Zooplankton in the Ligurian Sea: Part I. Characterization of their dispersion, relative abundance and environment during summer 1999

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Received July 22, 2002; accepted in principle August 26, 2003; accepted for publication July 19, 2004; published online August 20, 2004

The distributions of temperature, salinity, chlorophyll and zooplankton were measured in the Ligurian Sea, north of Corsica, in August 1999. To characterize the physical environment, hydrographic and fluorometric profiles were collected. A net and two acoustic systems were used to measure the distribution of small (<5 mm) and large (>5 mm) zooplankton. Highest chlorophyll values were strongly associated with a dome of dense water in the center of the Ligurian Basin. Small zooplankton (copepods and smaller), in contrast, appeared to be associated with the periphery of the basin and were negatively correlated with chlorophyll. Large zooplankton were not correlated with either chlorophyll or small zooplankton. Large zooplankton migrated vertically hundreds of meters every night, while small zooplankton did not appear to migrate much. The physical observations were consistent with (i) a well-documented geostrophically driven cyclonic coastal current (the Ligurian Current) fed by sources in the Algerian Basin and Tyrrhenian Sea and (ii) upwelling in the central Ligurian Basin. Large zooplankton, being strong vertical migrators, were potentially insulated from the effects of the currents and therefore stayed resident.

INTRODUCTION

Physical and biological data were collected as part of the Sound, Oceanography, and Living Marine Resources (SOLMAR) program, a multidisciplinary study of the Ligurian Sea which aims, among other things, to understand the environmental factors affecting the distribution of marine mammals. Since these factors undoubtedly include physical environment and food availability, the Lower Trophic Level and Oceanography (LTLO) component of the program maps basic physical variables, phytoplankton and zooplankton throughout a large part of the Ligurian Sea. By characterizing the large zooplankton habitat, LTLO aims to identify the controlling factors and processes that control the distribution of the large zooplankton population and, in turn, the marine mammal population in this area.

The Ligurian Sea is bounded on the northeast by the Italian Riviera, on the northwest by the French Côte d'Azur and on the south by Corsica. It is open on the southwest to the Algerian Basin and on the south to the Tyrrhenian Sea via the Corsican Channel. Two major surface currents flow into the southern part of the basin: the West Corsica Current brings modified Atlantic water from the Algerian Basin and the Tyrrhenian Current brings water north through the Corsican Channel from the Tyrrhenian Sea (Béthoux *et al.*, 1982; Millot, 1987; Astraldi *et al.*, 1994). Water flows counterclockwise along the Italian and French Coasts (Stocchino and Testoni, 1977; Béthoux *et al.*, 1982), exiting the Ligurian Basin as the Ligurian Current and flowing toward the Gulf of Lions and the Catalan Sea. This cyclonic circulation is a permanent feature of the Ligurian Sea, but all three of these currents vary throughout the year (Stocchino and Testoni, 1977; Béthoux *et al.*, 1982; Taupier-Letage and Millot, 1986). In August, the Ligurian Current moves $\sim 1.3 \times 10^6$ m^3 s^{-1} of water, with $\sim 1.1 \times 10^6$ m^3 s^{-1} of that coming from the West Corsica Current and 0.2×10^6 m^3 s^{-1} from the Tyrrhenian Current (Béthoux

doi:10.1093/plankt/fbh132, available online at www.plankt.oupjournals.org

et al., 1982). Near Nice, current speeds are ~23 cm s^{-1} at the surface in August, declining with depth to ~4 cm s^{-1} at 300 m depth (Béthoux *et al.*, 1982; Taupier-Letage and Millot, 1986). The central Ligurian Basin appears to be characterized by low currents in the summertime (Taupier-Letage and Millot, 1986) and by upwelling (Hela, 1963). Gostan and Nival (Gostan and Nival, 1967) and Pinca and Dallot (Pinca and Dallot, 1995) observed a dome of dense water in the center of the basin, with nutrient levels higher near the surface in the central basin than in the peripheral zone, consistent with central basin upwelling. An important geostrophically maintained density front exists between the peripheral zone, where flows the Ligurian Current, and the central Ligurian Basin (Boucher *et al.*, 1987; Sournia *et al.*, 1990; Pinca and Dallot, 1995).

