartition est plus complexe : on observe bien un maximum de chlorophylle dans la zone de convergence, par contre le maximum de zooplancton et de micronecton se trouverait en plein upwelling. Cette divergence avec le maximum de «biomasse acoustique» pourrait simplement provenir d'une différence d'efficacité de l'échantillonnage au filet et au sondeur, particulièrement pour des couches relativement fines. Enfin, les statistiques de pêche au thon montrent globalement une bonne relation entre bons secteurs de pêche et forte intensité de la SSL, ce qui plaide en faveur de son rôle dans la chaine trophique des thons.

Oceanologica Acta, 1993. **16**, 3,261-272.

INTRODUCTION

The Eastern Atlantic equatorial current system is more productive than adjacent areas. This enrichment and its mechanisms have been studied intensively during many cruises, especially in three well-known programmes : *Equalant* (1963), *Gate* (1974), *Ciprea* (1977-1979). During some of them the presence and the strength of migrating scattering layers were recorded (Gerlotto, 1975; Gerlotto *et al.*, 1978).

In the mid-1970s, a new surface tuna fishery was established to exploit new areas along the equator. In order to locate pelagic fish concentrations, an acoustic survey was carried out in the area bordered in latitude by 3°N and 6°S and in longitude by 2° and 10°W in March-April 1976 by the R/V *Capricorne* (cruise CAP 7604), following a grid of 6 meridian, 90 nautical miles-spaced transects.

A second cruise (*Echopreg II*) was carried out in July-August 1977 with more methodological objectives to prepare for the *Ciprea* programme. It was restricted to a single transect along the 4°W meridian from 5°N to 4°30'S in two directions.

At this time, we did not have sufficient data on environmental conditions and tuna abundance. Later, a comprehensive description of the equatorial system, including primary and secondary production levels, was provided, and this is analysed below. In addition, tuna fishery has grown in the area, and catch statistics allow us to map the distribution of tuna abundance. All this knowledge brings us to a better understanding of the acoustic data. So, from the steady composition of the micronekton and the macroplankton in the area, as described by Roger (1982) confirming our own observations, we derive the possibility to convert SSL volume scattering strength into biomass (relative or absolute). Then, its fluctuations in time and space could be investigated in relation with the environment and as potential standing stock of tuna prey (Blackburn, 1969).

MATERIAL AND METHODS

Equipment

The following acoustic equipment was used :

- echosounder Simrad EKR 38 with a 30 x 30 cm nickel transducer (7 x 7° beam angle);
- analog echo-integrator Simrad QM Mark II.

During both cruises, the same equipment with the same settings was used. No significant alterations of the performances were recorded between the cruises (*see* Tab. 1).

A ten-foot Isaacs Kidd Midwater Trawl (IKMT in this paper) with an opening-closing device (Bourret, 1976) was used during the second survey.

Table 1

Performances and settings of the echosounder: frequency, transmitted frequency; SL + VR, source level and voltage response measured with a calibration sphere; pulse, pulse length in millisecond; beam, equivalent two-ways beam, 10 log of ψ; threshold, threshold used at the integrator input.

Performances et réglages de l'échosondeur : «Frequency», fréquence d'émission ; «SL + VR», niveau d'émission et sensibilité à la réception mesurés avec une cible standard ; «Pulse», durée de l'émission en millisecondes ; «Beam», angle équivalent émission-réception, 10 log de ψ ; «Threshold», seuil utilisé à l'entrée de l'intégrateur.

Frequency kHz	SL + VR dB	Pulse ms	Beam dB	Threshold dB	TVG max dB
38	116.0	0.6	-20.7	-60.9	64.5

Data acquisition method

There are two channels on the integrator. One was selected as the main channel, with constant gain and threshold, and the interval of integration was set according to the depth of the SSL: not strictly, but in the range where the layer appeared, in order to reduce unwanted echoes or noise. The second channel was used either with different settings (for example, higher gain in low response) or with an other integration interval to watch over other layers.

After squaring, the echo-signal voltages corresponding to the scattering layer identified on the paper-recorder were integrated on a two-nautical miles distance (ESDU: Elementary Sampling Distance Unit as defined by Burczynski, 1982).

Acoustic data were recorded day and night continuously, except for the two first transects of the first cruise for which day-time acoustic data were missed.

Table 2

Computation of the average target strength (in dB) and the corresponding arithmetic value for 1 g of a mixture containing 64 % Euphausiids and 36 % Pisces. *Dw, average dry weight in mg; L, length in cm; %, dry weight percentage of the group; TS, target strength computed from the equations of Greene* et al. *(Euphausiids) and Love, 1977* (Pisces)*; 10 log N, ten times the decimal logarithm of the number of organisms/g of micronekton; TSg, target strength of 1 g of organisms of each group, or total.*

Calcul de la valeur moyenne de l'index de réflexion «TS» (en dB) et de son équivalent arithmétique pour 1 g d'un mélange contenant 64 % d'Euphausiacées et 36 % de Poissons. «Dw», poids sec moyen en milligrammes ; «L», longueur en centimètres ; «%», pourcentage du groupe en poids sec ; «TS», index de réflexion calculés à partir des équations de Greene *et al.* (Euphausiacées) et de Love (Poissons) ; «10 log N», dix fois le logarithme décimal du nombre d'organismes par gramme de micronecton ; «TSg», index de réflexion de 1 g d'organismes de chaque groupe, ou au total.

Class	Group	Dw	L	%	TS	10logN	TSg	$10^{TSg/10}$
Euphausiid	Large	13	1.8	24	- 75.1	+ 12.6	- 62.5	5.623 10^{-7}
	Small	1.8	0.1	40	- 83.4	+ 23.6	- 59.9	1.023 10^{-6}
	Total			64			- 58.0	1.585 10^{-6}
Pisces	Large	520	6	21	- 50	- 4.0	- 54.0	3.981 10^{-6}
	Small	20	2.2	10	- 58	+ 6.9	- 51.1	7.762 10^{-6}
	Larvae	3.6	13	5	- 62	+ 11.4	- 50.6	8.709 10^{-6}
	Total			36			- 46.9	20.452 10^{-6}
TOTAL				100			- 46.6	22.037 10^{-6}

Hydrological observations were restricted to a continuous surface temperature record for both cruises and a series of 20 nautical-miles spaced bathythermogram sets for the first cruise.

During *Echopreg II*, twenty-eight one-hour hauls at a speed of two knots were performed with the IKMT. Unfortunately, misfunctions in the opening-closing device and in the acoustic pinger made the depth of the catches very uncertain.

Data processing

Acoustic data

The output of the integrator may be regarded as proportional to the integrated volume backscattering strength of the layer named "column scattering strength" (Urick, 1975; Clay and Medwin, 1977) :

$$S_{vc}\ R1\text{-}R2 = \int_{R1}^{R2} Sv$$

$$= 10 \log M + C_s + C_I$$

with S_{vc} = column scattering strength
S_v = volume backscattering strength
M = graphic output of the integrator
C_s = echosounder constant
C_I = integrator constant
R1, R2 = minimum and maximum depth of the integrated layer.

Biomass

From the analysis of the IKMT hauls and corresponding echointegration, it appeared that only larger *Crustacea* and *Pisces* give valuable acoustic contributions. However, Euphausiids, which largely dominate the *Crustacea* class, give an echo intensity 12.8 times lesser than *Pisces*, weight for weight (*i. e.* - 11 dB for the scattering volume). The overall proportion (wet weight) was 63 % of *Crustacea* and 37 % of *Pisces* (excluding the other groups).

