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Surface megafauna related to western Mediterranean circulation

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Abstract

The present results come from the campaigns of the international multidisciplinary programme conducted by P. La Violette (Naval Oceans Research and Development Activities, NORDA), the Western Mediterranean Circulation Experiment. The mesoscale instabilities of the Mediterranean circulation induce meanders, gyres and eddies acting on the production potential of living resources. These resources are evidenced here through the cetaceans and other large organisms directly observable in the surface waters of the sea, along the track of the cruise NORDA 706 (May-June 1986), and through the underlying biomasses detected by an echo sounder, 12 kHz fishfinder. Acoustics detection was continuous, set at the same level by day and night for 15 days interrupted only when the ship stopped for hydrological measurements at 87 CTD sampling stations. The pattern of hydrological sampling was designed in order to identify the intermediate water veins in the Algerian Basin. The three sets of field data - daily visual census, continuous echo-sounding and hydrological profiles - were compared and processed in statistical factorial and multiregression analyses. These show that presence of cetaceans coincides with highly concentrated echos; other large organisms observed are distributed at random, without any link with the concentrated echos. It results that cetaceans have the ability to detect acoustically the same biomasses as humans do with a 12 kHz echo-sounder; this is an argument for the "echolocation of the Odontoceta" and "vocalization of the Mysticeta"; up to now, such processes are not accepted by all cetologists. Four examples of echogram are reported here associated with fin whales, sperm whales, pilot whales and dolphins. Dynamical analysis of the Mediterranean circulation before and during the cruise by contemporaneous remote sensing imagery (CZCS and NOAA 9) enables deduction of the dynamic characteristics of the areas where high densities of acoustical detection co-occur with the presence of cetaceans. Such areas are enriched by the intermediate water by a shearing effect against the edge or the bottom of an eddy, *i.e.* at the contact between two water bodies moving in opposite directions; it can also happen on the edges of two eddies where they become tangential. Thus, four areas of high productivity of living resources (high trophic-chain levels) are evidenced here in the Algerian Basin. One is linked with the frontal process of the Almeria-Oran Front; the three others, not previously described, concern the influx of levantine intermediate water into the Western Mediterranean Basin.

Keywords: Mediterranean circulation, acoustical detection, living resources, deep biomass, cetaceans.

Mégafaune de surface en relation avec la circulation ouest-méditerranéenne.

Résumé

Les résultats rapportés ici proviennent des campagnes océanographiques du programme international pluridisciplinaire d'expérimentation sur la circulation de la Méditerranée occidentale (Western Mediterranean Circulation Experiment). L'instabilité à moyenne échelle de la circulation méditerranéenne entraîne la création de méandres, de gyres, de tourbillons visibles en surface et de modifications de la position des veines d'eau intermédiaire, d'origine levantine ou nord-méditerranéenne. Cette instabilité induit des répercussions sur les ressources vivantes, qui sont détectées ici à travers des observations de la mégafaune visible en surface : cétacés, requins, tortues, bancs de thons ou autres poissons pélagiques. En même temps qu'une vigie continue de jour, est réalisée une détection acoustique unifréquentielle à 12 kHz de 0 à 1 000 mètres de fond, en continu jour et nuit pendant 15 jours au cours de la campagne NORDA 706 conduite par P. Pistek (mai-juin 1986); le but étant d'identifier les veines d'eau intermédiaire du bassin algérien, un plan d'échantillonnage de 87 profils hydrologiques a été établi, nous permettant de voir à quel type de profil sont liés les cétacés et autres grands organismes. Une étude statistique montre que les cétacés sont concomitants de toutes les très fortes concentrations d'échos révélées par l'échosondeur, alors que les autres grands organismes se trouvent répartis au hasard. On en déduit que les cétacés peuvent détecter acoustiquement les biomasses profondes avec des moyens qui doivent ressembler aux nôtres, tel un sondeur de 12 kHz; cela plaide en faveur d'un procédé acoustique non encore totalement admis chez les cétologues, nommé « écholocation » chez les odontocètes et « vocalisation » chez les baleines. Des échogrammes types sont rapportés ici, liés aux rorquals, cachalots, globicéphales et dauphins. Une analyse dynamique de la circulation méditerranéenne par des images satellitaires (CZCS et NOAA, mai et juin 1986) permet d'établir les caractéristiques des zones de forte détection acoustique et donc de coïncidence avec les cétacés; un lien apparaît avec l'eau intermédiaire et des tourbillons détachés du courant atlantique : les zones riches intéressant les cétacés sont à la périphérie de tourbillons, à la friction de deux tourbillons ou d'un tourbillon en friction profonde avec une masse d'eau intermédiaire se déplaçant en sens contraire. Quatre zones de forte production de ressources vivantes sont trouvées ici dans le bassin algérien : l'une est liée au front Almeria-Oran; les trois autres n'avaient pas été mentionnées à ce jour et concernent l'entrée d'eau intermédiaire d'origine levantine.

Mots-clés : Méditerranée, détection acoustique, ressources, biomasse, cétacés.

INTRODUCTION

Megafauna (*i.e.* cetaceans and other large organisms) constitute the highest level of pelagic food chains, as they feed on zooplankton, micronekton, and herbivorous or carnivorous nekton. Moreover, owing to their large displacements, their predation results in transferring biomass to great distances and recycling it in remote oligotrophic areas (Schlitz and Cohen, 1984). Their relationship with oceanic primary production has been studied (Le Guen and Chevalier, 1982; Bergh *et al.*, 1985; Smith *et al.*, 1986). Oceanographic campaigns performed in the Mediterranean area in various programs (MEDIPROD 5, W.M.C.E., FRONTAL, ALMOFRONT) showed that the high primary productivity of the Mediterranean is confined to very localized areas linked with mesoscale oceanographic structures, such as upwellings, fronts, eddies, etc. (Béthoux and Prieur, 1983; Millot, 1987*a* and *b*; Taupier-Letage and Raimbault, 1988; Prieur *et al.*, 1988; Arnone, 1988; Lohrenz and Wiesenburg, 1988; De Palma *et al.*, 1988; Sournia *et al.*, 1990). Hence megafauna plays an important role in consuming biomass in eutrophic areas as competitors of exploited fish populations, and recycling nutrients in oligotrophic ones, then monitoring aquatic living resources at a global scale.

Other oceanograhic approaches have focused on tuning, or matching, of primary and secondary production with the spatial and temporal scales of the driving physical phenomena (Legendre, 1981; Legendre and Demers, 1984, 1985; Le Fèvre and Frontier, 1988; Mann and Lazier, 1988). The present paper focuses on these problems, aiming to show precisely, among the data from an oceanographic cruise in the Mediterranean in 1986 (Western Mediterranean Circulation Experiment, W.M.C.E.), the co-occurrence of surface visible megafauna, echosounded biomass and mesoscale oceanographic structures.

Our observations before 1985 in the North-Western Mediterranean (Viale, 1985) aimed to make a stock assessment of various cetacean species, using a strip-transect method (Hammond, 1986). From 1985 on, a line-transect method (Hiby and Thompson, 1985) was preferred, giving a relative abundance index for the successive segments of the performed transects. Such index allows a comparison of abundance from one area to another, as realized by various authors in other seas (Ainley, 1985; Smith *et al.*, 1986, etc.).

Later, studying cetacea in the framework of the FRONTAL (CNRS) programme, the random sampling method (random drawing of transects) was abandoned and, on the contrary, we tried to observe the greatest possible number of cetacea in the Ligurian Sea through searching them in the vicinity of Corsican and Ligurian oceanographic fronts (Viale, 1991). Indeed, whaling grounds have long been linked with sharp thermohaline gradients (Uda, 1954; Uda and Dairokuno, 1957; Nasu, 1963 1966; Gaskin, 1976, 1982; Whitehead, 1981; Whitehead *et al.*, 1985). Our results indicate a density of sightings in areas of the oceanographic features of four times that which is obtained when observing at random.

It appeared necessary to confirm theses results in other areas, and particularly in the southern part of the Western Mediterranean basin. Ten Toulon-Gilbraltar or Toulon-Suez cruises were performed with IFREMER oceanograhic ships, in the framework of the French TRANSMEDICET program. Such cruises aimed at identifying water masses in which cetacea are observed, through continuous records of surface temperature and salinity, continuous echosounding of underlying biomass when a sounder (such as a fishfinder) is functioning on board, and simultaneous undisrupted daytime megafauna sighting. The collected data showed (Viale, 1991) that cetacea are clearly localized in areas containing important deep biomasses, associated with some physical mesostructures, namely in the North Eastern edge of Almeria-Oran front, the Catalonian slope front, and the Northern edge (along Spain) of the first gyre of Alboran Sea (Viale and Terris, unpubl.).

The southern area of the Western Mediterranean basin was studied, aiming to link the presence of megafauna with some aspects of the general or mesoscale circulation, during a multidisciplinary campaign in the area, the NORDA 706 cruise (conducted by P. Pistek), in the context of the Western Mediterranean Circulation Experiment (WMCE), on board the US NS ship “Lynch”. The transects have been determined by the context of this cruise (*see* Methods), and for that the megafauna sightings were not equivalent to a statistical sampling, hence they by no means allow a stock assessment. Along the track, visible coincidence between the sightings and the echogram characteristics of the water body were determined when cetaceans were observed diving for food. Indeed, when observing whales, the feeding behaviour is clearly distinct from moving, playing or mating activities. During our cruise, the behaviour observed was essentially diving for feeding, not any case of mating, and very few cases of playing.

METHODS

Data sampling

Three kinds of field data have been gathered: oceanographic measurements, visual census of megafauna, and acoustic detection of underlying living resources.

The method used in our preliminary cruises (Viale, 1991) had to be adapted to this multidisciplinary experiment, our purpose being a comparison between megafauna observations, acoustical detection of underlying biomass by means of echo-sounding, physical measurements at eighty seven well localized casts, and hydrodynamical contemporaneous structures. The sampling pattern was designed by P. Pistek (*see* chart *fig.* 1) according to a previous hypothesis about the presence of Intermediate Water veins in the Algerian basin. Our transects for visual census were imperatively fixed by this pattern, and hence correspond neither to any stratified sampling (because it includes no previous hypotheses concerning megafauna), nor regular, nor random sampling. Such an approach did not allow any orthodox statistical inference for stock assessment - but stock assessment was not our purpose. Marchal *et al.* (1990) and Macauley *et al.* (1990) used also an acoustical assessment compared with the patterns of physical oceanography.

Surveys were continuously performed from May 23 to June 12 1986, in the Alboran and the Algerian basins. Target species were surface visible organisms, including cetacea, sharks, tuna or other big fishes, turtles and birds. Observers were on watch twelve hours a day during the entire cruise.

The observations were possible up to one nautical mile avay from each side of the track for the largest organisms, and half a nautical mile for the isolated or paired dolphins; important schools of dolphins were visible up to one mile.

The presence of underlying resources is detected acoustically by a continuous synchronized registration of echo-soundings (Holliday *et al.*, 1990; Marchal, 1990; Masson, 1990). The echo-sounder used here was an "EDO Fish Finder" unifrequential of 12 kHz. The power output and the amplification remained set at the same level throughout the most part of the cruise, as shown in *figures* 3, 5, 6. The speed of the ship "in route" remained 9 knots. The paper band rate is indicated as the horizontal scale (time scale) of the record, as in *figures* 3 to 6. In *figure* 4, the rate of the paper band is two times faster than in the other figures, according to the high density of the detection in this area, the ship’s speed being unchanged; the vertical scale is also modified in that *figure* 4.

Acoustic detection was registered on a 22 m long paper band, on which 89 one-hour sequences have been sampled, corresponding to the 87 oceanograhic casts and two more samples between casts 59 and 60 (*fig.* 1). Target organisms, which can be detected at 12 kHz, are large individuals such as sharks, dolphins and large whales, squids up to 0.75 m long, or dense aggregations of micronektonic or zooplanktonic organisms. Phytoplankton cannot be detected. The census was obviously interrupted by night (although echosounding and hydrological data remained available) and was also interrupted by bad weather conditions.

Dynamics of Mediterranean circulation was contemporaneously studied by remote sensing imagery coming from the Remote Sensing and Prevision Laboratory of NORDA in Bay Saint Louis, USA. During the cruise, we had at our disposal some Nimbus CZCS images from May 1986 and infrared NOAA-9 photographs from 3, 4, 5, 9 and 10 June 1986; simultaneous field data have been reported on these figures (*fig.* 16).