Model predictions of the phytoplankton distribution indicate that the spring bloom begins along this front (Goffart *et al.*, 1995). As the summer progresses and the water stratifies, the flux of nutrients to the photic zone is decreased, and surface levels of chlorophyll decline, leading to a subsurface maximum. This maximum spreads from the frontal zone toward the central basin. Data from the late spring collected near Nice also appear to support this model (Baussant *et al.*, 1992).

Pinca and Dallot (Pinca and Dallot, 1995) found that copepods account for 70% of the zooplankton biomass in the Ligurian Sea in the spring. *Centropages typicus* and *Clausocalanus* spp. adults and *Paracalanus* and *Clausocalanus* copepodites were most abundant. Pinca and Dallot (Pinca and Dallot, 1995) also reported higher abundances in the peripheral and frontal zones than in the central zone. The large zooplankton in this region are primarily *Meganyctiphanes norvegica* (Franqueville, 1971; Wiebe and D'Abramo, 1972; Andersen *et al.*, 1998). The krill (as well as small fish and squid) are important in the diets of top predators including fin whales (Orsi Relini *et al.*, 1994; Panigada *et al.*, 1999). So in order to determine how marine mammals may react to man-made sounds, it is necessary to understand the factors controlling the distribution of their primary food source. By studying the physical and biological environment of the Ligurian Sea, we hope to understand better which factors are most important in controlling the distribution of krill in this area. In this paper, we describe the Ligurian Sea zooplankton community in the summer of 1999 and related physical and biological factors that characterized the environment. In a second paper (Warren *et al.*, 2004) we describe the situation in the summer of 2000, including additional measurements and analysis.

METHOD

Data were collected at 37 stations and while underway aboard the Italian Navy's hydrographic ship *Ammiraglio Magnaghi* from 2 to 13 August 1999 (Fig. 1). Profile stations were separated by ~22 km. Volume backscatter data were collected between stations using a split-beam 120 kHz echosounder (Simrad EY500). Profile data were measured using a conductivity, temperature and depth (CTD) probe (Idronaut, Model 317), a fluorometer (Seapoint Sensors, SCF) and a multifrequency acoustic profiling system [BAE SYSTEMS, Tracor Acoustic Profiling System (TAPS)]. The profiling package was lowered at a rate of 0.2 m s^{-1} from the surface to 150 m depth. Thereafter, it was lowered at a rate of 1.0 m s^{-1} from 150 to 600 m depth and then recovered at several m s^{-1}. The two-speed descent strategy permitted both a detailed examination of the photic zone and a profile of the physical properties of the deeper water column, all in less than a half-hour. Only the data from the surface to 150 m descent are presented herein. At least one profile was made during daylight at each station (Fig. 1). We revisited as many stations as we could by night in an effort to make day/night comparisons of vertical distributions. Because the nights were much shorter than the days, not all stations could be revisited.

CTD and fluorescence measurements were made twice a second, while the TAPS collected acoustic volume