Besides, the micronekton of this area has been surveyed intensively during the programme *Ciprea*, which consisted of a number of stations along a transect on the 4°W meridian from 2°N to 10°S during the two main seasons. Zooplankton and micronekton were sampled using an "Omori" net (Roger, 1982). An important result was that the proportion of the groups or families was very steady at the observed time-space scale. In addition, this proportion was very close to our own findings, with 64 % *Crustacea* (mainly Euphausiids) and 36 % *Pisces* in weight, excluding other groups.

So, this very good agreement in the two sets of observations, and the permanence in the proportion of organisms in the area convinced us to use these properties in an endeavour to assess the biomass of the SSL. The basic idea is to settle an average TS (Target Strength) for 1g of mixture of the layer (Euphausiids and *Pisces*), from a couple of equations and the finite proportion of these organisms. For Euphausiids, we use the equation settled by Greene *et al.* (1989) and the KRIDA model (Dalen and Kristensen, 1990); for the *Pisces* the Love's equation (Love, 1977). The proportions are found in Roger (1982). Results are in Table 2.

RESULTS

Depth and diel migration of the SSL

In the water column (0-500 m) the presence of a somewhat narrow SSL was almost constant. Its general diel pattern was the same for both seasons : deep in the daytime at 350-450 m and close to the surface during the night (Fig. 1, Tab. 3).

During the daytime, the layer reached its maximum depth at nearly 10 a. m. and remained more or less stable until 3 p. m. and located below 300 m for about nine hours. Its average thickness was 36 m in March-April and 45 m in July-August, but the difference was not significant.

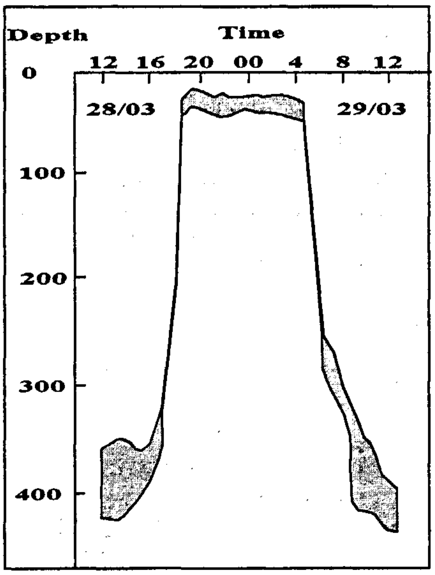

Figure 1

Position of the Sound Scattering Layer (SSL) during a 24-hour period. Cruise CAP7604, *28-29 March 1976, 5°W transect, from 0°20' S to 4° 10' S. Depth in metres, local time (= GMT time).*

Position de la couche diffusante acoustique (SSL) au cours d'une période de 24 heures. Campagne *CAP7604*, 28-29 mars 1976, radiale 5°W, de 0°20'S à 4°10'S. Profondeur en mètres, heure locale (= heure GMT).

The upward movement of the layer began at 5 p. m., its minimum depth was reached soon after 7 p. m., so the ascension from 350 to 50 m or less lasted about two hours, giving an average ascendancy rate of 2.5 m/mn or 4 cm/s. During night-time the depth of the layer was strongly related to the maximum thermal gradient, or thermocline (Fig. 2). This point will be discussed below. In the absence of a well-marked thermocline, the layer was close to the surface. Figure 3 shows the good fit between the depths of the averaged mid-point of the layer and the isotherm 23°5 C

Table 3

Thickness of the SSL according to the period of the year and day/night situation : n, number of data; t, average thickness of the layer in metres; sd, standard deviation.

Épaisseur de la couche diffusante acoustique (SSL) selon la période de l'année et la situation jour/nuit ; «n», nombre de données ; «E», épaisseur moyenne de la couche en mètres ; «sd», écart-type.

Period	Day/Night	n	t	sd
March-April	Day	9	36.0	9.3
July-August	Day	7	46.0	11.1
March-April	Night	32	14.4	5.6
July-August	Night	20	21.0	7.9

which corresponded to the mid-point of the thermocline during the first cruise (CAP 7604). There was no evidence of any influence of the lunar cycle, either during the fifteen days centred on the new moon or during the second period, centred on the full moon, with a mean depth of the layer closer to the surface.

The average thickness of the layer during the night was 14 m in the warm season and 21 m in the upwelling season. This difference may be related to the absence of a marked thermocline in the central part of the upwelling (*see* below). The layer remains for about ten hours at the upper level. It starts to sink around 5.30 a. m. just before sunrise and then drops quickly. The 300-350 m depth is reached after two hours. Thus, the sinking and ascending speeds are comparable.

It is clear from the echograms that all the organisms were not beginning their migration at the same time and moving at the same speed, as is evidenced in the appearance of several distinct layers which can cross without mixing. The gap between layers was no more than a few tens of meters. During the migration, scattering from these layers became less intense, especially between 150 and 75 m: this interval

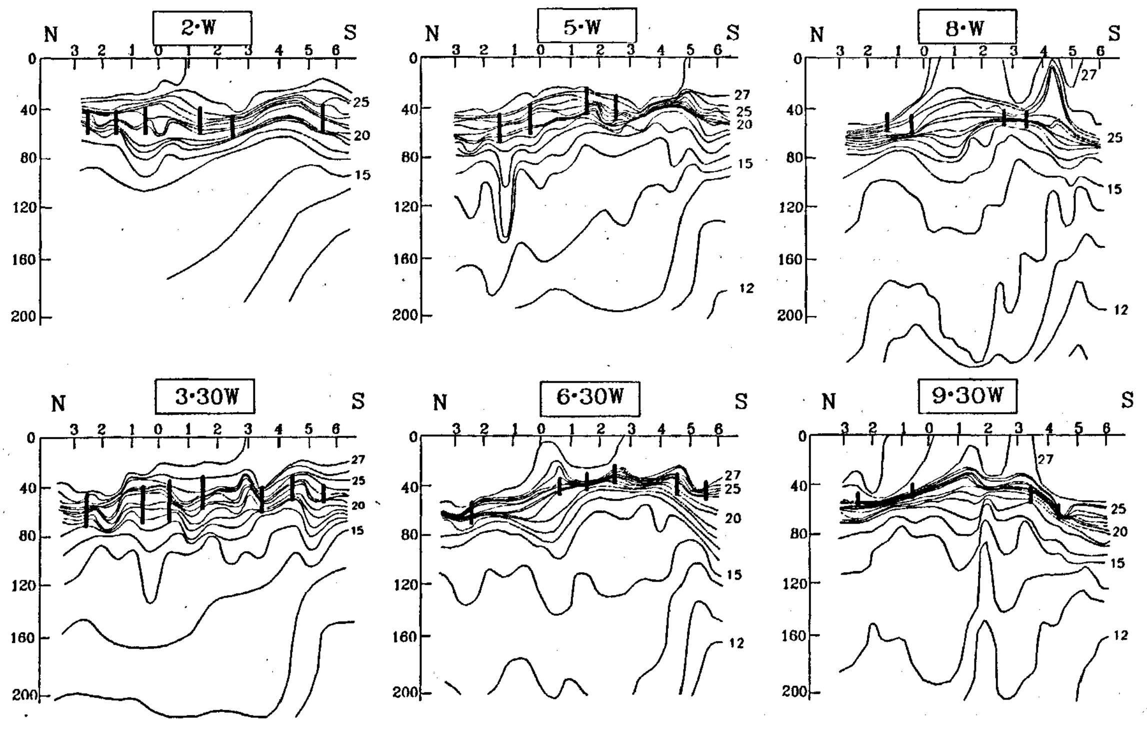

Figure 2

Night position of the SSL and thermal structure along six meridian transects. Cruise CAP7604, *March-April 1976. Vertical bars show the extension of the layer.*

Position nocturne de la SSL et structure thermique le long de six radiales méridiennes. Campagne *CAP7604*, mars-avril 1976. Les barres verticales indiquent l'extension de la couche.