Data processing

A stastistical analysis of coincidences between surface megafauna and the main characteristics of the echo sounding profile of the water layer 0-1 000 m was performed. Aiming at a statistical analysis, the oceanograhic transects observed by day (with a constant ship speed) were discretized into one-hour time intervals. Thus 914 nautical miles were surveyed for 178 hours. Each time interval contains one hydrological cast, or is intermediate between two casts. These are chosen as "sampling units" and include both visual census of surface megafauna, and echo registration. The echo profile did not vary much within a one-hour track.

45 samples units, out of 178, contained megafauna, namely 19 with cetacea only, 15 with megafauna other than cetacea, and 11 with both. 452 individuals pertaining to 7 species of cetacea were observed;

other megafauna was considered globally for the statistical treatment. Moreover, 44 more units without any megafauna were randomly chosen as controls.

Echos in each sampling unit were described in a set of water layers according to a conventional semi-quantitative scheme, and noted as follows: Echos X1 and X2 are Surface Scattering Layers (or SSL) at respectively 0-50 m and 50-100 m depth; X3 to X6 are Deep Scattering Layers (or DSL) at 100-200 m, 200-300 m, 300-450 m, and deeper than 450 m. Moreover, spots interpreted as fish schools have been noted X7 to X10 at 0-75 m, 75-200 m, 200-500 m and deeper than 500 m. Analogous methods had been used by Piatt *et al.* (1989) in Newfoundland.

A semi-quantitative index of echo density for SSL and DSL was: "0" is absence of echos, "1" is sparse and weak echos, "2" is continuous and more dense, "3" is concentrated, "4" is a very noticeable concentration. For discrete schools, "0" is absent, "1" is scarce, "2" is fairly abundant, "3" is very abundant. Such appreciations of echos were made always by the same scientist, according to predetermined figures, and gave an approximate but *reproductive* scaling for presumed biomass abundance along the same cruise, allowing a statistical comparison with the megafauna sightings.

Then, ten index values (2 SSL, 4 DSL, and 4 water layers for discrete schools, each index being between 0 and 4), have been gathered for each one-hour track, displaying an echo sounding profile of each sampling unit. Finally, summing these 10 index values gives a *global index B* for underlying biomass.

Three cross-checked numerical analyses have been used here, (i) *Multiple Factorial Correspondence Analysis* (which is a Factorial Correspondence Analysis applied to tables of "0 or 1" values: Volle, 1993; Flos *et al.*, 1987; Escoffier and Pagès, 1988), (ii) *Cluster Analysis* using Gower's similarity index (Gower, 1971, 1987; Legendre and Legendre, 1985), (iii) *Multiregression.*

Factorial and Cluster Analyses resulted in a classification of the sample units according to the main characteristics of their echo profiles. As a second step, the presence or absence of all whale species have been compared to that classification, giving the main figures of echos in the underlying water masses when cetacea are present at the surface. Finally a multiregression gives an approximate prediction for the surface megafauna abundance.

RESULTS

Sightings results

Table 1 summarizes 97 observations of megafauna: whales (65% of the total observations), sharks (2%), turtles (2%), birds (16.5%), squids (9%) and fishes (only large surfacing schools) (5%). Sighted birds were 10 schools of 50 or 60 *Larus argentatus*; 2 groups of 50 to 100 oceanids *(Hydrobates pelagicus)*; 2 schools of *Puffinus puffinus* and *Calonectris diomedea*; 4 sightings of migrant small passeriforms. Isolated individuals were not counted. Sighted fishes at the sea surface were 5 schools of tunas, 8 groups of undetermined species, 6 groups of few individuals of the planktophagous species *Mola mola*, 10 small groups of *Dactyloptera* sp. and one specimen of the abyssal species *Trachypterus* sp.

Table 2 gives the relative proportions of cetacea respectively in the Gibraltar, Alboran and Algerian areas, *i.e.* 91, 82 and 50% of the sightings. The number of sighted individuals are reported to unit of sighting effort (*i.e.* one hour) in the three areas mentioned, respectively 85/14=6.07; 195/205=0.95; 481/914=0.52 individual.hour^{-1}. Such averages must be weighted by the estimate of biomass by way of individual mean weight of each whale species, using growing curves of species found in the literature (*see* Seargent, 1969; Viale, 1985); results for the three areas are then respectively 0.69, 21.00 and 11.22 tons.hour^{-1}. Gibraltar whales were overall small species such as the delphinid *Tursiops truncatus*; in contrast, Algerian whales were large species. When related to the linear

Table 1. – Visible surface megafauna sighted during the NOAA cruise 706 (May 23 to June 12, 1986) in the southwestern Mediterranean. Three areas are principally compared: (i) area around the Gibraltar Strait, (ii) the Alboran Sea, (iii) the Algerian basin.

Letters for megafauna: *see figure* 2; moreover Ox are marine birds living in herds, Po are large schools of fishes sighted at the surface.

H: time (hours) passed watching along the line transects. M: number of nautical miles covered surveying by daylight. By species and area, S is the number of groups of aminals observed, I is the number of individuals sighted (N indicates too large a number impossible to count).

Area	H	M		T	S	D	B	P	G	g	d	To	R	Ox	Sq	Po	Total
Gibraltar:	14	126	S	9	0	0	0	0	1	1	0	0	0	0	0	1	12
			I	80	0	0	0	0	3	2	0	0	0	0	0	N	
Alboran Sea:	20	205	S	4	1	1	1	0	9	4	4	1	0	2	0	2	29
			I	67	5	5	4	0	75	13	26	1	0	90	0	N	
Algerian Basin:	144	583	S	3	1	7	4	3	3	5	2	1	2	14	9	2	56
			I	19	30	103	11	7	16	12	3	1	2	500	N	N	
Total cruise:	178	914	S	16	2	8	5	3	13	10	6	2	2	16	9	5	97
			I	166	35	108	15	7	94	27	29	2	2	N	N	N	

Table 2. – Percentages of whales (W) and other megafauna (O) among the surface sightings in the three areas investigated. Estimated weight (E in tons) of whales per hour of track.

H is watching time in (hours). M is number of miles watched. N is total number of sightings. I is total number of individuals sighted. U is mean number of individual cetacea recorded by sampling unit (= 1 hour watching).

Area	H	M	N	I	W	O	E	U	E/N	E/M
Gibraltar Strait:	14	126	12	55	92 %	8 %	9.7	6.07	0.69	0.77
Alboran Basin:	20	205	29	286	82 %	18 %	423.5	9.75	21.18	2.07
Algerian Basin:	144	583	56	701	50 %	50 %	1 616	2.09	11.22	2.77

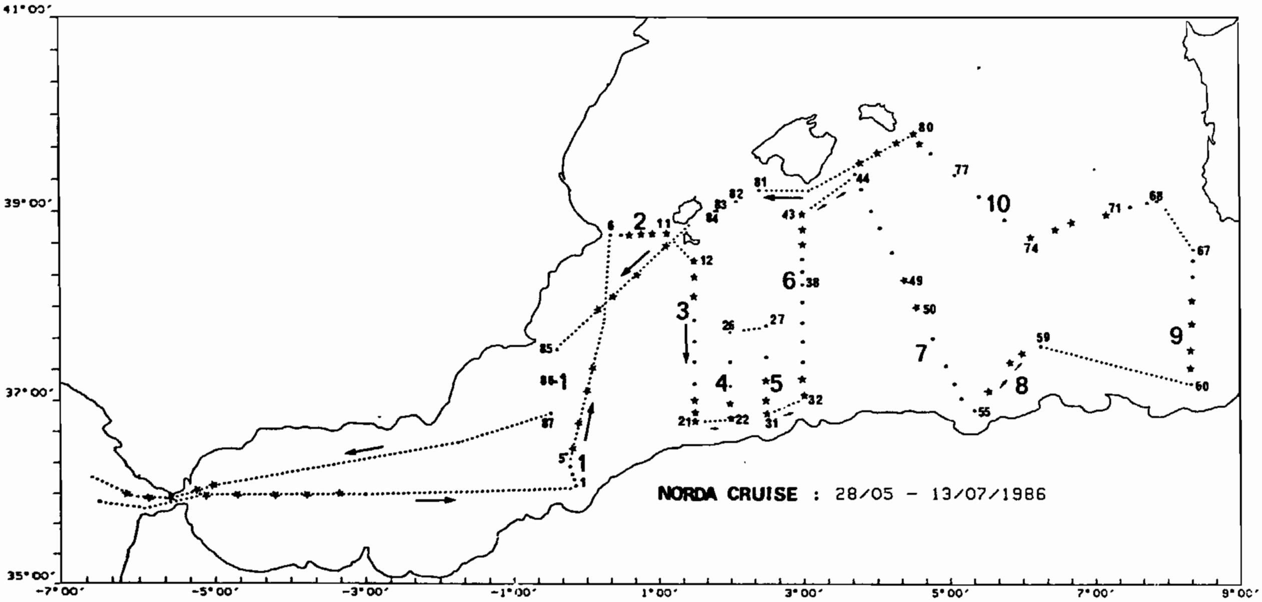

Figure 1. – Trajectory of the campaign of the US NS "Lynch" in the Alboran Sea and the Algerian basin (NORDA 706 cruise), May-June 1986. Large numbers 1 to 10 are hydrographic transects. Small numbers 1 to 87 are oceanographic casts (CTD measurements). Dots are CTD by day. Stars are CTD by night. Dotted lines are tracks without CTD. Arrows indicate the sense of the trajectory.

mile of visual census, the estimated biomass of sighted whales appears greater in the Algerian basin than in the Alboran sea. Sightings of cetacea and other megafauna are statistically independent as shown by the following contingency table, giving a non-significant $\chi_1^2 = 1.22$.

	Stations with other megafauna present	absent	total
Stations with cetacea present	11	19	30
absent	15	44	59
. total	26	63	89

Figure 1 shows the ship's track, and all the sightings are reported on *figure* 2. The spatial distribution of megafauna appears strongly heterogeneous, as follows:

(i) *Empty areas.* Very few sightings of megafauna were reported in sections 3, 4, 5, 6 *pro parte* (casts 32 to 35) and 7 (casts 52 to 55). Several squids were visible by night, attracted by the lighthouse of the ship during casts 31 and 32. One turtle (*Caretta caretta*) was sighted at cast 36.

(ii) *Areas with abundant surface fauna*: casts 38 to 39, 49, 77, 86 to 87. Four species of cetacea, out of seven living in the Mediterranean, are present, a good number being observed feeding in casts 86 and 87 : 7 fin whales *Balaenoptera physalus*, 14 pilot whales *Globicephala melaena*, 13 Risso dolphins *Grampus griseus*, and 20 common dolphins *Delphinus delphis.*

(iii) *Coastal areas* are intermediate, having a quantitatively and qualitatively different megafauna. Four dolphin species, *Tursiops truncatus, Delphinus delphis, Stenella coeruleoalba* and *Grampus griseus* were observed in the Gibraltar Strait, and between the islands of Mallorca and Ibiza (casts 81 to 83). The Algerian coastal area at stations 1 to 3 shows both submarine biomass and dolphins such as *Tursiops*