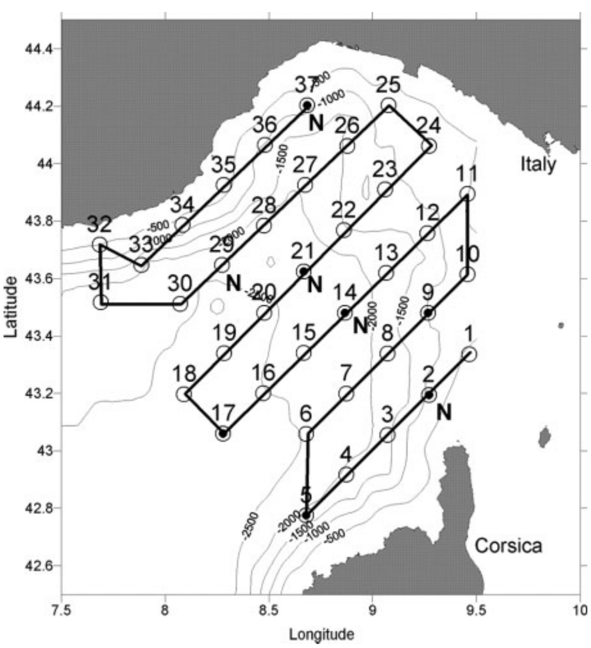

Fig. 1. *Magnaghi*'s nominal track during the 1999 Sound, Oceanography, and Living Marine Resources (SOLMAR) field study. Numbered stations indicate where conductivity, temperature and depth (CTD)/fluorescence/Tracor Acoustic Profiling System (TAPS) profiles were made. Open circles indicate daytime stations, and smaller black circles indicate nighttime stations. Vertical plankton net samples were collected at those stations marked with an N. A 120 kHz echosounder collected underway data between all stations, with complete daytime coverage and partial nighttime coverage.

backscattering data (S_v with units of dB re 1 m^{-1}) once every 2 s at six frequencies: 265 kHz, 420 kHz, 700 kHz, 1.1 MHz, 1.85 MHz and 3 MHz. Profile data were averaged in 1 m depth bins for processing. The CTD, fluorometer and TAPS were calibrated before and after the cruise.

The volume backscattering data from the TAPS were transformed into estimates of small zooplankton abundance as functions of size class using a matrix inversion algorithm employing the non-negative least squares (NNLS) method (Lawson and Hanson, 1974; Holliday, 1977; Greenlaw and Johnson, 1983). The inversion algorithm provided an estimate of biovolume, measured in $mm^3\ m^{-3}$, as a function of size class. Size classes were defined in terms of equivalent spherical radius (ESR), the equivalent radius of an animal if it were turned into a sphere of the same volume (Greenlaw and Johnson, 1982; Parsons *et al.*, 1990). An artifact of the inversion process, due to the finite upper limit of the acoustical frequencies used, was that the smallest size classes may have been underrepresented. Larger zooplankton may also have been underrepresented due to the small sampling volume of the TAPS (~5 L). The scatterers were divided into four broad size ranges: 0–0.725 mm ESR, 0.725–1.725 mm ESR, 1.725–2.475 mm ESR and 2.475–3.0 mm ESR. All further analyses were carried out using these four size ranges.

At some stations (Fig. 1), plankton were sampled using a conical net of 0.5 m diameter, 2.5 m long with 202 μm mesh. The net was lowered to depth and then hauled vertically up at a nominal speed of 1 m s^{-1} to the surface. Given the size of the net and the vertical speed of the tow, large zooplankton were likely to avoid capture. A sample was taken from 150 m to the surface, immediately followed by a sample from 600 m to the surface, whenever bottom depth permitted. Net stations were typically occupied around midday and then revisited around midnight, permitting day/night comparison. Net samples were collected only every 2 days because of processing constraints. Samples were preserved in 4% formalin solution. Ten plankton samples were analysed following the cruise (Table I).

Table I: Numerical density (individuals m^{-3}) of the different taxa collected with the 0.5 m plankton net from stations 2, 14 and 21