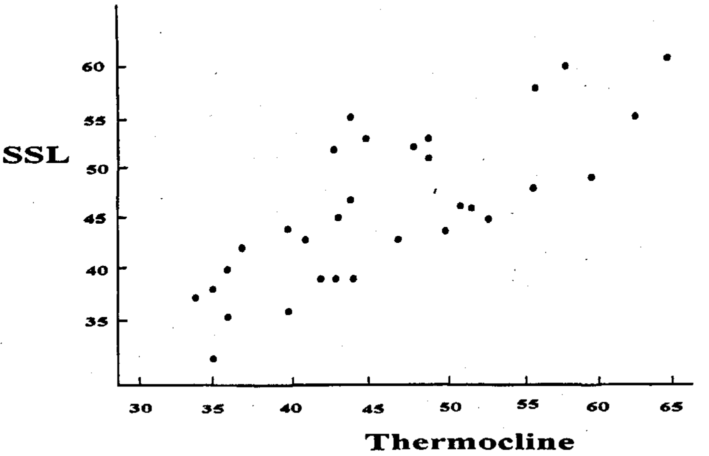

Figure 3

Depth of the night SSL (mid-point) and depth of the thermocline (23°5C isotherm), all transects, cruise CAP7604.

Profondeur de la SSL (point moyen) de nuit et profondeur de la thermocline (isotherme 23°5 C), toutes radiales confondues, campagne *CAP7604.*

Table 4

Day and night average integrated values. For the first period, transects 1 and 2 were discarded (no record during day-time). For the second period, the data of the two transects are put together. m, average integrator output (relative units); n, number of values (ten nautical miles averaged for the first period, thirty nautical miles averaged for the second); sd, standard deviation.

Valeurs moyennes intégrées de jour et de nuit. Pour la première période, les radiales 1 et 2 ont été éliminées (manque d'observations de jour). Pour la seconde période, les données des deux radiales ont été réunies. «m», sortie moyenne de l'intégrateur (en unités relatives) ; «n», nombre de valeurs (moyennées sur dix milles marins pour la première période, sur trente milles marins pour la seconde) ; «sd», écart-type.

Period	Night			Day			Ratio
	m	n	sd	m	n	sd	
March-April	16.44	77	10.31	15.80	91	13.71	1.04
July-August	22.90	20	13.24	22.90	9	12.42	1.00

corresponds to the fastest phase of the movement when the organisms are tilted and dispersed. Non-migratory layers, either deep or near the surface, were recorded, but their reverberation level was low.

This leads to the question of the magnitude of the migration. Since the averaged column scattering strength of the SSL was not different between day and night for both cruises, despite the difference of depth (*see* Tab. 4), it is assumed that all organisms move. The possible influence of the depth on the target strength is considered later. However, the great homogeneity in the averaged day and night values allowed us to take them into account for purposes of description.

Scattering volume and hydrological structure

Warm season (Tab. 5)

The hydrological situation found in March-April 1976 is very similar to the Typical Tropical Structure (TTS) as des-

Table 5

Column scattering strength and biomass estimations for cruise CAP 7604. *M, average integration of the SSL (graphical output of the Simrad QM MK II echo-integrator); SVc, average column scattering strength of the SSL, in dB; B1, average biomass of Pisces and larger Crustacea expressed in gram of dry weight per square metre (g/m²); B2, same value, in fresh weight : B2 = B1 x 5; B3, average biomass of all organisms expected in the SSL, extrapolation according to Roger (1982), in g/m² of dry weight : B3 = B1 x 1.25; B4, same value, in fresh weight : B4 = B3 x 5; Z, average value for the total area, as sum of transect averages divided by the number of transects (6); sd, standard deviation of the mean.*

Index de réverbération intégré de la «SSL» et biomasses estimées correspondantes, campagne *CAP7604.* «M», intégration moyenne de la «SSL» (sortie graphique de l'intégrateur Simrad QM MK II) ; «SVc», index de réverbération intégré de la «SSL», en dB ; «B1», biomasse moyenne de poissons et de crustacés supérieurs exprimée en grammes de poids sec par mètre carré (g/m²) ; «B2», même valeur en poids frais : B2 = B1 x 5 ; «B3», biomasse moyenne de la totalité des organismes présents dans la «SSL» en g/m² de poids sec,, extrapolée selon Roger (1982) d'après la formule : B3 = B1 x 1,25 ; «B4», même valeur en poids frais : B4 = B3 x 5 : «Z», valeur moyenne pour toute la zone, pondérée par radiale (somme des moyennes par radiale divisée par le nombre de radiales) ; «sd», écart-type de la moyenne.

Transect	Longitude	M	SVc	B1	B2	B3	B4
1	2° 00 W	7.09	- 53.2	0.219	1.095	0.274	1.370
2	3° 30 W	17.61	- 49.2	0.549	2.745	0.686	3.430
3	5° 00 W	15.11	- 49.9	0.468	2.340	0.585	2.925
4	6° 30 W	12.24	- 50.8	0.380	1.900	0.475	2.375
5	8° 00 W	16.59	- 49.5	0.513	2.565	0.641	3.205
6	9° 30 W	20.28	- 48.6	0.631	3.155	0.789	3.945
Z		14.82	- 50.0	0.458	2.290	0.572	2.860
sd		4.63					

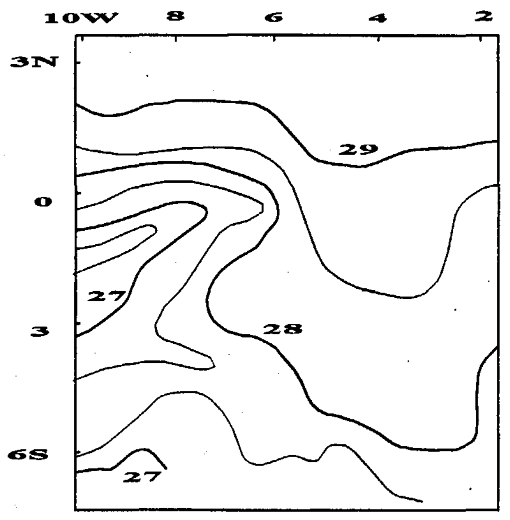

Figure 4

Surface temperatures, cruise CAP7604, *March-April 1976.*

Température de surface, campagne *CAP7604*, mars-avril 1976.