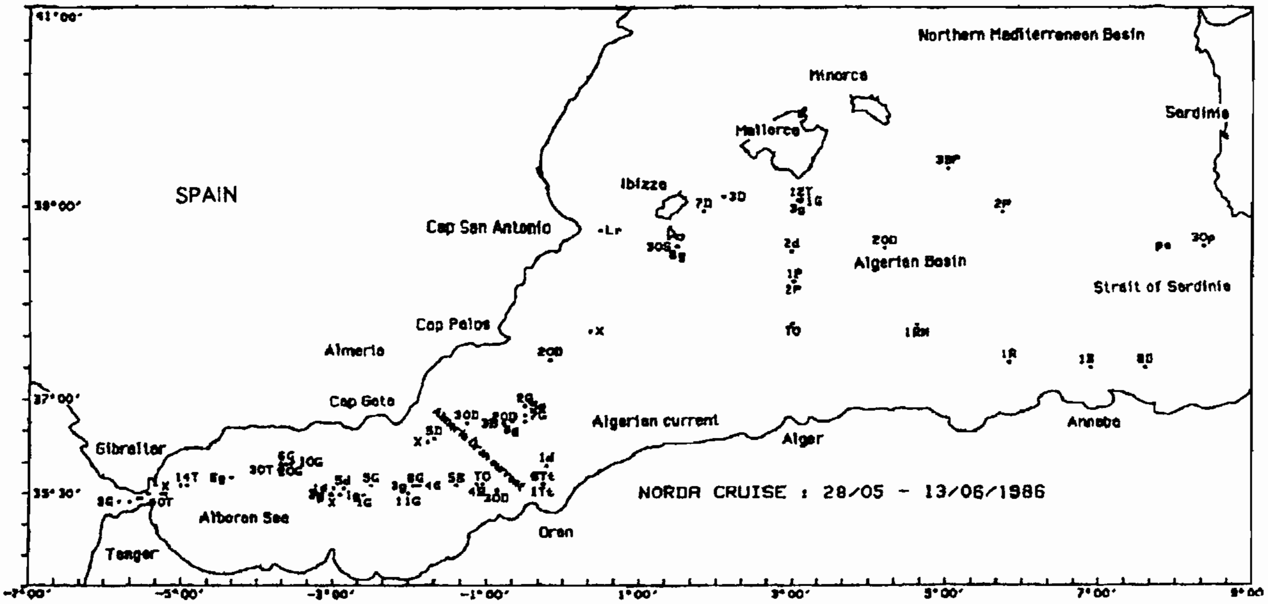

Figure 2. – Location of the observations of surveyed species (visible superficial megafauna).
B are fin whales *Balaenoptera physalus*. **P** are sperm whales *Physeter macrocephalus*. **G** are pilot whales *Globicephala melaena*. **g** are Risso dolphins *Grampus griseus*. **D** are common dolphins *Delphinus delphis*. **S** are striped dolphins *Stenella coeruleoalba*. **T** are grey dolphins *Tursiops truncatus*. **d** are unidentified dolphins. **IA** and **Ir** are marine birds in schools. **p** are puffins. **R** and **Rm** are sharks. **Sq** are squids. **To** are turtles *Caretta caretta*. Numbers before letters are numbers of individuals sighted.
W are observations of fin whales made by D. Wiesenburg in May 1986. **X** are changes of route or transitions night/day.

truncatus; they were observed in spite of a stormy weather and high seas during our passage.

Echo-sounding results

Echo sounded biomass appears as really heterogeneous in localization as well as density and diversity of the registered signs (*fig.* 3 to 6). Punctual echos are present on all the figures. Vertical dashes (*fig.* 3 and 4) co-occur with presence of dolphins or sperm whales at the surface: they can be seen below 1,000 m depth, and at that depth, they are presumed to be due to squids. Schools of fishes or swarms of krill such as euphausids appears as "V-shaped" signals (*fig.* 4 to 6). Effectively, the co-occurrence of some registered echos with some types of cetacea leads to a presumption about the submarine biomass content that determined these echos. Dense Scattering Layers (below: DSL) are generated by a large number of organisms living in a group, located at greater or lesser depth in relation to the time of the day (Jacques and Tréguer, 1986; Piatt *et al.*, 1989; Marchal, 1990; Holliday *et al.*, 1990; Macaulay *et al.*, 1990). Particularly highly concentrated DSL (*see fig.* 4 and 6) were found in ten sequences during the entire cruise: all were concomitant with cetaceans. Four of these cases are represented in *fig.* 3 to 6. On *fig.* 4, the echo of one of the three fin whales simultaneously watched can be seen exactly at the same level as the highly concentrated biomass. Such co-occurrences argue for these echos being due to euphausiacean swarms, as the fish capelin *(Mallotus villosus)* does not exist in the Mediterranean. Three species of fishes are caught in important swarms in the Mediterranean, namely *Trisopterus minutus capelanus* (Gadidae), *Centracanthus cirrus* (Maenidae) and *Capros aper* (Zeidae), but they were not identified in the few stomach contents analyzed here. Up to now, the stomach contents from Mediterranean fin-whale carcases showed monospecific swarms of *Meganyctiphanes norvegica*, and little pieces of muscle of unidentified isolated small fishes. Another argument comes from Marchal (1990), who described pelagic aggregative structures by means of acoustics, with 15 and 50 kHz. Wiebe *et al.* (1990) reported empirical studies of zooplankton and nekton with a 120 and 420 kHz acoustical system, and showed that the back scattering is modified by the form, the length and the weight of zooplanktonic or micronektonic individuals. Thus our echo-sounding results from 12 kHz sounder allow only the detection of concentrated swarms; the echo from a 20 m long whale appears in *fig.* 4 as an horizontal dash remaining during 1.6 minutes.

Factorial Analysis of Correspondence

Comparison between surface megafauna and echosounding data is analyzed by Factorial Analysis of Correspondence and Cluster Analysis. These statistical analyses will indicate significant coincidences between cetacea sightings and the more concentrated echos,

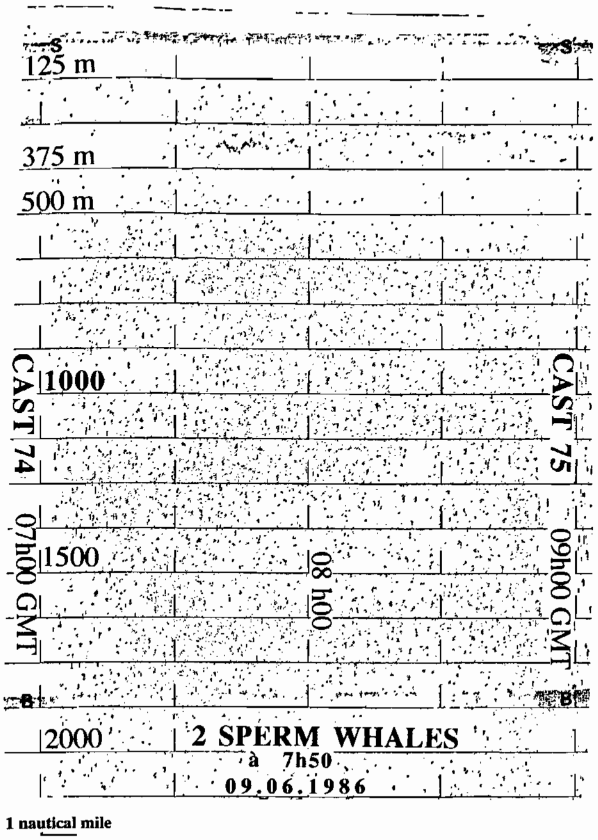

Figure 3. – Echo sounded biomass from 0 to 1 000 m between casts 74 and 75, co-occurring with the observations of two sperm whales at 07 h 50 GMT, on 9th June. Vertical axis is depth from 0 to 1 000 m (between two horizontal lines are 65 m). Horizontal axis is time (between two vertical dashed lines is half an hour).

Four dense layers can be considered at the levels 150, 300, 560 and 820 m. Note the co-occurrence of sperm whales with concentrated biomass at 150 m. BB′ is the second echo of bottom. SS′ is an echo due to the disturbance from waves and ship motor.

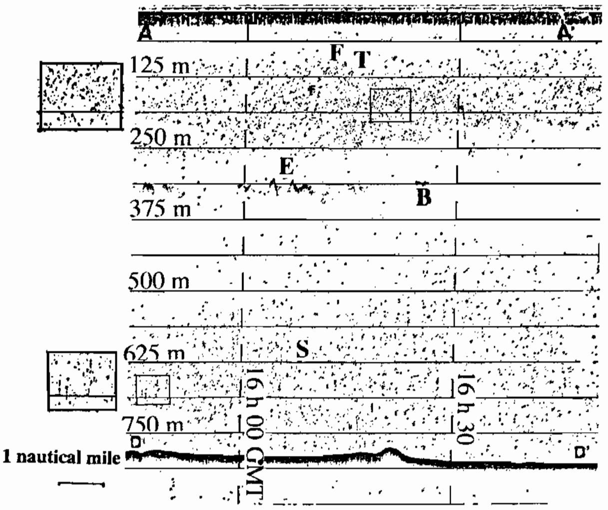

Figure 4. – Echo sounding sequence at cast 77, on 9th June. Three fin whales were observed between 14 h 10 to 17 h, one of them (**B**) being echo sounded under the ship. Different diffusive layers can be discerned, at 0-30 m (artefactual); 30-65 m (numerous spots such as **F** and **T**); 100-250 m (an important layer whose details are given in two enlarged windows, showing point-signals and "V-shaped" signals); 300-330 m (the most concentrated layer); and below 500 m (abundant biomass signals). This figure shows the twilight migration of pelagic biomass, beginning at 16 h, separating that biomass into two diffusive layers, one at the surface (SSL) and the other below 375 m (DSL).

E are assumed to be signals from euphausids (krill), **F** to be from fish schools, tiny vertical segments **S** to be from squids, **T** to be from schools of gathered organisms.

whereas megafauna other than cetacea give no significant relation.

The analyses were carried out from a table derived from the raw data table as follows. In order to eliminate too rare events, some index values have been grouped, namely: for scattering layers at 0-50 m, "2" and "3" have been clumped together; at 100-200 m, 200-300 m and 300-450 m, "3" and "4"; deeper than 450 m, "1" and "2" as well as "3" and "4"; for discrete schools at 75-200 and 200-500 m, "2" and "3".

Each event (*i.e.* a given index in a given layer) is represented by the value 1 "yes") or 0 ("no"), resulting in a matrix (not represented here) containing 89 lines (sample units: 89 one hour tracks) and 34 columns (0 or 1). *Multiple Factorial Analysis of Correspondence* was then performed.

26.75 % of the total inertia are concentrated in the first two factorial axes, and more than 50 % in the first five - that is, a fairly good result for Multiple Correspondence Analysis (Volle, 1993). Examination of the contributions of variates and samples to the inertia of both axes (*table* 3) clearly shows that the first axis represents the general richness of presumed underlying biomass determining the echo registered. "0" DSL values for many water layers, as well as "0" discrete schools, are well represented at one extremity of the first axis (38 % of its inertia). High densities of deep echos are well represented at one extremity of the first axis (38 % of its inertia). High densities of deep echos are well represented at the opposite extremity (56.7 % of inertia are due to 17 stations with an echo index "2" to "4" for scattering layers at all depths and index "2" or "3" for schools below 75 m).

Cetacea have been plotted on the corresponding station points. They were present at 16 out of 17 stations located in the "rich" extremity of axis 1, representing 57.7 % of the axis intertia. Out of 21 stations located at the "poor" extremity, cetacea (dolphins) were only at one. The correlation between presence of cetacea and dense underlying echo sounded biomass is thus well established.

The biological significance of axis 2 is less obvious. At one extremity, there are many "0" or "1" index values for several classes of echos, namely: no echo in SSL; scattered biomass in DST at all depths; schools absent or scarce between 0 and 200 m. At the other extremity of the axis there are some large values at great depth ("3" or "4" for DSL below 300 m;

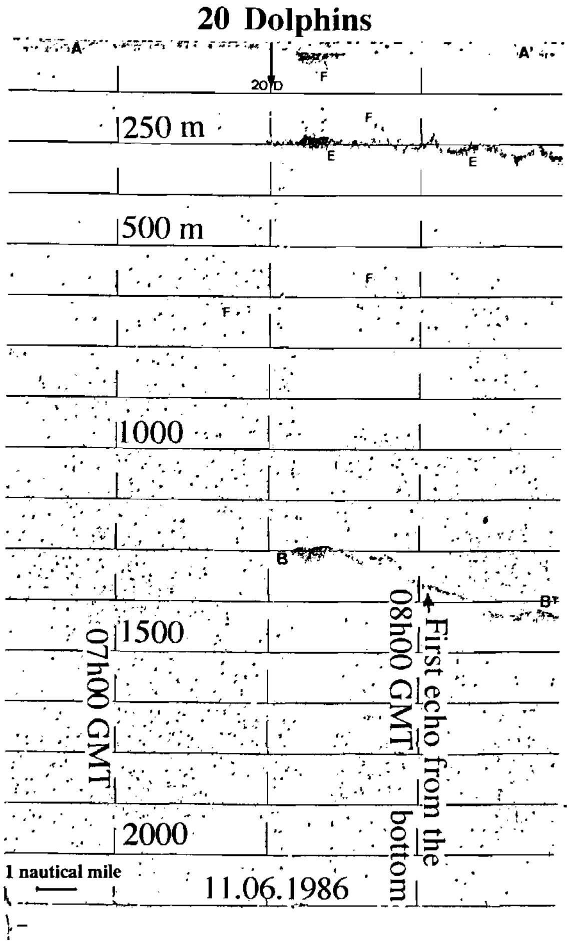

Figure 5. – Echo sounding sequence just before cast 86, on 4th June, from 07 h 35 to 07 h 45 GMT, ship in route.
20 dolphins were observed at 07 h 30, exactly at the beginnig of the most concentrated layer at 125 m depth. At 0-60 m, a few points are assumed to be fish schools. A 65-125 m, layer of points-echos and stick-echos. At 125-140 m, concentration of organisms giving "V-shaped" echos. At 130-200 m, low density of echos, with few isolated "V" echos. At 250-1 000 m, echos of diffuse biomass. Letters as in *figure* 4.