Taxa	Species	Station 2		Station 14				Station 21			
		Day S	Night S	Day S	Day D	Night S	Night D	Day S	Day D	Night S	Night D
Copepods	*Clausocalanus* spp.	64.7	70.1	372.4	108.4	95.9	60.9	206.2	65.2	69.6	90.6
	Clausocalanus spp. imm.	46.8	40.5	307	81	123	56.4	214.3	43	77.5	68.3
	Oithona spp.	36.4	20.4	31	7.1	3.8	1.9	7.1	0.8	1.4	2.6
	Copepodites uid.	16.9	7.6	26.7	5.3	6.5	3	2.7	1.1	0.8	1.5
	Centropages typicus imm.	2.4	0.5	7.1	1.1	2.4	1.9	6	0.8	4.1	3.3
	Eucalanus spp. imm.	4.6	3.8	4.4	1.9	1.6		4.4	2.2	1.4	
	C. typicus	4.9	2.5	5.4	1.4	5.4	0.5	1.1	0.1	0.3	1.4
	Calanus spp. imm.	2.2	4.1	3.8	0.3	0.8	0.4	3.8	1.2	1.1	1
	Corycaeus spp.	7.1	9.5	0.5	0.3	0.3			0.1	0.3	0.1
	Calanoid copepods uid.	2.2	1.1	3.8	0.7	1.4	0.1		0.3	0.3	
	Ctenocalanus spp. imm.	5.4	2.5				0.1		0.3	0.5	0.4
	Acartia clausi	3	0.8	1.6	0.3	1.4		0.5			
	Calanus spp.	0.6	1.7	1.6		0.3	0.1	2.7		0.3	0.3
	Ctenocalanus spp.	3.3	2.2	0.5		0.8	0.3		0.1	0.3	0.1
	Oncaea spp.	2.7	3.5		0.5				0.1	0.5	
	Eucalanus spp.		1.9	0.5			1.1				1.5
	Euchaeta spp.	3.5				0.3			0.4	0.3	0.1
	Pleuromamma spp.		1.9		0.2	1	0.4		0.3		0.7
	Euchaeta spp. imm.		3			0.5	0.4				
	Calanus tenuicornis imm.	0.3		3.3							
	Scolecithricella spp.	0.3	1.4			0.5	0.3		0.1		0.4
	Candacia spp. imm.	0.3	0.8	1.6	0.1						
	Temora spp.	1.9	0.6				0.1				
	Nauplii (GE = 0.4 mm)	0.8	0.5	0.5	0.3	0.3					0.1

(Continued)

Table I: Continued

Taxa	Species	Station 2		Station 14				Station 21			
		Day S	Night S	Day S	Day D	Night S	Night D	Day S	Day D	Night S	Night D
	Pleuromamma spp. imm.	0.8	0.5	0.5					0.4		
	Acartia spp. imm.	0.8	0.8		0.1	0.3					
	Calanus helgolandicus imm.				0.8				0.7		
	Microsetella spp.	0.5	0.3					0.5	0.1		
	Clytemnestra spp.		0.3	0.5	0.1				0.3		0.1
	Hemicalanus spp.	0.8									
	Sapphirina spp.	0.8									
	Temora spp. imm.					0.5	0.3				
	Heterorhabdus spp.		0.3				0.1				0.3
	Acartia spp.		0.3			0.3					
	Aetideus spp.		0.3			0.3					
	Candacia spp.	0.3	0.3								
	C. tenuicornis			0.5							
	Hemicalanus spp. imm.		0.3								
	Lucicutia spp.	0.3									
	Neocalanus spp.					0.3					
	C. helgolandicus								0.1		0.1
	Scolecithricella spp. imm.						0.1				0.1
	Gaetanus spp.								0.1		
	Haloptilus spp.				0.1						
	Harpacticoid copepod				0.1						
Cladocerans	*Evadne* spp.	24.2	3.5			0.5	0.1	2.2	0.4	2.5	1.1
	Penilia spp.	0.5									
	Podon spp.			0.5							
Euphausiids	*Euphausiid calyptosis*	1.6	1.1	0.5	0.1						0.3
	Euphausiid uid.				0.3	0.1		0.1			0.1
Ostracods	Ostrocods (GE = 0.4; LT = 0.8 mm)	0.3	1.4		0.3			0.5	0.1		
Amphipods	Gammarid amphipods imm.		0.3			0.5					
	Amphipod uid. imm.									0.3	
Crabs	Crab zoea		0.3				0.1				
Decapods	Decapod uid. imm.				0.1	0.3					
Larvaceans	*Oikopleura* spp.	28.6	4.1					0.5		0.3	0.1
	Fritillaria spp.	15.8	5.7					0.5		0.3	
Chaetognaths	Chaetognatha (GE = 6 mm)	2.2	0.5	1.1	0.1	0.5	0.5		0.1		0.4
Fish	Eggs (25–50 mm diameter)	0.3		1.1	0.4			0.5	0.8		
Polychaets	*Polychaeta* spp.	0.8		1.6							0.1
	Polychaeta spp. imm.				0.1						
Molluscs	*Bivalvia larvae*				0.1						
Not counted											
Siphonophores		x	x		x	x	x		x		
Medusae			x								
Pteropods		x	x		x	x	x				
Fish larvae							x		x		
Isopods		x									
Doliolids		x	x								

Taxa are listed in order of decreasing abundance. S, tows to 150 m depth; D, tows to 600 m depth.