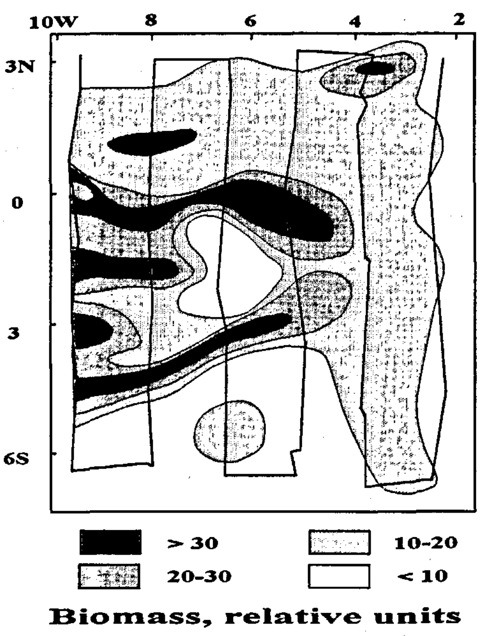

Figure 5

Map of the biomass (average integrator output), cruise CAP7604, *March-April 1976.*

Carte de répartition de la biomasse (sortie moyenne de l'intégrateur), campagne *CAP7604*, mars-avril 1976.

cribed by Herbland and Voituriez (1977). A strong stratification was observed with a homogeneous 30-50 m surface layer, a well-marked thermocline of 20 m average thickness, followed by a slight thermal gradient. The "thermal ridge" around 3° S as described by these authors was not definitely found during our survey, probably due to the late season. On the other hand, the thermocline showed a marked dome from the transect 5° W and westwards (Fig. 2). This thermal dome spread over 1° N to 5° S with its summit between 2° and 4° S, depending on the transects. Southwards, the thermocline sank. On a meridian section, the thermocline showed a few waves, suggesting sometimes a slight ridge around 4° 30' and 3° S on the westernmost transects. The surface temperature showed a clear drop westwards, in the doming area (Fig. 4).

The distribution of the highest integrated values, or relative column scattering strength of the layer, follows closely the distribution of lowest temperature values (Fig. 4 and 5).

The comparison of the distribution of these values with the depth of the thermocline characterized by the 23°5 isotherm along the meridian transect 9° 30' W, shows clearly

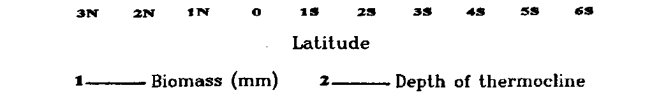

Figure 6

Biomass (average integrator output) and depth of the thermocline, transect 9° 30W, cruise CAP7604, *March-April 1976.*

Biomasse (sortie moyenne de l'intégrateur) et profondeur de la thermocline, radiale 9°30W, campagne *CAP7604*, mars-avril 1976.

Table 6

Column scattering strength and biomass estimations for cruise Echopreg II. *Transects concern the 4° W meridian. Transect 1 (T1) was southwards, from 3° 45 N to 4° 22 S, transect 2 (T2) was northwards, from 4° 22 S to 4° 45 N, we call T2c the common part with T1. Calculations and symbols are the same as in Figure 5, plus n, which is the number of observations (ESDU on transects, or transects).*

Index de réverbération intégré de la «SSL» et biomasses estimées correspondantes, campagne *Echopreg II.* Les radiales étaient situées sur le méridien 4°W. La radiale 1 (T1) a été parcourue du Nord vers le Sud, de 3°45'N à 4°22'S ; la radiale 2 (T2) a été parcourue du Sud vers le Nord, de 4°22'S à 4°45'N ; la partie de cette radiale commune avec T1 a été indiquée «T2c». Les calculs et les symboles sont les mêmes que pour le tableau 5, avec en plus «n», qui indique le nombre d'observations (ESDU par radiales, ou radiales).

Transect	n	M	sd	Svc	B1	B2	B3	B4
T1	204	22.22	11.53	- 48.7	0.616	3.08	0.770	3.85
T2c	208	22.68	14.90	- 48.6	0.631	3.15	0.789	3.94
T2	181	22.32	14.23	- 48.7	0.616	3.08	0.770	3.85
T1-T2	2	22.45	0.32					

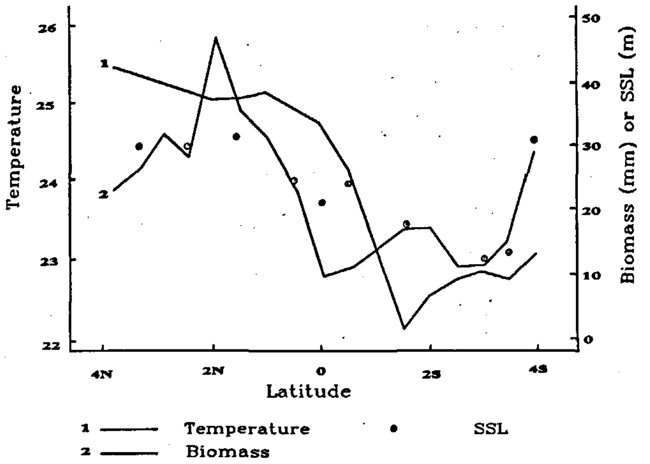

Figure 7

Biomass (average integrator output), surface temperature and position of the SSL, 4° W transect, from north to south. Cruise Echopreg II, *July-August 1977.*

Biomasse (sortie moyenne de l'intégrateur), température de surface et position de la SSL, radiale 4°W, du Nord au Sud. Campagne *Echopreg II*, juillet-août 1977.

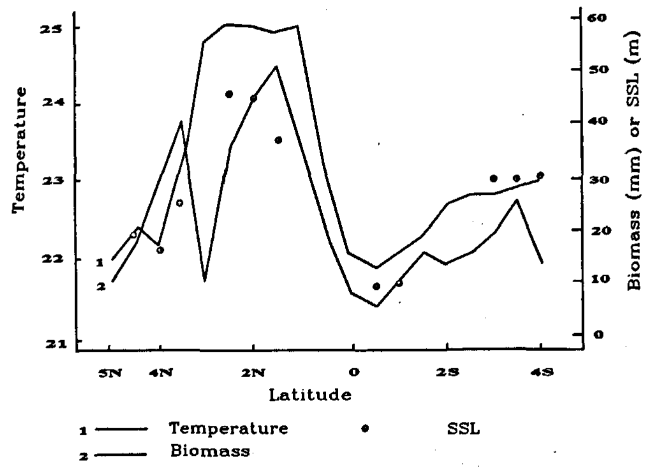

Figure 8

Biomass (average integrator output), surface temperature and position of the SSL, 4° W transect, from south to north. Cruise Echopreg II, *July-August 1977.*

Biomasse (sortie moyenne de l'intégrateur), température de surface et position de la SSL, radiale 4°W, du Sud vers le Nord. Campagne *Echopreg II*, juillet-août 1977.

this coincidence between high integrated values and dome of the thermocline (Fig. 6)

At this season, the average column scattering strength of the SSL was found to be - 50.0 dB (or 14.8 in relative units of echointegration).

Cool season (Tab. 6)

In July-August 1977, we found a typical equatorial upwelling season along the meridian 4° W transect. As mentioned earlier, this transect was sailed twice. Southwards (Fig. 7), the measurements started only at 4° N. Between this point and 1° N, the surface temperature was quite stable around 25°C, then dropped gradually to 22°C on 1° 30' S and then increased to 23° 5 at 4° S. Northwards (Fig. 8), we found 22°C at 1° N (with a minimum between 0° 30' S and 0° 30' N) where there was a well-marked thermal front, the temperature reached 25°C in a few nautical miles. Beyond 4° N, the temperature dropped again and remained at 22°C up to the continental shelf. Then, the equatorial upwelling was clearly marked, but its northern border moved two degrees of latitude northwards in an eight-day period, changing the structure of the front between cool upwelled waters and warm ones of the northern convergence that spread over two to three degrees of latitude centred around 2° N.