"3" for schools below 500 m). Cetacea are almost equally distributed on both sides of the second axis, as different species: *Balaenoptera physalus* B are only on the axis extremity displaying many "1" echos, and teutophagous species *Physeter macrocephalus* P, *Grampus griseus* g, *Globicephala melaena* G principally at the other extremity, simultaneous with a very dense scattering layer and very abundant schools in the deep layers. So the presence of a deep pelagic echo-sounded biomass appears to be a restrictive condition for high cephalopod biomass, foraged by some specialized cetacea species. On the other hand, the predominance of "0" and "1" echos in more superficial water layers shows that poor superficial biomass is negatively correlated with dense deep biomass: in other words dense deep biomass is excluded from areas containing too low biomass at the surface.

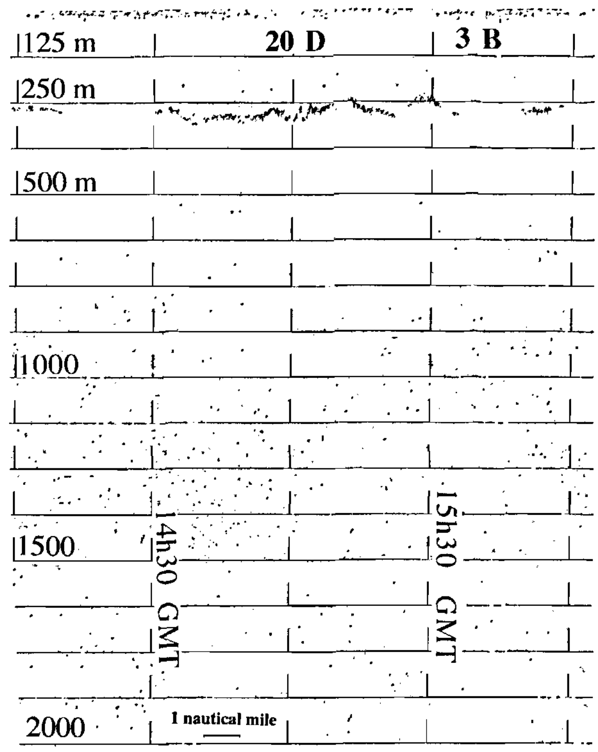

Figure 6. – Echo sounding sequence at cast 87, on 11th June, from 14 h 00 to 16 h 00 GMT.
Occurrence of 3 fin whales (**3B**) and 20 common dolphins, (**20D**) respectively sighted at 14 h 00 and 15 h 50. At 0-65 m, isolated echos. At 60-250 m, points and vertical sticks. At 150 m, is a concentrated layer made of "V" signals.

Variable-points (*i.e.* the various values of the echo indices in the various water layers) are plotted in 1-2 factorial plane in *fig.* 7. Single lines represent the SSL (2 layers) and DSL (4 layers). Double lines represent the discrete schools (4 layers). The data show two different patterns. The one (single or double continuous lines) displays a "horse shoe" or Gutman effect (Volle, 1993; Gower, 1987), suggesting three sets of data: "0" echos are located on the left side of axis 1; "1" are at the upper part of axis 2; big echo values are at the right-hand side of axis 1, associated with low coordinates on axis 2. Another pattern (single or double dashed lines) is a diagonal distribution for SSL and for the discrete schools of the two more superficial layers. Nevertheless, "2" to "4" values for 100-200 m, and "3-4" values for 200-300 m, have been shifted from the first to the second pattern.

The first pattern clearly corresponds to an increasing biomass along both axes 1 and 2. According to the contribution to inertia of axes, the second pattern suggests a negative correlation between deep dense biomass and the value "1" for the DSL, and schools at lower depths, as seen above.

Table 3. – Main variables and main stations contributing to the inertia of axes 1 and 2 (% are percentages of inertia of axes). Presence of cetacea species at the various stations are indicated (**B** is *Balaenoptera physalus*, **P** is *Physeter macrocephalus*, **G** is *Globicephala melaena*, **g** is *Grampus griseus*, **d** are dolphins *Delphinus delphis*, *Stenella coeruleoalba* or *Tursiops truncatus*). DSL is Deep Scattering Layer. SSL is Surface Scattering Layer.

Axis 1 (16.57 % of the total inertia). 87.5 % if the inertia of the axis is explained by the following variables and 87.9 % by the following stations.

Coordinates (+)		**Coordinates (–)**	
%	Variables	%	Variables
3.6	SSL 50-100 m = 2		
4.6	DSL100-200 m = 3 or 4	5.4	DSL100-200 m = 0
4.0	DSL200-300 m = 2	7.4	DSL200-300 m = 0
8.2	DSL300-450 m = 2	5.4	DSL300-450 m = 0
2.0	DSL 300-450 m = 3 or 4		
2.1	DSL > 450 m = 1 or 2	5.2	DSL > 450 m = 0
8.4	DSL 300-450 m = 3 or 4		
2.6	schools 75-200 m = 2 or 3	3.3	schools 75-200 m = 0
9.0	schools 200-500 m = 2 or 3	6.3	schools 200-500 m = 0
2.1	schools > 500 m = 2	5.0	schools > 500 m = 0
9.1	schools > 500 m = 3		
Total = 49.5 %		Total = 38.0 %	

%	Stations	Cetacea	%	Stations	Cetacea
6.0	20	**P**	2.3	68	
5.6	35	**g**	2.0	15	
5.6	36	**G**	1.9	4	
5.6	38	**g**	1.9	9	
5.6	39	**G**	1.8	5	
5.1	41	**B**	1.8	67	
4.0	42	**d**	1.8	93	
3.2	43	**d**	1.6	24	
2.3	21	**B**	1.5	1	
2.1	31	**d**	1.5	58	
2.1	32	**g**	1.4	69	
2.1	55	**g**	1.4	62	
2.0	18	**B**	1.3	60	
1.7	11	**d**	1.3	14	
1.4	34	**d**	1.2	74	
1.3	49		1.2	2	
1.0	47	**P**	1.2	58	
			1.1	10	
Total = 56.7 %			1.0	56	**d**
			1.0	57	
			1.0	82	
			Total = 31.2 %		

Table 3. – (*continued*).

Axis 2 (10.00 % of the total inertia). 83.6 % if the inertia of the axis is explained by the following variables and 83.5 % by the following stations.

Coordinates (+)		**Coordinates (–)**	
%	Variables	%	Variables
2.6	SSL 0-50 m = 0		
1.9	SSL50-100 m = 0		
7.8	DSL100-200 m = 1	1.9	DSL 100-200 m = 2
11.8	DSL200-300 m = 1		
10.9	DSL 300-450 m = 1	1.9	DSL 300-450 m = 3 or 4
11.2	DSL > 450 m = 1	3.5	DSL > 450 m = 0
		2.1	DSL > 450 m = 3 or 4
6.8	schools 0-75 m = 0	3.9	schools 0-75 m = 2
2.1	schools 75-200 m = 0		
2.2	schools 75-200 m = 1	4.8	schools 75-200 m = 2 or 3
		2.1	schools 200-500 m = 0
6.5	schools > 500 m = 2	5.3	schools > 500 m = 3
Total = 64.0 %		Total = 19.6 %	

%	Stations	Cetacea	%	Stations	Cetacea
8.5	16		4.8	20	**P**
7.8	34	**d**	2.0	6	
4.5	50		1.9	55	**g**
4.2	87		1.9	36	**G**
3.5	19	**P**	1.9	38	**g**
3.2	54		1.9	39	**G**
2.9	18	**B**	1.9	73	
2.5	51		1.2	61	
2.5	84		1.2	66	
2.5	49		1.2	75	
2.4	48	**P**	1.1	58	
2.3	53		1.1	74	
2.2	86		1.0	23	**d**
2.1	72				
1.9	55	**g**	Total = 23.1 %		
1.6	91				
1.3	95	**B**			
1.2	52				
1.2	88				
1.1	45	**B**			
1.0	83				
Total = 60.4 %					

According to axis 2, "0" values are neither negatively nor positively correlated with deep dense biomass because their coordinates on that axis are near 0. Both kinds of data are negatively correlated between them only following the axis 1. In the Discussion below, an oceanographic interpretation of the negative correlation between deep dense biomass and low echo values near the surface will be proposed.

Megafauna presence or absence has also been plotted on the 1-2 factorial plane, as supplementary variables in the analysis. Absence of cetacea and other megafauna (small stars), and presence of megafauna other than cetacea (big star with letter M) are clustered near the barycentre, signifying that these variables are independent of axes 1 and 2. Presence of the various cetacean species (big stars with letters) are scattered on the right part of the graph, emphasizing their correlation with high echos as a whole. Large whales (B and P) are on the upper part of axis 2, and among the teuthophagous species, the series "P, g, G" seem to follow a gradient of requirements for deep

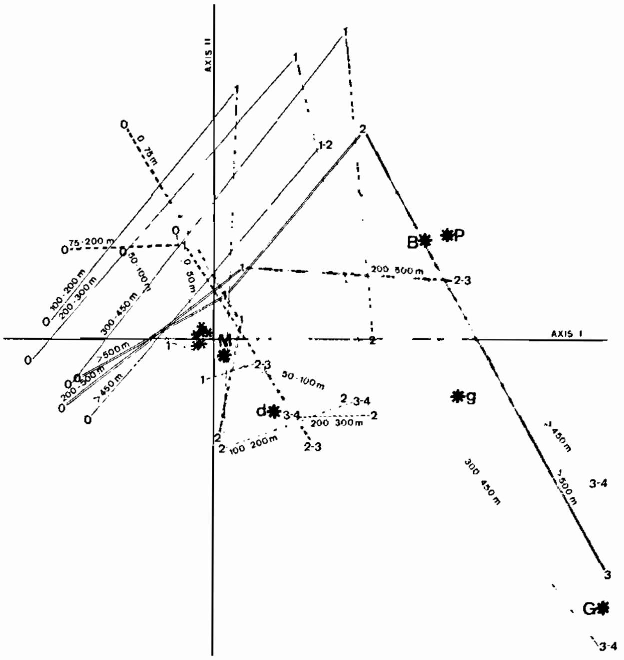

Figure 7. – Projections of the variable-points (descriptors of echos) on the 1-2 factorial plane of Multiple Factorial Correspondence Analysis. Lines correspond to various water layers examined. They display two patterns (respectively continuous and dashed lines). Simple (continuous or dashed) lines are SSL at 0-50 and 50-100 m and DSL at 100-200, 200-300, 300-450 and >450 m. Double (continuous or dashed) lines are discrete echos at 0-75, 75-200, 200-500 and >500 m. Numbers are the codified "echo-values". For SSL and DSL was: "0" is absence of echos, "1" is sparse and weak, "2" is continuous and more dense, "3" is concentrated, "4" is a very noticeable concentration. For discrete schools, "0" is absent, "1" is scarce, "2" is fairly abundant, "3" is very abundant.
Big stars with letters indicate the presence of megafauna (supplementary variables of the Factorial Analysis). **B** are fin whales *Balaenoptera physalus*. **P** are sperm whales *Physeter macrocephalus*. **G** are pilot whales *Globicephala melaena*. **g** are Risso dolphins *Grampus griseus*. **d** are small dolphins. **M** are surface megafauna other than cetacea.
Small stars are absence of the same.

dense biomass. Finally small dolphins (d) are near the origin, hence poorly correlated with both axes.

Stations with cetacea have been plotted on 1-2 plane in *fig.* 8. The "cetacea-variates" (supplementary variables) are plotted again (big stars, letters as above) after a barycentric transformation (*i.e.* multiplying each coordinate by the square root of the corresponding eigenvalue, so that each "cetacea-variable" becomes the barycentre of the stations where the species has been sighted). It can be seen that, with the exception of the small dolphins, stations with cetacea are located in the right half of the factorial plane. Stations with dolphins are scattered along axis 1, and mainly localized facing a small segment of the lower part of axis 2. They are hence largely independent of the echo density, and surprisingly seem to avoid both diffuse ("1") and the strongest ("3" or "4") echos of the deep layers.