The samples were chosen to be representative of the center of the gyre (Stations 14 and 21) and the shelf (Stations 2).

The echosounder was used to survey the distribution of large (>5 mm) acoustic scatterers. The split-beam transducer was mounted to a towing foil and deployed behind the ship. Data were indexed with time and geographic location and were post-processed using SonarData EchoView V1.5. Towing speeds were typically 3 m s^{-1}, at which speed the foil towed at a depth of ~5 m. The 120 kHz acoustic signals used for the underway survey were 1 kW pulses of 1 ms duration. Volume backscattering data (S_v in dB re 1 m^{-1}) were recorded in 0.33 m depth bins from 5 to 155 m depth. The 120 kHz system was calibrated using standard targets immediately before the cruise. Volume backscattering data from the EY500 were filtered to remove transmit pulse noise, bubble reflections, transient and background noise and bottom reflections. The data were then used directly to map the relative density of large zooplankton as a function of depth and distance along trackline.

RESULTS

The Ligurian Sea was well stratified during the entire study period of 2–13 August 1999 (Fig. 2). Isopycnal surfaces indicated a subsurface dome of dense water in the center of the basin. The temperature (13.3°C) and salinity (38.5) of this water suggest that it was a water

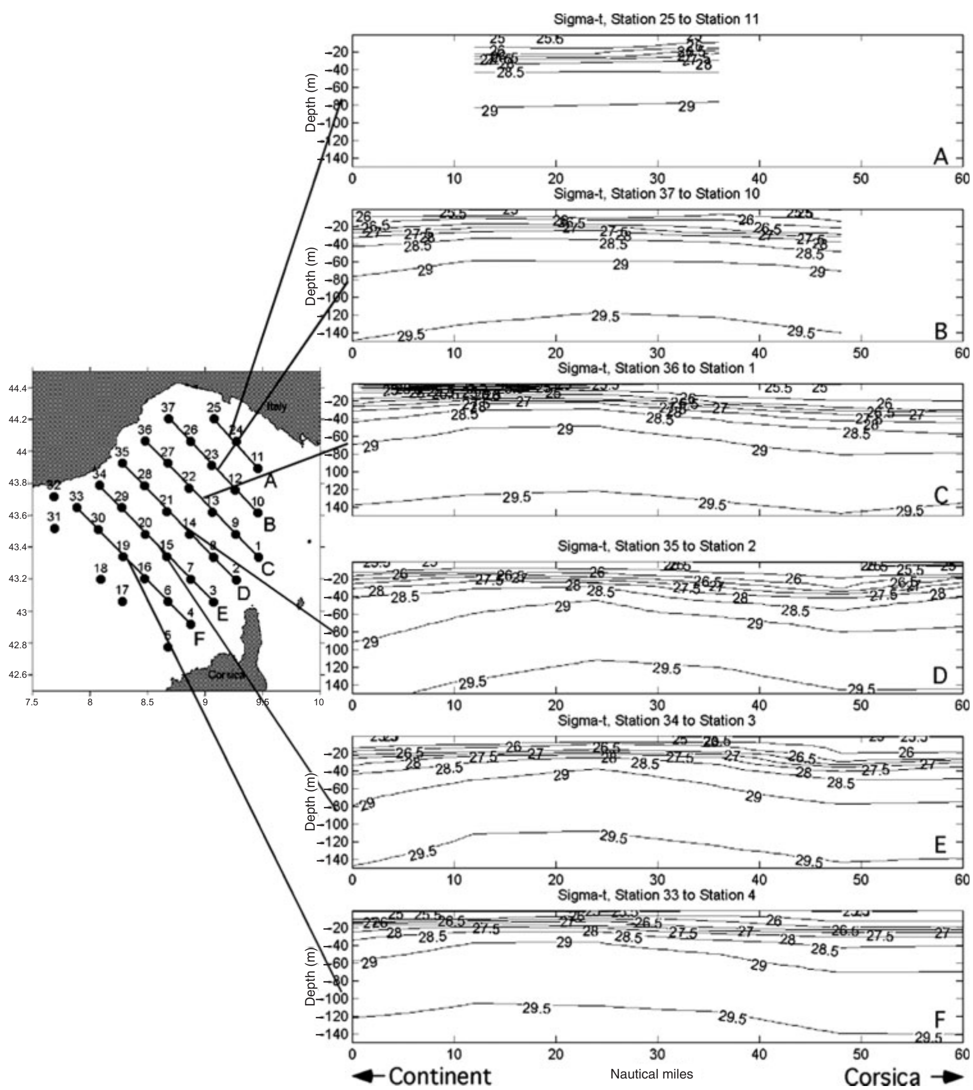

Fig. 2. Density transects across the Ligurian Basin show a dome of dense water in the center of the basin, consistent with previous observations of counterclockwise geostrophic circulation. Transects C, D and E also show a slight rise in the deep pycnoclines near Corsica, suggesting a countercurrent flowing southwest.