The distribution of the column scattering strength of the layer along the transects was very similar in both directions. The average relative values for the common part (*i. e.* excluding the part north of 4° N) are 22.2 and 22.7 respectively. This distribution highlights the preponderance of low values in the upwelling area and high values in the northern convergence. It is noteworthy that the rapid modification of the frontal structure did not cause any disturbance in the distribution pattern of the scattering layer.

At this season, the average column scattering strength was found to be - 48.7 dB (22.4 relative units of integration)

Biomass

Figures of the expected biomass are given in Table 5 for the warm season and in Table 6 for the cool season. Obviously, the standard deviation of the mean shows the distribution of the values but not the precision of the mean. This is particularly clear on the second cruise. As seen above, there was a strong stratification in rich and poor areas along the transect, giving a high intra-transect standard deviation. On the other hand, the duplicate transect standard deviation was very low, despite a gap of nine days between the beginning and the end of the transects. So, the second experiment with duplicated transect proves the data reliability and the distribution pattern consistency.

The output of the integrator and the corresponding column scattering strength must be seen as valuable but relative abundance indices. Absolute values of biomass in g/m^2 are discussed below.

DISCUSSION AND INTERPRETATION

Location of the layer during a 24-hour period

During daytime the depth of the micronektonic organisms is closely related to light levels. This was established by Clarke and Backus (1956) who showed that the migration of the organisms towards the surface is triggered by a precise level of illumination. In the same way, the split of the SSL during its upwards and downwards movement at different speed is also related to difference in light sensivity (Clarke, 1971).

On the other hand, SSL location during night-time is more controversial. Illumination may play the same part and the moon cycle could influence the depth reached by the organisms. But this is not obvious, according to our observations : the first cruise was centred on new moon and the second on full moon; and on average the layer was closer to the surface during the second one.

The very good fit between the depths of the thermocline and of the layer seems not to have been pointed out previously, except by Clarke (1933, 34 *in* Clarke and Backus, 1956) concerning the role of the thermocline on the night migration of copepods in the Gulf of Maine.

A very comprehensive survey entitled "Biological sound scattering", edited by Farquhar (1977), considers several factors which could influence the migration of the SSL. Besides light, he noted temperature modifications, density gradients, pressure and trophic behaviour.

In our case, the question is whether the migration is stopped directly by the thermal gradient or by some factors related to it. Obviously, in this area most of the factors cited by Farquhar coincide with the thermocline and the top of the nitracline (Voituriez and Herbland, 1979) and most of the time with the highest values of chlorophyll.

Roger (1982) pointed out the higher concentration of macroplankton and micronekton in the first one hundred metres during night but could not be more precise due to his sampling mode. We stress the fact that during night-time, the SSL was located at a depth which corresponds to the maximum thermal gradient and trophic accumulation. In addition, the thickness of the layer is also dependent on the intensity of the thermal gradient.

Influence of the 24-hour cycle

Classical observations of the SSL show that generally the column scattering strength is higher during the night, when the layer is close to the surface (Farquhar, 1977). However, this is not relevant to our observations because we used a higher frequency than in previous studies. According to Chapman and Marshall (1966), the difference between integrated scattering volume from 850 m depth in daytime to the surface at night depends on the frequency and decreases from 2 to 12 kHz. For higher frequencies, the difference is no longer significant. In addition, many authors consider the total column from a given depth to the surface rather than the scattering layer itself: layers located deeper during daytime, might move upwards and "contaminate" the data during night-time.

In fact there are two questions: one is related to the directivity of the targets, the other to their modification with depth, mainly for fish with swimbladders. Concerning the fish attitude, dive observations from submarine devices are rather controversial and led Barham (1971) to define two types of Myctophids: the first one, with a well developed swimbladder or without it, swims actively, realizes diel migrations and its body remains horizontal; it is found in inter-tropical and sub-tropical areas. The second one has a swimbladder filled with an adipose tissue in the adult phase. It is not very active, performs no migrations or at least not into the upper layers and its body is dark and often in a vertical position; it is mainly found in temperate and cold waters. Large differences in the day-night acoustic response of the Euphausiids have been noted by different authors. According to Sameoto (1980), night values might be seven times lower. Everson (1982) observed similar differences in the antarctic krill *Euphausia superba*. On the other hand, Sameoto (1980) did not notice any influence of depth on the acoustic response, from 70m to 120m. All these observations on Euphausiids are at 120 kHz.

For the fish, the resonant frequency of the swimbladder is well below 38 kHz, even at 400 m. Using the simplified formula given by Weston (1967) the resonant frequency for a fish of 4 cm at 400 m should be:

$$fr = \frac{8.Po^{1/2}}{L} = \frac{8.400^{1/2}}{4} = 12.6 \text{ kHz}$$

But the scattering section of the fish decreases with depth if the size of the swimbladder decreases with increasing pressure. According to Farquhar (1977), there would be two types of response:

- constant mass of gas, leading to a constriction of the swimbladder and then to a reduction of the scattering section (physostom);
- constant volume maintained by secretion or absorption of gas and then with a scattering strength independant of the depth (physoclist). The Myctophids should belong to the second type.

However, Ona (1990) found a decrease in the volume and to a lesser degree in the dorsal area of the swimbladder with an increased pressure under experimental condition simulating "a rapid downward migration" by three physoclist gadoids.

Gjosaeter (1978) did not notice any significant difference between day and night integrated reverberation volume of a SSL moving from 250-300 m to less than 50 m in Arabian Sea. The layer was mainly composed of Myctophids, according to catch data. In this case, the frequency in use was 38 kHz, the same as in our surveys. So, at least at this frequency, the assumption of independence of the target strength of these fishes in regard to the depth and to their day-night behaviour is rather consistent with

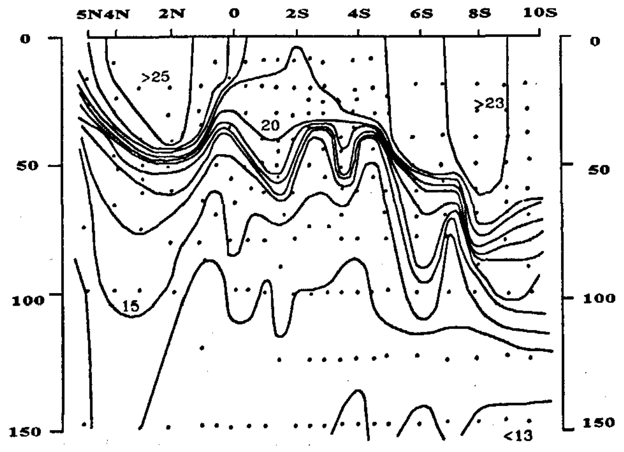

Figure 9

Temperatures on 4° W transect, August 1978, cruise Ciprea I *(Roger, 1982).*

Température le long de la radiale 4°W, août 1978, campagne *Ciprea I* (Roger, 1982).