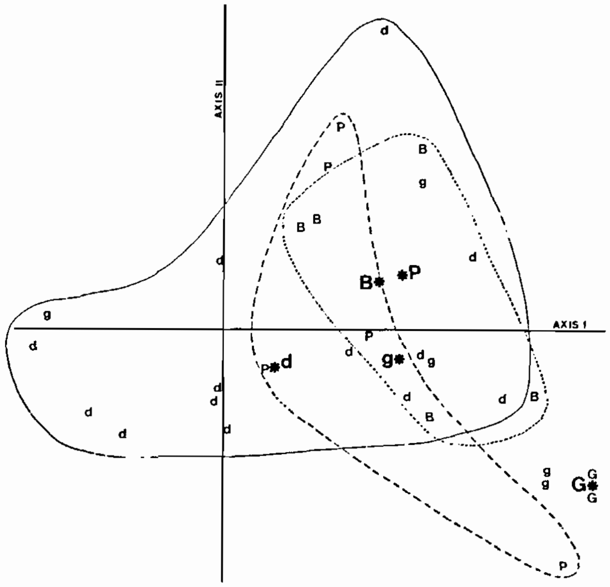

Figure 8. – Projections of the station-points on the 1-2 factorial plane of Multiple Factorial Correspondence Analysis, indicating only the stations with megafauna (abbreviations as in *figure* 7). Stars with bigger letters are barycentres of the corresponding species. Contours are approximately outlining the distributions of small dolphins (continuous), *Balaenoptera* (dotted) and *Physeter* (dashed).

In *fig.* 9 the distributions of stations showing surface megafauna other than cetacea (stars), and stations without any megafauna sighted (circles), are visible. The first ones are scattered in the whole plane,

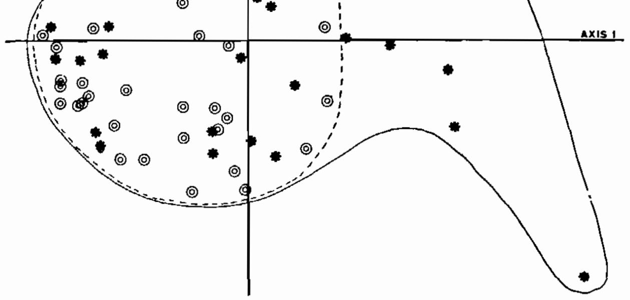

Figure 9. – Projections of the station-points on the 1-2 factorial plane of Multiple Factorial Correspondence Analysis, indicating only the stations with no megafauna (circles) and with megafauna other than cetacea (stars). Contours are approximately outlining the distribution of both.

denoting a total absence of correlation with either axis. The second ones are distributed on the left part of the plane, then are clearly linked with the weakest echos in all water layers, and were completely independent of axis 2.

As a conclusion:

(i) Complete absence of megafauna only occurs in sampling units where the echos registered by our device were zero or very weak on the whole water column;

(ii) When echos are registered, cetacea co-occur with dense subjacent agreggations, whereas megafauna other than cetacea are distributed without any link with the echo vertical structure;

(iii) Distribution of large or medium-size cetacea depends on the underlying pelagic biomass in a way that clearly differs from that of dolphins, probably because the food of the latter is localized in the surface water, in contrast with the deep foraging of krill and squid feeders;

(iv) Dolphins avoid certain kinds of echos, the reason for which remains unknown;

(v) Following the above remarks, the clear difference between cetaceans and other large organisms argues for the proper ability of cetacea to detect submarine biomass, as we do with our device, *acoustically*, and probably with a frequency close to 12 kHz.

Cluster analysis

The clustering results in a dendrogram represented in *fig.* 10. At a 0.2 similarity level, five groups emerge, called "A" to "E". At a higher level, "A1", "A2", "E1" and "E2" are recognized. Presence of cetacea and other megafauna (letters as above) are plotted at the bottom of the dendrogram, facing the stations or sample units. For clarity of the graph, stations are numbered 1 to 89 following their ordering by the dendrogram, and the corresponding oceanographic casts are given in *table* 4. The number of sightings of cetacea and other megafauna (more than one individual are frequently censed as one sighting) in the seven main clusters are:

Clusters	A1	A2	B	C	D	E1	E2	Total
Number of sample units	6	11	28	8	16	6	14	89
Number of cetacea sightings	0	2	3	4	6	6	9	30
N° of other megafauna sight.	1	4	6	3	8	0	4	26

The mean numbers of cetacea sightings per station are significantly different among the 7 clusters of stations ($\chi^2_6=29.58$, significant at 0.1 level). Those of other megafauna are not significantly different ($\chi^2_6=7.48$).

The "mean echo profile" in the 7 groups of stations can be calculated by averaging the values of the ten echo indices among each group. Results are given in *fig.* 11, displaying seven typical profiles (the percentages of stations containing cetacea have been indicated, facing each echo profile). It can be seen that, globally, the higher the various echo indices are in the water column, the more frequent the sighting of cetacea.

Table 4. – Correspondence between the oceanographic stations (visible on *figure* 1) and the ordering of stations by the dendrogram of *figure* 10.

Den-drogr. order	Ocea-nogr. stations	Den-drogr. order	Ocea-nogr. stations	Den-drogr. order	Ocea-nogr. stations	Den-drogr. order	Ocea-nogr. stations
1	85F	26	31	51	80B	76	59A
2	42	27	45	52	43	77	36
3	41	28	22	53	54	78	34
4	50	29	12	54	87A	79	59C
5	46	30	9	55	87	80	35
6	47	31	10	56	85E	81	26
7	65	32	6	57	85D	82	32
8	40A	33	7	58	85C	83	27
9	59A	34	57	59	85A	84	37
10	83	35	17	60	63	85	60A
11	67	36	21	61	87E	86	33
12	28	37	20	62	87F	87	87A
13	83A	38	18	63	87B	88	84
14	19	39	56	64	85B	89	89
15	11	40	40	65	87D		
16	39	41	51	66	77A		
17	48	42	2	67	70		
18	66	43	1	68	74		
19	45	44	16	69	74A		
20	52	45	13	70	87C		
21	25	46	14	71	75A		
22	80A	47	15	72	70A		
23	44	48	23	73	61		
24	49	49	53	74	77		
25	38	50	60	75	55		

Finally, a rough abundance index B of the underlying echo sounded biomass was calculated at each station by summing the ten observed indexes. The mean value for a group of stations, say $\overline{B}$ has been compared with the mean number of sightings reported to 100 stations. Results are:

		Number of sightings per 100 stations:	
Cluster	$\overline{B}$	Cetacea	Other megafauna
A1	6.67	0	17
A2	10.27	18	36
B	5.32	11	21
C	11.63	50	38
D	15.88	38	50
E1	21.83	100	0
E2	13.86	64	29

These data result in a positive correlation coefficient (weighted by the number of stations in each group)

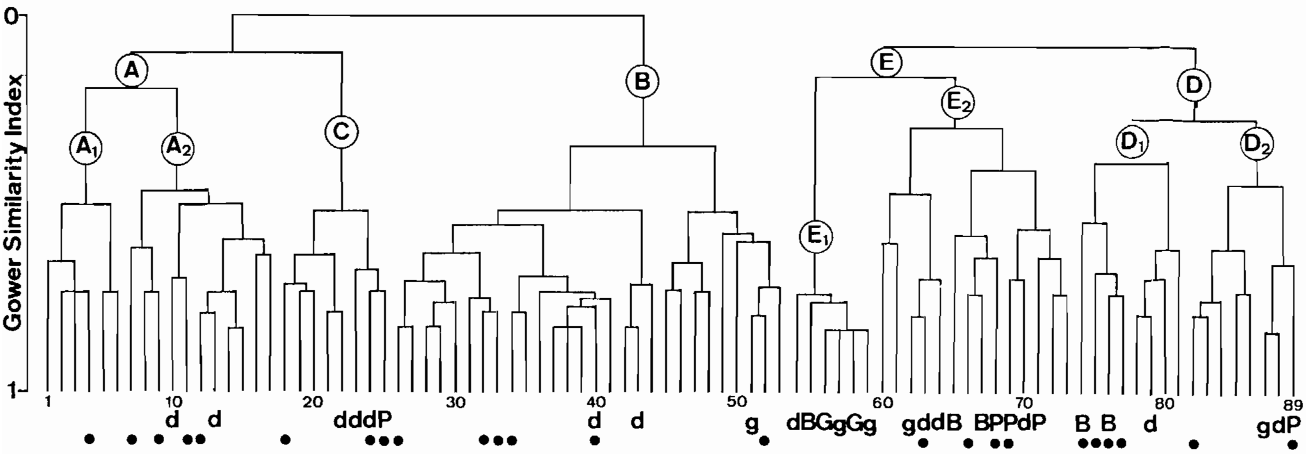

Figure 10. – Clustering the 89 samples (45 with megafauna, and 44 without any megafauna as prooves) following Gower's similarity index Seven groups of stations appear, noted A1, A2, B, C, D, E1, E2. The stations have been numbered from 0 to 89 following the order in the dendrogram. Correspondence with oceanographic stations are given in *table* 4.
Observations of cetacea are indicated beneath the station ranks, showing that clusters differ a lot concerning the associated megafauna (abbreviations as in *figure* 7, spots indicate non-cetacea megafauna).

$r=0.874$ (highly significant) between the mean number of cetacea sighted in 100 stations and the global index for pelagic echo sounded biomass. The regression line, accounting for 76.4 % of the variance of the observed frequency of cetacea is $C\%=4.747\,\overline{B}-17.16$.

Multiregression analysis

A multiregression equation can be calculated for estimating the presence of cetacea (variate is $c=0$ or 1 for absence or presence in a single station), starting from the echo values encoded by variates **X1** to **X10**:

$$c = 0.257\,\mathbf{X5} + 0.158\,\mathbf{X7} + 0.092\,\mathbf{X10} - 0.088\,\mathbf{X8} + 0.063\,\mathbf{X3} - 0.044\,\mathbf{X4} + 0.034\,\mathbf{X2} - 0.014\,\mathbf{X1} + 0.014\,\mathbf{X9} + 0.008\,\mathbf{X6} + 0.067$$

The multiple correlation coefficient $R^2=0.4652$, that is, 46.52 % if the variance of the "cetacean-variate" c (presence or absence, say 1 or 0) is predicted by the ten "echo variables" (0 to 4).

The echos which are predominant for the prediction of presence or absence of cetacea are indicated by the equation: the first five terms account for 95.8 % of the variance of the estimated c, hence 45 % of the observed c. The first variable **X5**, or DSL between 300 and 400 m, is the more predictive one, accounting for 55.3 % of the variance of the estimated c. The second one **X7**, or schools between 0 and 75 m, accounts for 13 %. The following three **X10**, or schools below 500 m, **X3**, or DSL between 100 and 200 m, **X8**, or schools between 75 and 200 m, account for 6 to 9 % - the latter accounting for a negative correlation.

DISCUSSION

Heterogeneous distribution of living resources along our track

Some comments are needed here about the field data sampling, which appears to be inoperative by night. The only megafauna species that can be seen at night are dolphins which come to eat the squids attracted by the vessel's spotlight, and dolphins or other cetaceans detected when diving below the sounder at dusk or dawn, as they did in casts 71, 74 and 77. As it appears obvious in our continuous report of 15 night-and-day echo-sounding, large concentrated swarms do not occur by night, but only by day. Indeed, every day, many individuals join together to undertake a vertical diurnal migration down to deep water layers (Jacques and Tréguer, 1986, and here *fig.* 3 to 6), and come back to the superficial water layers after 15 h GMT.

With their echolocating system, toothed whales are supposed able to detect even tiny organisms in dense aggregations (*see* for example Sergeant, 1969). Baleen whales are thought to have no echolocating system, but to use vocalizations to detect euphausid swarms and they feed on them either when the swarms start diving, or come back to the shallowest layers just before euphausids scatter at the surface by night. Large swarms such as aggregative populations of *Meganyctiphanes norvegica* are currently observed in the Mediterranean.