mass with characteristics derived from both Levantine intermediate water and Mediterranean winter water (Hela, 1963; Pinca and Dallot, 1995). Such water is normally found at depths >200 m in the Mediterranean [(Nielsen, 1912) as cited in (Sverdrup *et al.*, 1942; Wüst, 1961)]. The presence of this dome was consistent with the strong, geostrophically driven counterclockwise flow observed by other researchers working in the Ligurian Sea [(e.g. Nielsen, 1912) as cited in (Sverdrup *et al.*, 1942; Stocchino and Testoni, 1977; Béthoux *et al.*, 1982)].

Chlorophyll *a*, as measured by fluorescence, exhibited a subsurface maximum throughout the basin (Fig. 3) closely associated with the σ_t = 29.00 kg m^{-3} isopycnal (Fig. 4). Total chlorophyll integrated from the surface to 150 m showed generally higher levels in the basin center than near the coast (Fig. 5), although some near-coastal stations (Stations 12 and 23) also showed high levels of chlorophyll.

Small zooplankton as measured by the TAPS were dominated at all locations by the smallest size range (0.05–0.725 mm ESR). Net samples showed the dominant organisms in this size range as the small copepods *Clausocalanus* spp. and *Oithona* spp. (Table I). The vertical distribution of small zooplankton did not show any clear pattern, although several stations exhibited shallow maxima and others exhibited maxima at depths that may have been associated with the chlorophyll maximum (Fig. 6). The very high values observed just beneath the