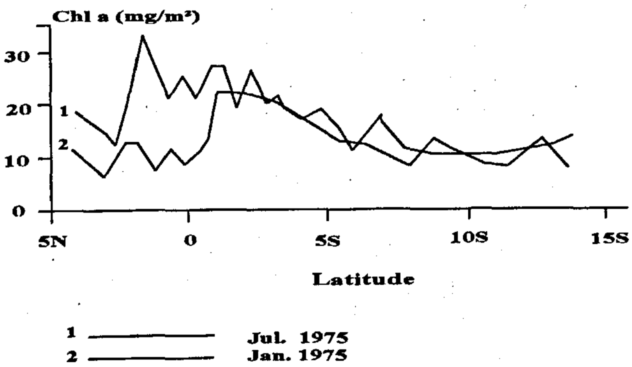

Figure 10

Integrated amount of chlorophyll a on 100 m (mg/m²) along 4° W transect in warm (January 1975) and cool (July 1975) seasons (Voituriez and Herbland, 1977).

Quantité intégrée sur 100 m de chlorophylle *a* (en mg/m²) le long de la radiale 4°W en saison chaude (janvier 1975) et en saison froide (juillet 1975) : Voituriez et Herbland, 1977.

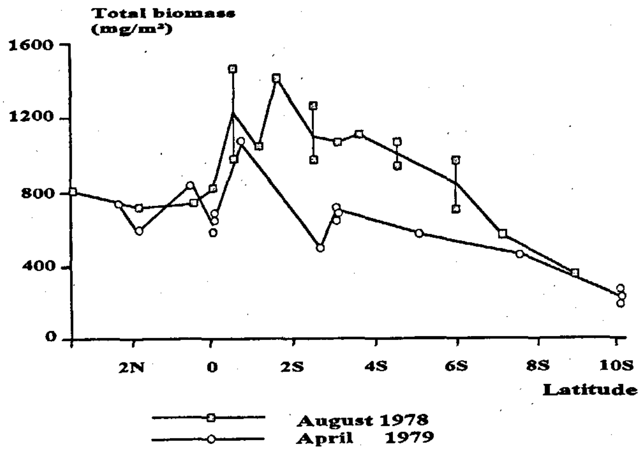

Figure 11

Macroplankton-micronekton in mg (dry weight) per square metre along 4° W transect (Roger, 1982).

Macroplancton-micronecton en milligrammes de poids sec par mètre carré le long de la radiale 4°W (Roger, 1982).

the observations. As far as Euphausiids are concerned, their contribution to the response is so weak in comparison to fish that their variation may be neglected. Also, we failed to consider any significant contribution from other organisms, such as Siphonophores, whose gas bubbles could be resonant at 38 kHz (Barham, 1963).

"Acoustic biomass" and hydrological structure

We call "acoustic biomass" the relative arithmetic expression of the averaged column scattering strength. During warm season, the biomass maximum was observed below the coolest waters, whereas it was below the warmest waters during cool season. Obviously, the surface temperature is only an indicator of the underwater hydrological phenomenon, and this apparent contradiction can be understood from the study of the thermal profile. In TTS situation, the lowest temperatures found at the surface correspond to a dome of the thermocline which is clearly related to the highest biomass values. In cool season, the lowest temperatures correspond to the new upwelled waters without marked thermocline, whereas the warmest temperatures correspond to the stable north convergence area with a well-marked thermocline similar to the TTS situation. This is clear on the thermal profile made on the same transect in August 1978 (Fig. 9). The rapid evolution of the thermal front in the space of a few days must be understood as the displacement of the meanders of the equatorial surface current and of the under-current, following a fifteen-day periodicity, as was described by Düing *et al.* (1975) and later observed by Herbland and Le Bouteiller (1982). The biomass maximum seems localized north of the northern point reached by this displacement, leading to the idea that the stability of the superficial system is a condition for the formation of a dense SSL.

"Acoustic biomass" and biological production

In Typical Tropical Season (TTS), the top of the nitracline is situated just below the strongest density gradient, which is practically the same for the temperature (Voituriez and Herbland, 1977). At this level, the chlorophyll and zooplankton biomass maxima are also found (Le Borgne, 1977). There is then a complete correspondence between these trophic levels and the position of the SSL during night-time. On a depth profile along the 4° W meridian (Fig. 10), we can see that the chlorophyll *a* maximum is located south of the equator in the equatorial divergence (Voituriez and Herbland, 1977). This "rich" sector extends from 1° to 5° S. According to Le Borgne (1977) the abundance of zooplankton fits well with that of chlorophyll. An assessment of micronekton biomass has been made by Roger (1982) from hauls of "Omori" plankton net made at a number of stations along this transect. The maximum biomass integrated from 400 m to the surface was found between 0° 30' S and 4° S around the "thermal ridge" (Fig. 11). The very good agreement between the pattern of trophic abundance and that of the "acoustic biomass", particularly along the transect with a marked thermal dome, is noteworthy.

In boreal summer, various situations occur : equatorial upwelling extends approximately from 0° 30' N to 3° S; northerly and southerly a similar situation to the TTS with a strong thermal stratification especially marked in the northern convergence (Voituriez and Herbland, 1977). In the upwelled waters, the nitracline disappears and nitrates are no longer the limiting factor for the primary production. However this production is reduced by water turbulence. In the stable situations found on both sides, the nitracline occurs again with the peak of chlorophyll at this level. Obviously, this maximum is higher than in the upwelling area (Minas *et al.*, 1983). According to Voituriez and Herbland (1977) this should be caused by the sinking of the enriched upwelled waters below the warm waters of northern convergence. On the other hand, the maximum of zooplankton biomass occurs in the upwelling area (Le Borgne, 1977) as well as macroplankton-micronekton, with a biomass 50 % more than in the northern convergence (Roger, 1982; Fig. 11). This is inconsistent with the pattern of distribution of the "acoustic biomass" observed in that season. The question revolves around the efficiency of each method. Relevant points to be considered are sampling methods and the spatial distribution of the organisms. Net hauls were made obliquely at constant speed from a given depth to the surface. If the biomass is concentrated in a rather narrow layer fluctuating in density and thickness, the discrete and small sample caught by a plankton net may be inadequate. On the other hand, the echosounder samples the layer in a quasi-continuous way and gives an average of the density along the course of the vessel. In addition, the size of each sample taken by the echosounder (each transmission) is much greater than the net haul (say sixty times more at 50 m depth for exemple, sixty times or more by minute). Clearly, when scatterers with low target strength (like plankters, krill, small fish, *etc.*) are spread over a large volume, the net is more efficient. On the contrary, when these scatterers are concentrated in a rather thin layer, then echointegration is much more efficient.

Seasonal variations

Roger (1982) found a ratio of 1.2 between upwelling and cool seasons for the micronekton biomass. This is very consistent with the seasonal ratio of 1.3 we found for the acoustic biomass. Primary production and chlorophyll indices show a seasonal variation of the same amplitude (Voituriez and Herbland, 1977; Herbland *et al.*, 1983). It is difficult to know whether this difference is actual or casual.

Absolute biomass assessment

Obviously, absolute biomass computation is based on a number of assumptions not fully confirmed. In particular, Euphausiids TS is very controversial. According to recent papers (Foote *et al.*, 1990; Greene *et al.*, 1991), it could be some 10 dB less than our value. Nevertheless, the acoustic contribution of krill is so small in comparaison with that of fish that even an order of magnitude could not significantly modify the global TS of the mixture, and hence the total biomass. Clearly, what we actually measure acoustically is the *Pisces* contribution, and we assess the total biomass from the average proportion of the organisms, which is a reasonable procedure due to the steady state of this proportion (Roger, 1982). Another problem is related to the actual TS of this kind of fish, which there is no direct measurement for. So, the absolute value of the biomass is doubtful and should be taken more as an order of size. However, the close average figures given by Roger (1982) for the same transect, using net sampling, are noteworthy: 3.6 g/m^2 instead of 3.2 for our data in warm season, 4.7 instead of 3.9 in upwelling season. These values are higher than those reported by Sund *et al.* (1981) for tropical waters, 0.6 to 1.0, but in the range given by Voss (1969) for the Gulf of Guinea, 6 g/m^2.