In the data reported here, the process begins with dusk, at 5.00 h GMT, or appeared at dawn. *Figures* 5 and 6 suggest the presence of migrating concentrations of planktonic and nektonic organisms in the shallowest layer. Simultaneously, visual censuses indicate (*fig.* 4 and 5) active diving of fin and sperm whales. That leads us to the conclusion that very little information is lost due to the unability to watch by night, as far

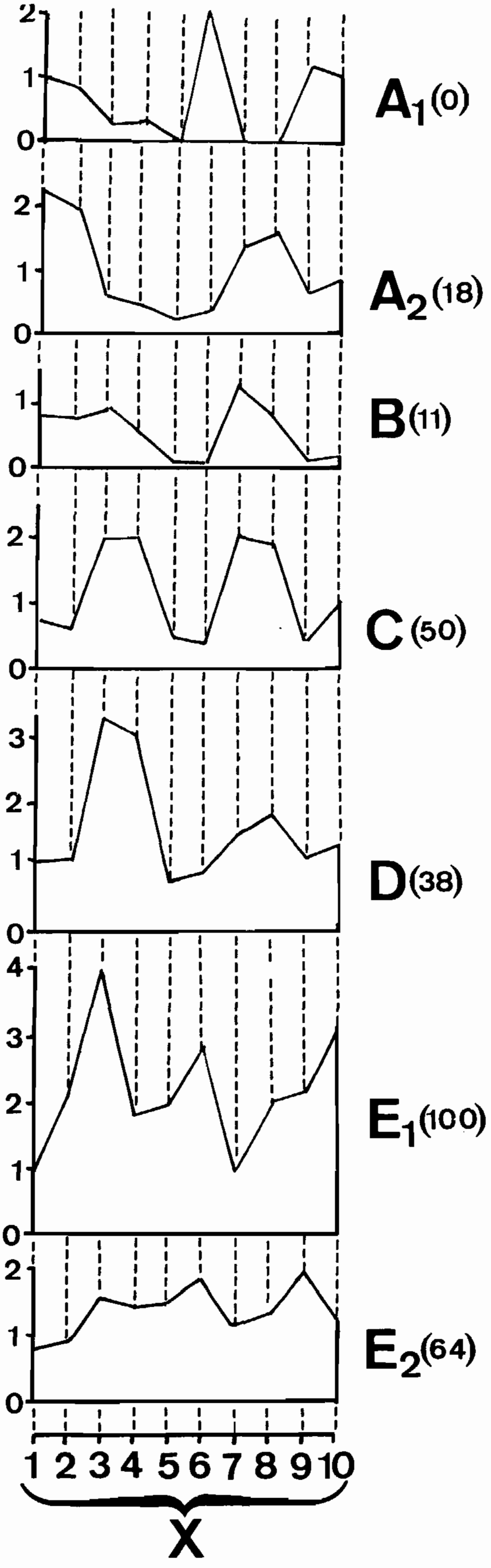

Figure 11. – Mean profiles of echo in the seven clusters of stations evidenced in *figure* 10, and number of cetacea sightings per 100 stations (in brackets).
Ordinates (scales at left) are the mean value, for the cluster, of the echo indexes **X1** to **X10**.
Abscisses are values of the ten variables. **X1** is echo index for the Surface Scattering Layer (SSL) at 0-50 m; **X2** for the SSL at 50-100 m; **X3** for the Deep Scattering Layer (DSL) at 100-200 m; **X4** for the DSL at 200-300 m; **X5** for the DSL at 300-450 m; **X6** for the DSL deeper than 450 m; **X7** for the discrete schools at 0-75 m; **X8** for the discrete schools at 75-200 m; **X9** for the discrete schools at 200-500 m; **X10** for the discrete schools deeper than 500 m.
Values of the ten variables are: for SSL and DSL, 0 is "absent", 1 is "diffuse and weak", 2 is "diffuse but dense", 3 is "concentrated", 4 is "very noticeable concentration"; for discrete schools, 0 is "absent", 1 is "scarce", 2 is "fairly abundant", 3 is "very abundant".

as only the probability of co-occurrence is concerned. Wishner *et al.* (1988) established the coincidence of whales and copepods in the Great South Channel, in the Northeastern Atlantic, because blue whales feed either on high densities of *Calanus finmarchicus*, or on swarms of capelins.

Conclusions of the numerical analyses

The most obvious conclusion from the three joint numerical analyses is that the presence of cetacea at the surface is strongly linked with dense echos in the underlying water - probably indicating a sufficiently abundant and concentrated biomass below the animals.

The global prediction for the presence of cetacea according to the underlying echos is less precise with the multiregression on the echo indexes, than with the overall biomass index *B* used above. But the multiregression provides information about the *hierarchy* among the predictive values of echos at a single station. Moreover, *B* cannot predict the ability of a single station to support cetacea: a particular distribution of echos in the water column (scattering layers and schools of fishes at various depths) is also required.

This result has to be compared with those of the Factorial Analysis. A particular influence of the weak, but not absent, echos from DSL and discrete schools, which are opposed, along axis 2, to the deep dense biomass, can be seen. Only a very particular echo profile allows the presence of large or medium-size cetacea species, particularly the teuthophagous ones: very noticeably concentrated DSL ("4") below 300 m and very abundant ("3") spots below 500 m are attractive for them. On the contrary, weak diffuse DSL ("1") from 100 m to deeper than 450 m, and fairly abundant discrete spots ("2") deeper than 500 m, seem to be avoided by teutophagous species. An interpetation can be attempted, related to the different patterns of concentration of deep pelagic biomass: the same biomass can alternatively be concentrated below 450 or 500 m by day, or scattered in upper water by night; only the first pattern is attractive for medium-size cetacea.

Small dolphins seem to be distributed independently from the pelagic biomass existing in the 0-1 000 m

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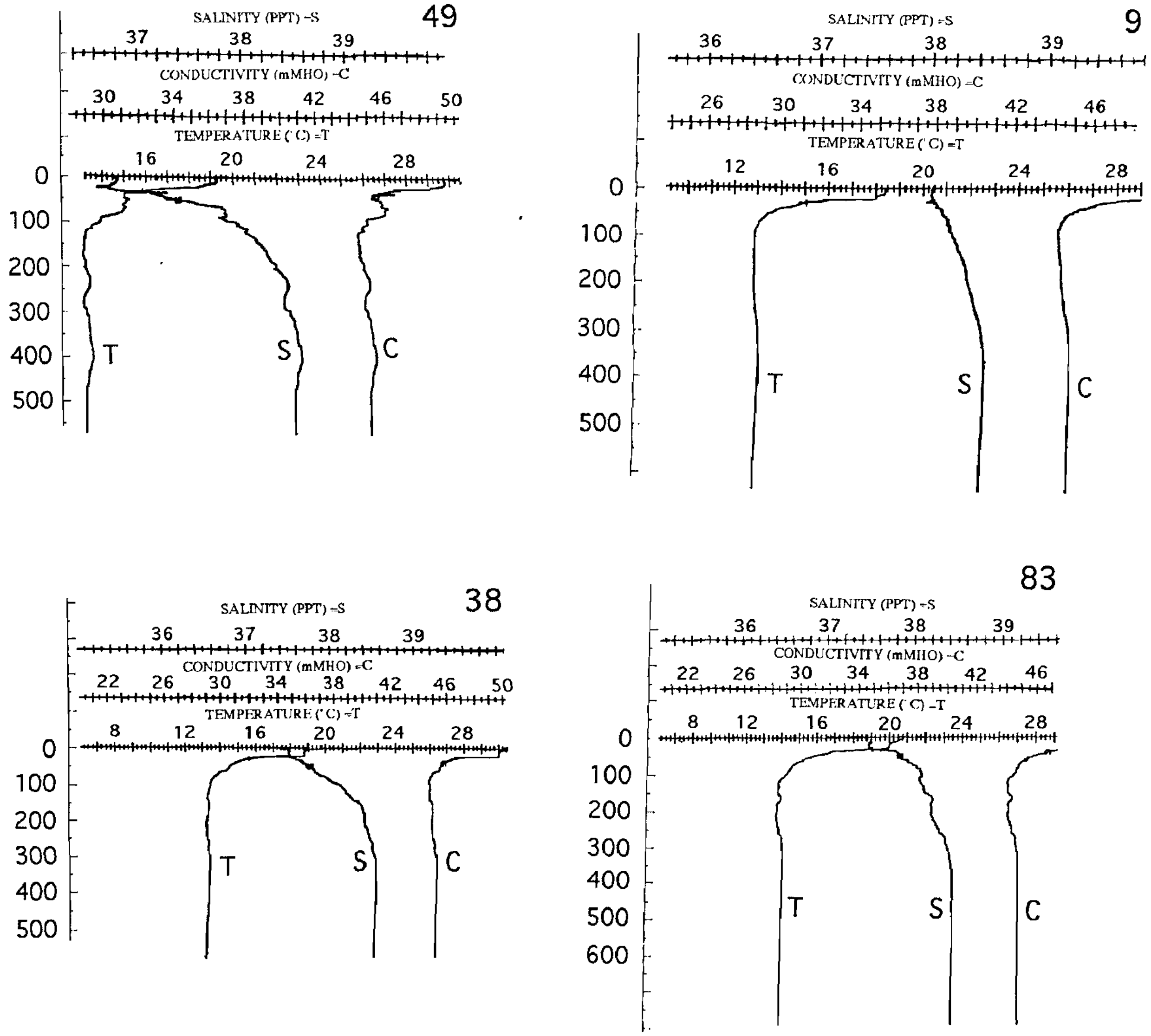

Figure 12. – Hydrological profiles (**T** is temperature, **S** is salinity, **C** is conductivity).
Station 49, showing a shearing between two water layers. The area is characterized by the presence of numerous squids at the surface, and schools of dolphins observed eating on them.
Station 38, showing a thermocline at 40 m and below it, up to 300 m, a stepwise sequence of more or less saline and warm layers. Below 300 m is Modified Intermediate Water (MIW). This profile co-occurs with sightings of three sperm whales diving to eat.
Station 9, as an example of area devoid of any surface megafauna. At 40 m is a thermocline separating superficial Mediterranean water, and mixed MIW present up to 300 m.
Station 83, an example of coastal zone.

layer, but clearly avoid the kinds of conditions shown at the two extremities of axis 2 - precisely those conditions which respectively favour, or hinder, teutophagous cetacea. The apparent independence of dolphins with respect to axis 1 is possibly due to the mixing of the sighting results the three dolphin species, which may display distinct behaviours.

Hydrological profiles corresponding to the presence of megafauna

Among the eighty-seven hydrological profiles of this cruise, some are enhanced by biological observations - surface sightings or echosounded biomass (*fig.* 12 to 15). What are the hydrological characteristics of these profiles?

Profile 49. A strong shearing appears between several alternating layers (each one 50 m thick: *fig.* 12), in which temperature and salinity are quite different. From 0 to 100 m, a well defined layer is identified as Modified Atlantic Water (MAW: 14.4 °C; 36.8 %). From 300 to 450 m, a layer shows the temperature and salinity of Levantine Intermediate Water (LIW: 14.0 °C; 38.5), and is identified as a lenticular mass of LIW (Perkins and Pistek, 1989).