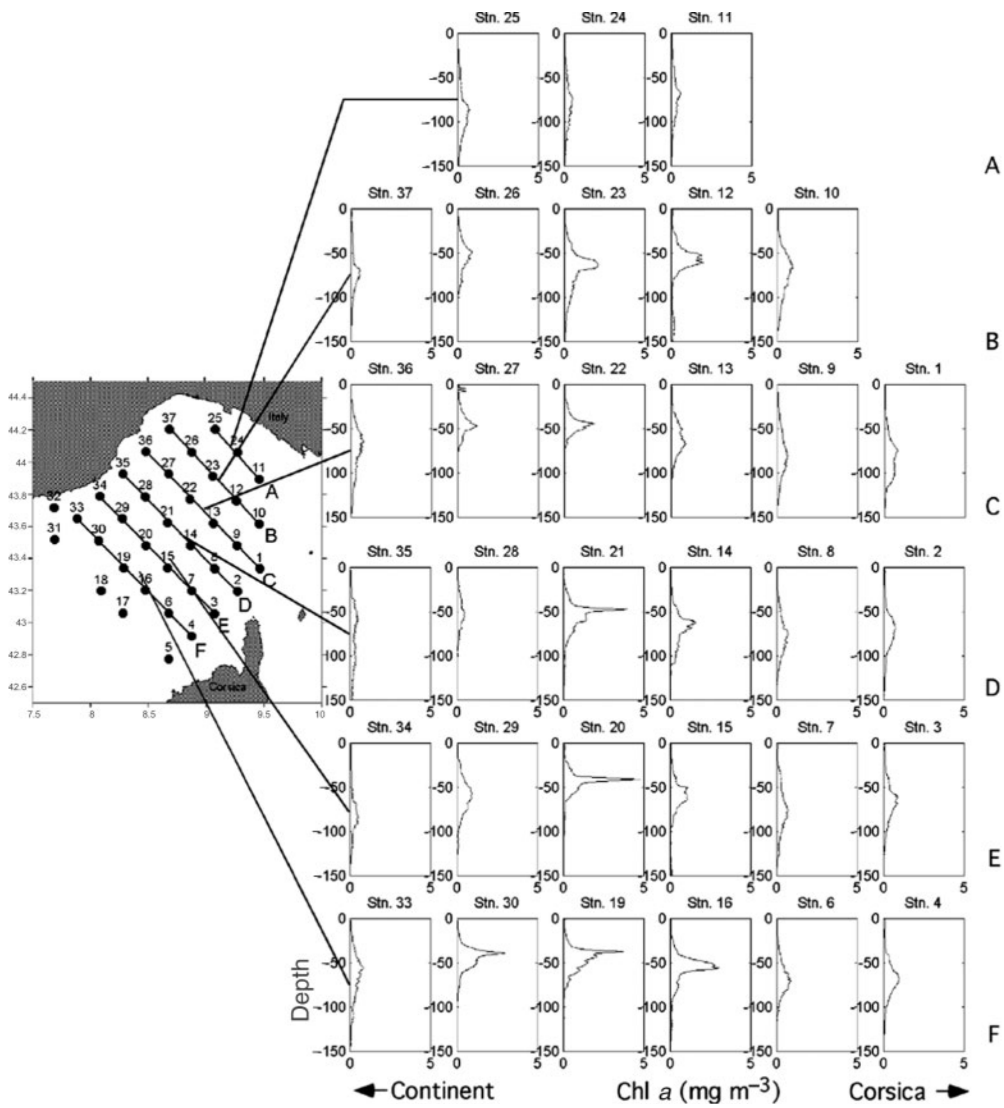

Fig. 3. Chlorophyll profiles for selected stations. The profiles suggest that the highest density of chlorophyll occurred in the center of the Ligurian Basin in August 1999. Also, peak values in the vertical chlorophyll profiles in the basin center occurred at shallower depths than they did around the periphery.