Tuna catches in the area

Data and information concerning tuna are mainly found in the well-documented paper "*Environnement et pêche thonière en Atlantique tropical oriental*" (Stretta, 1988). This area is mainly inhabited by big yellowfins (weight more than 30 kg). The maximum catch occurs from January to March south of the equator to about 3°-4° S. There is a clear westward movement of the concentration between December and April from the west of meridian 0° to 9°-17° W (Fig. 12). The distribution and abundance of the acoustic biomass found in March-April is consistent with this pattern.

During the boreal summer, there is no catch of tuna south of the equator. Almost all the big yellowfin are caught either near the coast of Ghana or in the warm waters of the northern convergence. This situation was regarded as rather paradoxical, since the upwelling area is considered as more productive than the warm waters. On the other hand, the acoustic biomass was found to be much more abundant in the convergence area. In a review of the relations between environment and tuna in the Pacific Ocean, Sund *et al.* (1981) wrote that "[yellowfins] are more abundant between 1° and 6°N than at the equator where the upwelling is centered. The explanation given is that the major drift of newly upwelled water is towards the northwest...The biomass maximum for the micronekton tuna should be, therefore, a few degrees north of the equator, with tuna aggregated on the forage. The expected forage maximum was found." This is exactely the situation we found during the upwelling season. The same type of situation occurs in fronts. It has been described from Cape Lopez, in the same geographical area (Frontier, cited by Stretta, 1988): tuna were found on the warm side of the

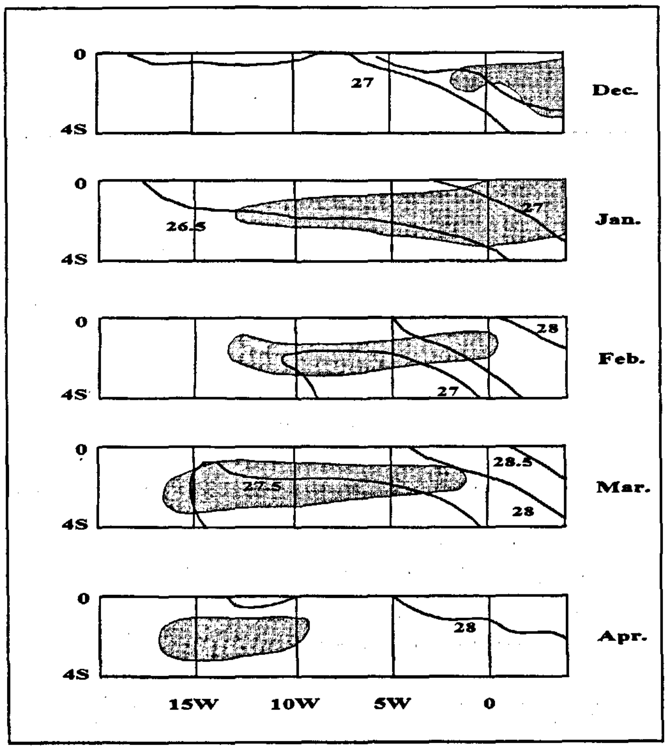

Figure 12

Distribution of monthly catch of big yellowfin tuna (over 30 kg) in the equatorial area of the Eastern Atlantic, December to April (Stretta, 1988).

Distribution des prises mensuelles de grands albacores (supérieurs à 30 kg) dans le secteur équatorial de l'Atlantique oriental, décembre à avril (Stretta, 1988).

thermal front, less productive but benefiting from the export of living material from the rich but newly upwelled cold waters. The role of fronts was underlined by Laurs *et al.* (1984) who note "The satellite images and concurrent albacore catch data clearly show that the distribution and availability of albacore are related to oceanic fronts".

In our case, the good fit between tuna catch and "acoustic biomass" suggest some kind of trophic relationship. From acoustic tracking experiments, Cayré *et al.* (1986) demonstrated the yellowfin is able to reach a depth of 250 m and the skipjack 300 m during daytime. But most of the time these fish did not exceed 100 m depth, except at sunset and sunrise when the skipjack sinks quickly down to 300 m for a short period. Although these observations were made in the Pacific Ocean, it is likely that the behaviour of those fishes is not different in the Atlantic Ocean. Obviously tuna are not able to feed on the SSL when it is deep. The question of their ability to feed during night-time is unclear. However, Bard and Pézennec (1990) after other observers, found fish of the SSL in the stomach contents of the tuna fished in the equatorial area. They could feed quickly on the ascending or descending SSL when light level is just enough : that could explain why tuna are reported to sink quickly at sunrise and sunset. This phenomenon was also recorded from sonic-tagged skipjack in Hawaï waters (Sund *et al.*, 1981). In this respect, the degree of concentration and patchiness of the layer probably play a very important role.

CONCLUSION

It has been shown that the location of the SSL observed permanently in the equatorial area of the Eastern Atlantic is closely related to the hydrological structure in its night phase. The absence of difference between day and night average column scattering strength of this layer supports the hypothesis of a nearly-total diel migration from 300-400 m to 20-60 m depth.

The night concentration of the layer is under the control of different factors : hydrological structure, type of water mass, and most probably degree of concentration of chlorophyll and zooplankton. The layer seems more concentrated in the Typical Tropical Season or in the convergence which is similar to (stable structure) than in the upwelling (unstable structure).

As far as the trophic use by upper levels is concerned, the degree of concentration or patchiness is probably more important than the average abundance in the total water column. This could explain why tuna, which are directly or indirectly micronekton feeders, are associated more with stable structures with a concentrated narrow layer than with productive areas having a more dispersed layer.

Finally, and despite uncertainties related to the tremendous difference within the acoustic response of the zoological groups, the acoustic approach has proved to be a quick and efficient method to identify areas which are rich and attractive to predators.

Acknowledgements

We wish to thank Alain Herbland, Director of CREMA (Centre de Recherche en Écologie Marine et Aquaculture de l'Houmeau, France), who encouraged us to publish this work. We also thank our colleagues Alain Fonteneau for his valuable comments on a first draft of the paper, Claude Roger and Robert Le Borgne who took an active part during one of the cruises. John Dolan has kindly revised the English of an advance copy.

We should not forget the two anonymous referees whose pertinent comments and remarks allowed us greatly to improve the original manuscript.

REFERENCES

Bard F.X. and O. Pezennec (1990). Analyse des contenus stomacaux des albacores (*Thunnus albacares*) pêchés à la senne dans le Golfe de Guinée. *Contribution to the Conference of the International Commission for the Conservation of the Atlantic Tunas, I.C.C.A.T., Madrid, 29 October-9 November 1990*, 8 pp.

Barham E.G. (1963). Siphonophores and the deep scattering layer. *Science*, **140**, 3568, 826-828.

Barham E.G. (1971). Deep-sea fishes lethargy and vertical orientation. in : *Proceedings of the International Symposium on Biological Sound Scattering in the ocean*, G.B. Farquhar, editor. Maurry Center Ocean Science, Washington D.C., 100-118.

Blackburn M. (1969). Conditions related to upwelling which determine distribution of tropical tunas off Western Baja California. *Fishery Bulletin, Fish Wild. Serv. US*, **68**, 147-176.