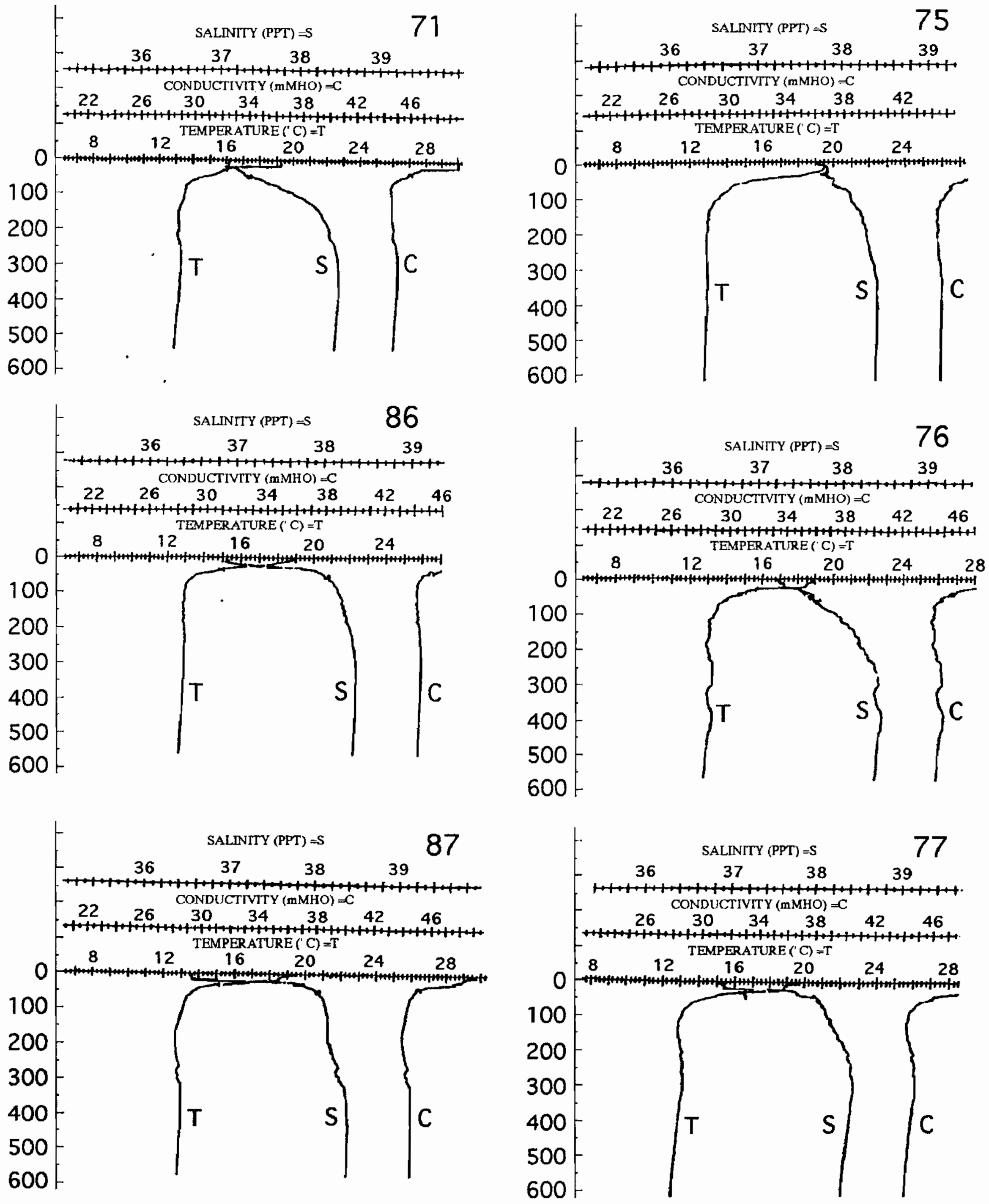

Figure 13. – Comparison of the hydrological profiles 71, 75, 76, 77, 86, 87. *See* text.

A thermocline occurs at 40 m, displaying a 5°C gradient: so the mixed layer reaches the euphotic layer, resulting in a favourable water structure for primary, and consequently secondary, productions. The latter is proved by the presence of dolphins, large squids, sharks and *Trachypterus* sp. - species of fish living between 600 and 1 000 m.

In contrast, *profile 9* (*fig.* 12) is a typical situation of cast without any biological content. The entire water column is homogeneous (Mediterranean Water: 38.32%, 21 to 22°C).

Profile 83 (*fig.* 12), with dolphins observed, shows also layers of turbulent mixing, but less intense than in the *49* one, and only in the first 50 meters. It

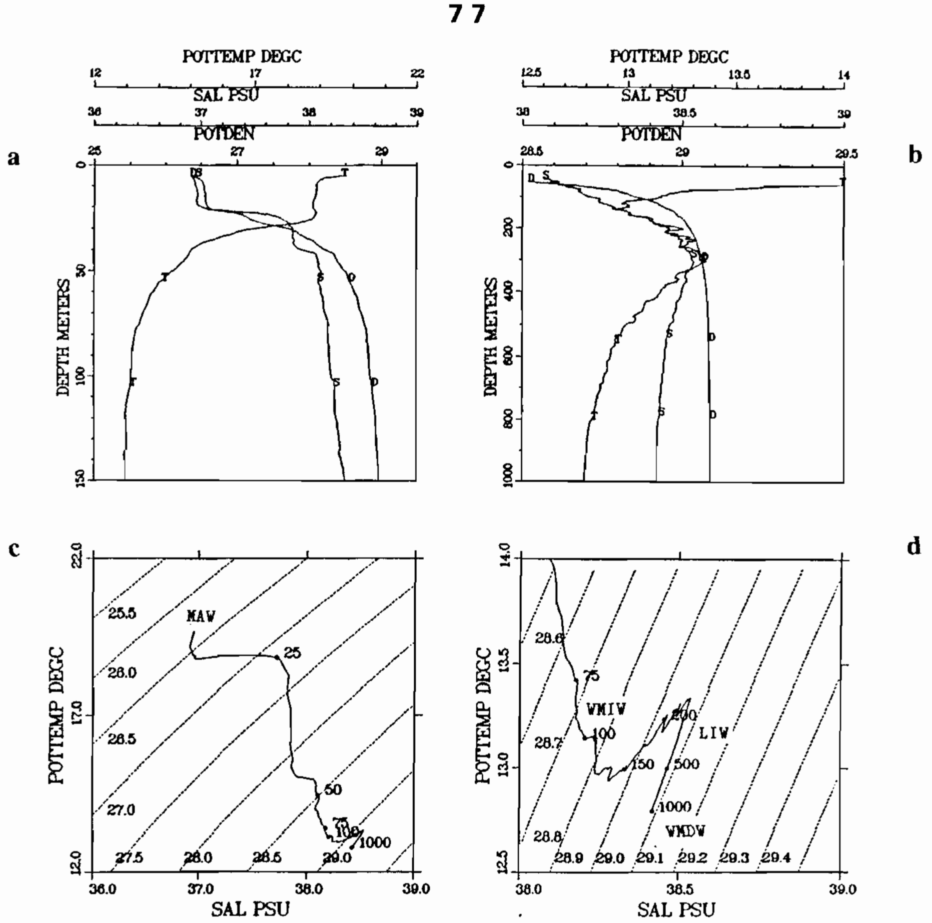

Figure 14. – Hydrological profile with two depth scales (**a** and **b**: T is temperature, S is salinity, **C** is conductivity) and T, S diagram (**c** and **d**: 0-50 m and 50-1 000 m) at station 77.
A well characterized Atlantic superficial water is present from 0 to 25 m. A shearing between Western Mediterranean Intermediate Water (WMIW), which exists between 50 and 200 m and reaches the euphotic layer, and Levantine Intermediate Water (LIW) existing between 200 and 600 m, is observed. Below the latter is the Western Mediterranean Deep Water (WMDW).

represents a coastal situation with superficial currents (Millot, 1988) and Mediterranean intermediate water identified as a MIW southward current (Perkins and Pistek, 1989).

Profiles 38 and 71 (*fig.* 12 and 13), where sperm whales were observed, show turbulent layers implying mixing with MAW, but without the high salinity gradient present on the following profiles.

Profiles 77, 86, 87 (*fig.* 13 to 15) are characterized by (i) a strong gradient of both temperature and salinity, (ii) a thermocline located between 25 and 50 m, and (iii) an "undulating" salinity profile linked to a turbulent shearing at the contact of three different water masses: MAW at the surface, mixed layer, and Modified Intermediate Water (MIW) below 300 m.

In *Profiles 70a, 71* (*fig.* 13), *77a* and *74*, LIW is visible above 300 m, probably caught by an old eddy hypothesized by Pistek and Perkins (WMCE Consortium, 1989). Echo registrations are statistically similar (*see* above).

Relation with the Western Mediterranean circulation

In fact, the biological potential of production of these hydrological features is to be considered within the framework of a dynamical study of the water masses. Indeed, the biological and hydrological profiles give static information and do not inform about mechanisms. However, the infrared satellite imagery allowed a dynamical approach to the Algerian basin during the ten days of the cruise (*fig.* 16), and even before the cruise, which gives information about what happened dynamically in the area.

Intensive secondary production is found only in some well located areas namely (a) stations 85 to 87 on the eastern boundary of the Almeria-Oran front; (b) stations around 70 and 71; (c) stations 73 and 74; (d) stations 76 to 77. Areas (b) to (d) are in the interval between Sardinia and Minorca. Two other areas appear with less intensive production, presenting co-occurrences of megafauna and deep biomas: station

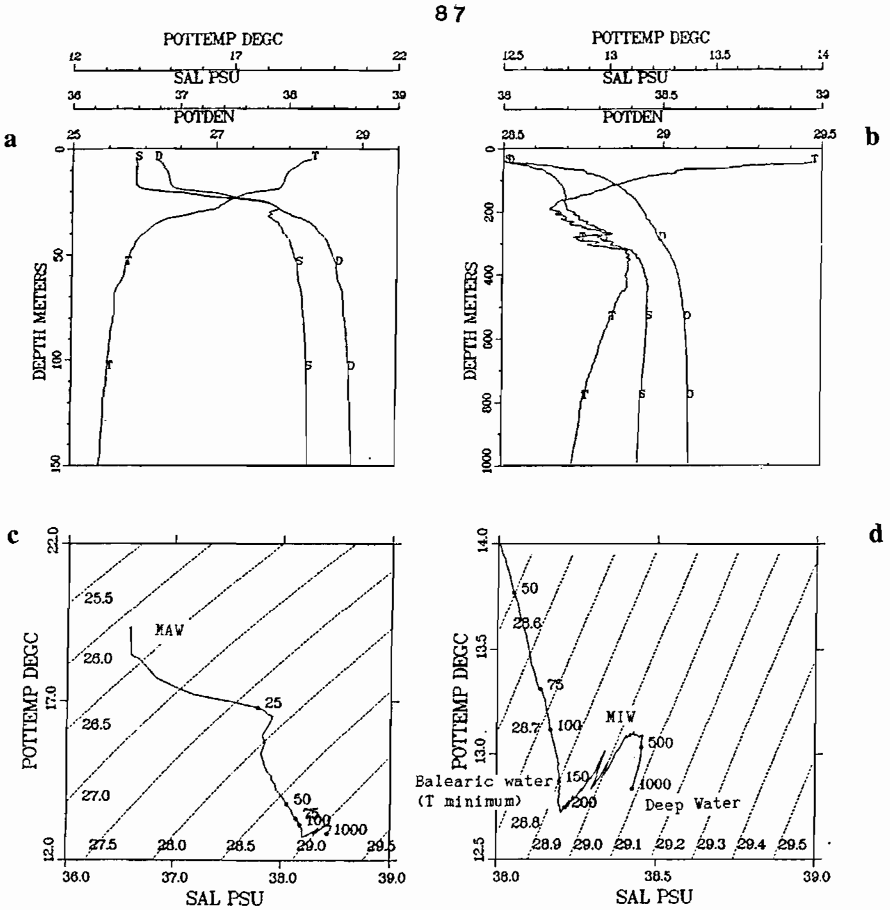

Figure 15. – Hydrological profile with two depth scales (**a** and **b**: T is temperature, S is salinity, C is conductivity) and T, S diagram (**c** and **d**: 0-50 m and 50-1 000 m) at station 87.
Cold water between MAW and MIW is seen.

49 (*fig.* 1) and the transect between stations 59 and 60 (casts called 59a, b and c) on the Strait of Sicily. These six cases concern offshore areas. They will be discussed now in order to identify common features among the richest stations of our first set of data, and to observe how they differ from stations without any biological observation.

The *Remote Sensing and Prevision Laboratory* of NORDA (at Bay Saint Louis) allowed us to study the AVHRR images as a movie. With the collaboration of Robert Arnone, we examined on the screen the infrared photographs from the ten days of the cruise. Evolutive features of the Mediterranean circulation are highlighted, with a surface signature changing in the Algerian basin from day to day.

An eddy can migrate eastwards for several months after leaving the Atlantic Algerian current (Millot, 1987*c*). According to Millot (1988) and other oceanographers of the Workshop in Bay Saint Louis (WMCE Consortium, 1989), the different water layers of an eddy are turning together without generating any vertical motion; therefore, no vertical transport of nutrients into the eddy occurs, but it is possible on its edge. Our data suggest that biological richness occurs in areas when and where turbulence occurs on the edge of an eddy, at the contact between the eddy and another water mass moving in the opposite sense. Such an encounter of two water masses generates, through turbulent mixing, an influx of nutrients, specially if LIW underlies. This hypothesis is supported by four examples, as follows:

(i) *Areas of casts 70 and 71 and cast 74.* If biomass is enclosed in an eddy where no vertical transport is generated to bring up new resources, its survival is questionable. Consequently the important biomass observed at cast 74, with regard to its probable age (euphausids and squids need several months to become adult), cannot belong to the eddy, but probably lives in its vicinity (see below). This argument arises from comparison of both infrared and CZCS imagery. Indeed, abundant chlorophyll is visible in this area on the 12th May CZCS image, suggestiong two anticyclonic eddies functioning in the channel between Sardinia and Minorca. Between these eddies, a central area shows a high primary production, likely due to the shearing of both, which results in a turbulent mixing and a possible vertical nutrient recovery. In the profiles 70 and 71 LIW was found, probably extracted from the LIW flow along Sardinia by the eastern eddy described above.