Bourret P. (1976). L'échantillonnage du micronecton profond avec description d'un nouveau chalut Isaacs-Kid 10 pieds ouvrant-fermant. Documents Centre ORSTOM Nouméa, 50 pp.

Burczynski J. (1982). Introduction to the use of sonar systems for estimating biomass. *FAO Fish. tech. Pap.*, **191**, Rev. 1, 89 pp.

Cayré P., J. Chabanne, G. Moarii and B. Uglini (1986). Premières expériences de marquages acoustiques et de poursuite de thonidés en Polynésie française. EVAAM, Pêche Document, 11, Papeete, Tahiti, 45 pp.

Chapman R.P. and J.R. Marshall (1966). Reverberation from Deep Scattering Layers in the Western North Atlantic. *J. acoust. Soc. Am.*, **40**, 405 pp.

Clarke G.L. (1971). Light conditions in the sea in relation to the diurnal vertical migrations of animals. in : *Proceedings of the International Symposium on Biological Sound Scattering in the ocean*, G.B. Farquhar, editor. Maury Center Ocean Science, Washington D.C., 41-50.

Clarke G.L. and R.H. Backus (1956). Measurements of light penetration in relation to vertical migration and records of luminescence of deep-sea animals. *Deep-Sea Res.*, **4**, 1-14.

Clay C.S. and H. Medwin (1977). *Acoustical Oceanography: principles and applications.* John Wiley and sons, London, 544 pp.

Dalen J. and K.E. Kristensen (1990). Comparative studies of theoretical and empirical target strength models of Euphausiids (Krill) in relation to field experiment data. *Rapp. P.-v. Réun. Cons. perm. int. Explor. Mer,* **189**, 336-344.

D'Aoust B.G. (1971). Physiological constraints on vertical migration by mesopelagic fishes. in : *Proceedings of the International Symposium on Biological Sound Scattering in the ocean,* G.B. Farquhar, editor. Maury Center Ocean Science, Washington D.C., 86-99.

Düing W., P. Hisard, E. Katz, J. Meincke *et al.* (1975). Meanders and long waves in the equatorial Atlantic. *Nature,* **257**, 280-284.

Everson I. (1982). Diurnal variations in mean volume backscattering strength of an antartic krill (*Euphausia superba*) patch. *J. Plankt. Res.,* **4**, 1, 155-162.

Farquhar G.B. (1977). Biological sound scattering in the oceans: a review. in: *Oceanic sound scattering prediction,* N.R. Andersen and B.J. Zahvranec, editors. Marine Science 5, Plenum Press, 493-527.

Foote K.G., I. Everson, J.L. Watkins and D.G. Bone (1990). Target strength of Antarctic krill (*Euphausia superba*) at 38 and 120 kHz. *J. acoust. Soc. Am.,* **87**, 1, 16-24.

Gerlotto F. (1975). Note sur les biomasses pélagiques évaluées par écho-intégration dans la zone équatoriale du Golfe de Guinée : premiers résultats. *Doc. scient. Cent. Rech. océanogr., Abidjan,* **6**, 2, 119-138.

Gerlotto F., R. Le Borgne, E. Marchal, C. Roger and B. Stequert (1978). Application au micronecton des méthodes d'estimation de biomasse par échointégration. Publication interne ORSTOM Brest, 10 pp.

Gjosaeter J. (1978). Aspects of the distribution and ecology of the Myctophidae from the western and northern Arabian Sea. *Dev. Rept Indian Ocean Progr.,* **43**, 2, 62-108.

Greene C.H., P.H. Wiebe and J. Burczynski (1989). Analyzing zooplankton size distribution using high-frequency sound. *Limnol. Oceanogr.,* **334**, 1, 129-139.

Greene C.H., T. Stanton, P. Wiebe and S. McClatchie (1991). Acoustic estimates of Antarctic krill. *Nature,* **349**, 110.

Herbland A. and A. Le Bouteiller (1982). The meanders of Equatorial currents. Influence on biological process. *Oceanogr. trop.,* **17**, 1, 15-25.

Herbland A. and B. Voituriez (1977). Production primaire, nitrate et nitrite dans l'Atlantique tropical. I: Distribution du nitrate et production primaire. *Cah. ORSTOM, sér. océanogr.,* **15**, 1, 47-55.

Herbland A., R. Le Borgne, A. Le Bouteiller and B. Voituriez (1983). Structure hydrologique et production primaire dans l'Atlantique tropical oriental. *Oceanogr. trop.,* **18**, 2, 249-293.

Laurs R.M., P.C. Fiedler and D.R. Montgomery (1984). Albacore Tuna catch distributions relative to environmental features observed from satellites. *Deep-Sea Res.,* **31**, 9, 1085-1099.

Le Borgne R. (1977). Étude de la production pélagique de la zone équatoriale de l'Atlantique à 4°W. II: Biomasses et peuplements du zooplancton. *Cah. ORSTOM, sér. Oceanogr.,* **15**, 4, 333-347.

Love R.H. (1977). Dorsal-aspect target strength of an individual fish. *J. acoust. Soc. Am.,* **49**, 816-823.

Minas M., A. Herbland and A. Ramade (1983). La production primaire dans les structures hydrologiques de la divergence équatoriale en saison d'upwelling (campagne *Ciprea I*). *Oceanogr. trop.,* **18**, 2, 319-329.

Ona E. (1990). Physiological factors causing natural variations in acoustic target strength of fish. *J. mar. biol. Ass. U.K.,* **70**, 107-127.

Roger C. (1982). Microplancton et micronecton dans l'Atlantique tropical. I : Biomasses et composition taxonomique. *Oceanogr. trop.,* **17**, 1, 85-96.

Sameoto D.D. (1980). Quantitative measurements of Euphausiids using a 120 kHz sounder and their *in situ* orientation. *Can. J. Fish. aquatic. Sci.,* **37**, 693-702.

Stretta J.M. (1988). Environnement et pêche thonière en Atlantique tropical oriental. in : Ressources, pêche et biologie des thonidés tropicaux de l'Atlantique centre-est, A. Fonteneau and J. Marcille, éditeurs. *FAO Doc. Tech. Pêches,* **292**, 269-316.

Sund P.N., M. Blackburn and F. Williams (1981). Tunas and their environment in the Pacific Ocean: a review. *Oceanogr. mar. Biol. a. Rev.,* **19**, 443-512.

Urick R.J. (1975). *Principle of underwater sound.* McGraw Hill, New York, 384 pp.

Voituriez B. and A. Herbland (1977). Étude de la production pélagique de la zone équatoriale de l'Atlantique à 4°W. I : Relations entre la structure hydrologique et la production primaire. *Cah. ORSTOM, sér. Océanogr.,* **15**, 4, 313-331.

Voituriez B. and A. Herbland (1979). The use of the salinity maximum of the Equatorial undercurrent for estimating nutrient enrichment and primary production in the gulf of Guinea. *Deep-Sea Res.,* **26 A**, 77-83.

Voss G.L. (1969). The Pelagic mid-water fauna of the eastern tropical Atlantic with special reference to the Gulf of Guinea, in: *Proceedings of a Symposium on Oceanography and Fisheries of the Eastern Tropical Atlantic,* UNESCO, Paris, 91-99.

Weston D.E. (1967). Sound propagation in the presence of bladder fish. in: *Underwater acoustics,* V.M. Albers, editor. Plemum Press, New York, 2, 55-88.