(iii) *Area of casts 77 to 78.* Infrared NOAA imagery (*fig.* 16) shows, in the area of cast 77, a clear curved plume of cold water, turning around Minorca at the North-East. Cast 78 is located at the southern edge of this cold water (*fig.* 16), at the interface between the cold northern Mediterranean water, and an anticyclonic eddy coming from the Algerian basin. A strong turbulence results from the antagonistic contact between the old southern eddy, and the Mediterranean water entering the Algerian basin from the North.

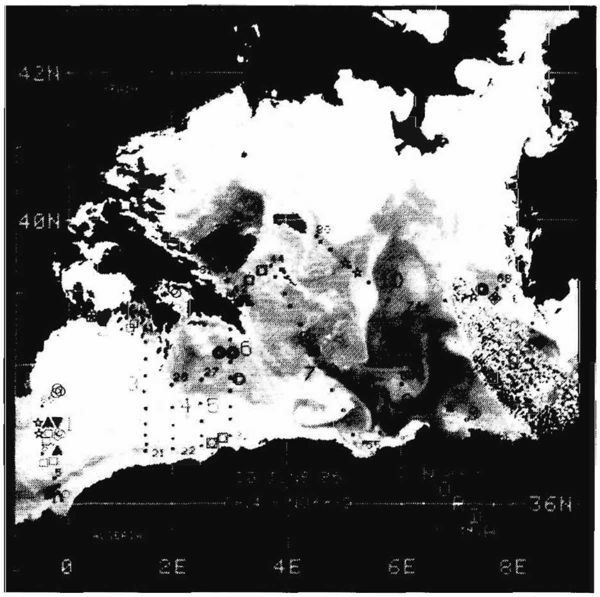

Figure 16. – Localization of the megafauna observations and hydrological casts plotted on the AVHRR-NOAA 9 images from the 19th June, 1986 (NORDA Remote Sensing and Prevision Laboratory, Bay Saint Louis, by courtesy).

☆ B: Fin whales *Balaenoptera physalus*
⊗ D: Common dolphin *Delphinus delphis*
○ d: Unidentified dolphin
▲ G: Pilot whale *Globicephala melaena*
□ g: Risso dolphin *Grampus griseus.*
⊠ LA or Lr: Marine birds in schools
⊠ p: Marine birds such as Puffins
✪ P: Sperm whales *Physeter macrocephalus*
◈ R or Rm: Sharks
✱ S: Striped dolphin *Stenella coeruleoalba*
◢ T: Grey dolphin *Tursiops truncatus*
▢ Sq: Squid in the surface
⊖ To: Turtle *Caretta caretta.*

(iii) *Area of casts 85 to 87.* A photograph from the NOAA-9 Band 4 of the Almeria-Oran front, on 29th April 1986, shows an anticyclonic instability on the eastern boundary (Lohrenz and Wiesenburg, 1988). An anticyclonic eddy is also seen on CZCS images of 30th April, 8th May, 12th May (1989), 17th May (Arnone, 1988), and is also visible on the infrared picture from NOAA-9 on the first days of June and on June 9 (*fig.* 16) and 10. Pictures of June 3 and 4 were concealed by clouds. Arnone and La Violette (1986), studying the Almeria-Oran front over several months, confirmed the regular presence of an anticyclonic eddy in this area. It cannot migrate either westwards against the front, nor eastwards because it is pulled by the newly generated eddies coming from the Algerian Atlantic flow (*fig.* 12). This process results in an interesting interface between (1) an energetic eddy coming from the Almeria-Oran current, (2) the older eddies moving westwards from the Algerian current, and (3) the Mediterranean and Balearic waters turning back from the Catalan current and entering the Alboran Sea (Perkins and Pistek, 1989). New fresh Atlantic water is regularly extracted from the Almeria-Oran current and visible on the hydrological profile 86, determining the high characteristic gradient of salinity discussed above.

This analysis is then historical, taking into account a set of simultaneous events of the Western Mediterranean circulation, and yields a hypothesis about a possible process able to explain the rich and sustained secondary production found in the area of casts 85-87.

(iv) *Area of stations 59b and c.* Similarly, it seems that the deep biomass encountered simultaneously with megafauna at casts 59b and c can be explained by an eddy, visible on NOAA picture of June 9 (*fig.* 16), confronting the Levantine water entering the Strait of Sicily.

In conclusion, anticyclonic eddies seem to be associated, in the area studied here, with all the processes able to generate a nutrient enrichment. This enrichment occurs at the contact of these eddies with other hydrological structures, mainly when and where they generate a friction and shearing against LIW or MIW veins moving in the opposite sense. The high biological production at stations 70 and 71 indicates a frontal production along the incoming flow of LIW (*fig.* 13), clearly identified at stations 68 and 69 (Pistek and Perkins, 1989). LIW appears at 200 m depth on *figure* 13.

Relations with chlorophyll *a*. Temporal aspects

During the cruise, cetaceans were absent along the Algerian current west from 4°E, despite the presence of underlying biomass detected in some places (stations 14, 17, 19, 23, 24, 26). Chlorophyll *a* measurements during the cruise have been made only at the surface. Maximum values, namely 2 mg.m^{-2}, have been found along the Algerian front or in coastal zones (Martinez *et al.*, 1990; *fig.* 17), without any link with the area of interest for the megafauna. That is in agreement wih the observations of Smith *et al.* (1986), which did not demonstrate any simple relation between chlorophyll and cetaceans as a whole in the California current. According to the latter, small delphinid species have been found significantly and positively correlated with surface chlorophyll concentration in the coastal areas only. The baleen whales have been found weakly correlated with chlorophyll. Sperm whales were negatively correlated with surface chlorophyll on the seaward side of the thermic front - that recalls our observations of sperm whales in cast 38 at the seaward side of the Algerian currrent front. Smith *et al.* (1986) also report that the presence of *Grampus griseus* is linked with medium chlorophyll concentrations.

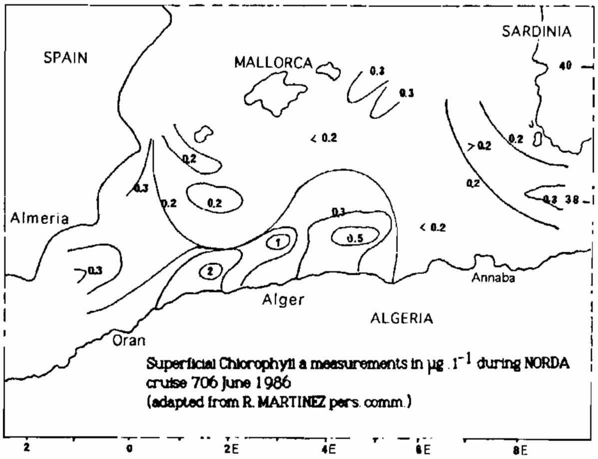

Figure 17. – Superficial (10 m depth) distribution of chlorophyll *a* during the NORDA 706 cruise (from R. Martinez, by courtesy).

In conclusion, the relation between cetacea and superficial chlorophyll is by no means univocal, probably because of the numerous trophic steps leading from phytoplankton to cetacea. The areas able to produce trophic chains up to the highest level, *i.e.* megafauna, in the Western Mediterranean, need a shearing between MIW or LIW and the adjacent waters allowing the former to penetrate the euphotic layer. Turbulence arising from this shearing then determines a vertical advective (or turbulent diffusive) transport of nutrients coming from the LIW or MIW, entering the Algerian and Alboran basins.

But it is not sufficient to consider only turbulence. The area of the strong Atlantic flow along the Algerian coasts, between 0 and 4 °E westwards from section 6 of the cruise (*fig.* 1), shows no cetaceans, in spite of the important primary production as measured by MEDIPROD 5 campaign (Taupier-Letage and Raimbault, 1987) or in our cruise (Martinez *et al.*, 1990). By contrast, eastwards from section 6, Dallot *et al.* (1988) show that an eddy studied at 4 °E presents a strong dominance of macroplanktonic species (high trophic levels), which suggests that this eddy is old, having evolved into an old diversified ecosystem. Productivity westwards from 4 °E in the Algerian current probably leads to short microheterotrophic chains because the periodicity of the instabilities does not allow any other kind of secondary production (Frontier, 1986; Le Fèvre and Frontier, 1988). As a matter of fact, NORDA cruises along the northern edge of the Atlantic current on May and June found a bacterial biomass 30 times greater at 0 °E than at 4 °E (Larock, 1988).

In the same way, temporal aspects are to be considered concerning the stations 74 to 75. NOAA pictures, confirmed by CZCS, from the end of May up to June 10, show between stations 74 and 75 a triangular zone in the middle part of the Sardinia-Minorca Strait, bounded westwards and eastwards by two old eddies (*fig.* 16). The shearing at the contact between eddies, able to generate an advective motion, was sufficiently steady to sustain a long food chain. Historically speaking, the duration of this process has been sufficient for the ecosystem to turn out to be an old and diversified one (Frontier, 1978), able to produce euphausids for squid and whale feeding. In conclusion mesoscale phenomena, in order to determine enough turbulence and nutrient enrichment to induce a diversified production, attractive for megafauna, have to be steady for at least three weeks, and preferably several months.

CONCLUSION: EVIDENCE FOR THREE NEW AREAS AS ERGOCLINES

According to our results and to statistical data processing, cetacea act as surface markers of high concentrations of underlying deep biomass - the latter being linked with some mesoscale events due to instabilities of the Mediterranean circulation. Ten sequences of particularly concentrated echos were found during the entire cruise: all were concomitant with cetaceans - an argument proving the acoustical detection of preys by cetacea, probably with a biological device detecting sounds at a frequency close to 12 kHz.

The spatial distribution of concentrated food sought by whales is strongly heterogeneous in the Algerian basin. Everywhere a co-occurrence between whales and underlying biomass is observed, there is an encounter of two water masses moving in opposite directions, such as MIW and LIW when entering the Algerian basin and encountering eddies extracted from the Atlantic current. Such eddies are living for a longer or shorter period according to their kinetic energy. Such antagonistic contacts are interfaces, sites of matter and energy exchanges, then *ergoclines* as defined by Legendre *et al.* (1984, 1985 and 1986). Four ergoclines areas were demonstrated in the present work, located (1) at stations 76 to 79, (2) at stations 58 to 63, (3) around station 71 along the LIW flow southeastwards from Sardinia, and (4) at stations 86 to 87.

Starting from the results of ECHOCET cruises of IFREMER on March, April and early May, 1986 (Viale, 1991), which revealed abundant cetacea in the fourth area mentioned above, this area as already presumed to be an ergocline. The origin of the enrichment was thought to be at the northern boundary of the Almeria-Oran front (Gascard and Richez, 1982; NORDA Workshop at Bay Saint Louis, 1988). But to explain the present result, it is necessary to take into account the clear difference between the station 85 and the stations 86-87, despite the fact that all are on the frontal edge. This suggests that the local high enrichment of 86 and 87 stations arises from a strong shearing at the triple confluence of the Almeria current northern edge, an anticyclonic eddy, and the Mediterranean water flow coming back into the Alboran Sea. The frontal edge alone (as in 85) does not provide any steady secondary production.

The three other ergocline areas had never been shown until now to be high secondary-productive areas. *Such areas are of interest for the living resources of the Western Mediterranean,* whose oligotrophy was generally assumed and sets a problem owing to the regular presence of large whales in the Western Mediterranean basin (Viale, 1985).

So the ability of a mesoscale event, in the Western Mediterranean circulation instabilities to produce some steady enrichment, is quickly "announced" by the presence of megafauna such as marine mammals. Cetacea act as markers of relatively high and sustained secondary production, in a manner similar to the way chlorophyll is a marker of recent primary production. Large whales are indicating the most quantitatively important areas for the production of krill (3th or 4th trophic level), hence they give temporal information on the streadiness of oceanographic events which result in an important deep biomass.

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