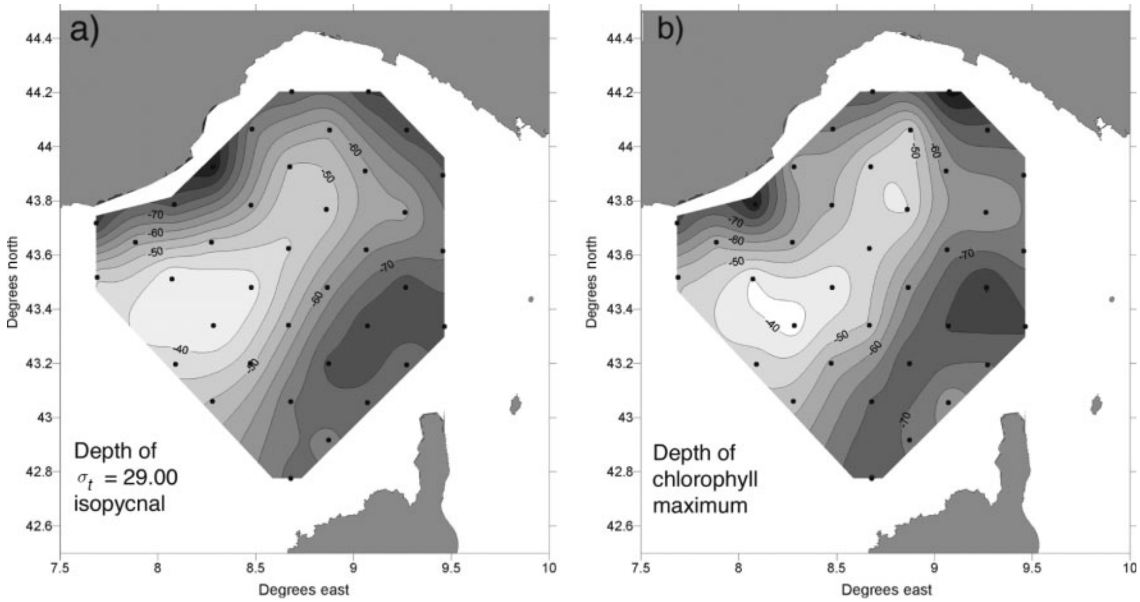

Fig. 4. There was a dome of dense water in the center of the Ligurian Basin in August 1999 associated with counterclockwise circulation. (**a**) Depth of the σ_t = 29.00 kg m^{-3} isopycnal. If this isopycnal is used as a marker for the base of the pycnocline/top of the deep layer, then deep nutrient-rich water came closest to the surface in the basin center. (**b**) Depth of the peak in the vertical chlorophyll distribution. Maximum local standing stock was closely associated with the top of the deep layer (σ_t = 29.00 kg m^{-3}).

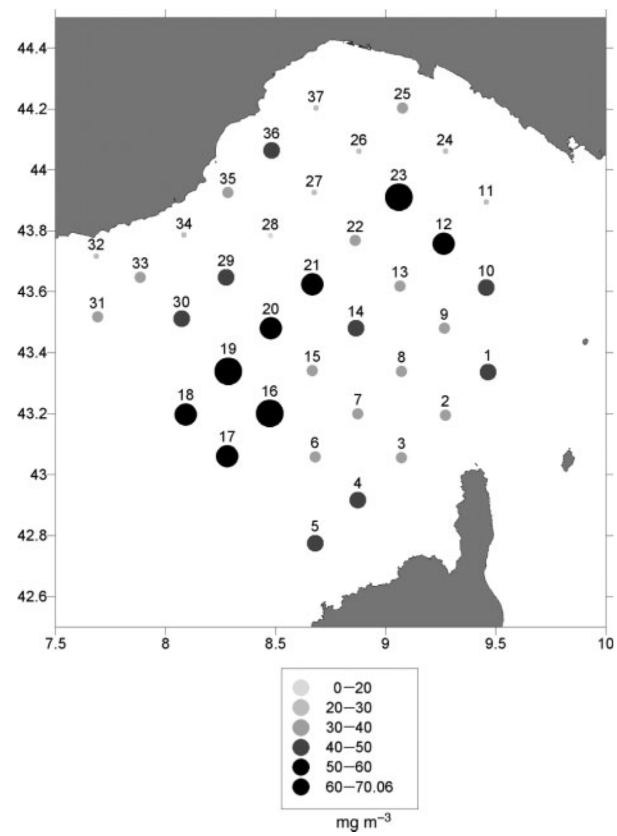

Fig. 5. Chlorophyll integrated from the surface to 150 m depth, August 1999. Highest concentrations were found in the center of the Ligurian Basin, although high concentrations were also found to the northeast.

surface at many stations were probably based on acoustic scattering from near-surface phenomena (e.g. bubbles, the surface and the ship) rather than from plankton.

In contrast to the concentration of chlorophyll in the basin center, total small zooplankton biovolume integrated from 15 to 150 m depth generally showed higher values near the coast than in the center of the basin (Fig. 7). Indeed, there was a significant negative correlation between total integrated small zooplankton biovolume and total integrated chlorophyll [$r = -0.56$, $0.0005 < P < 0.001$ using a one-tailed *t*-test (Zar, 1984)]. The vertical distribution of small zooplankton did not appear to change appreciably between day and night, suggesting that any vertical migration of these animals was small.

Large zooplankton were found in the upper 150 m of the water column almost exclusively at night, often aggregating at the depth of the chlorophyll maximum. As day approached, these strong vertical migrators would dive to depths >150 m, beyond the detection range of the echosounder. Our ability to map them was therefore compromised by the incomplete nighttime coverage. From what we observed though, the distribution of large zooplankton did not show the same clear patterns shown by either the chlorophyll or the small zooplankton (Fig. 8).

DISCUSSION

The governing paradigm for the Ligurian Sea is that of a counterclockwise surface current (the Ligurian Current) fed

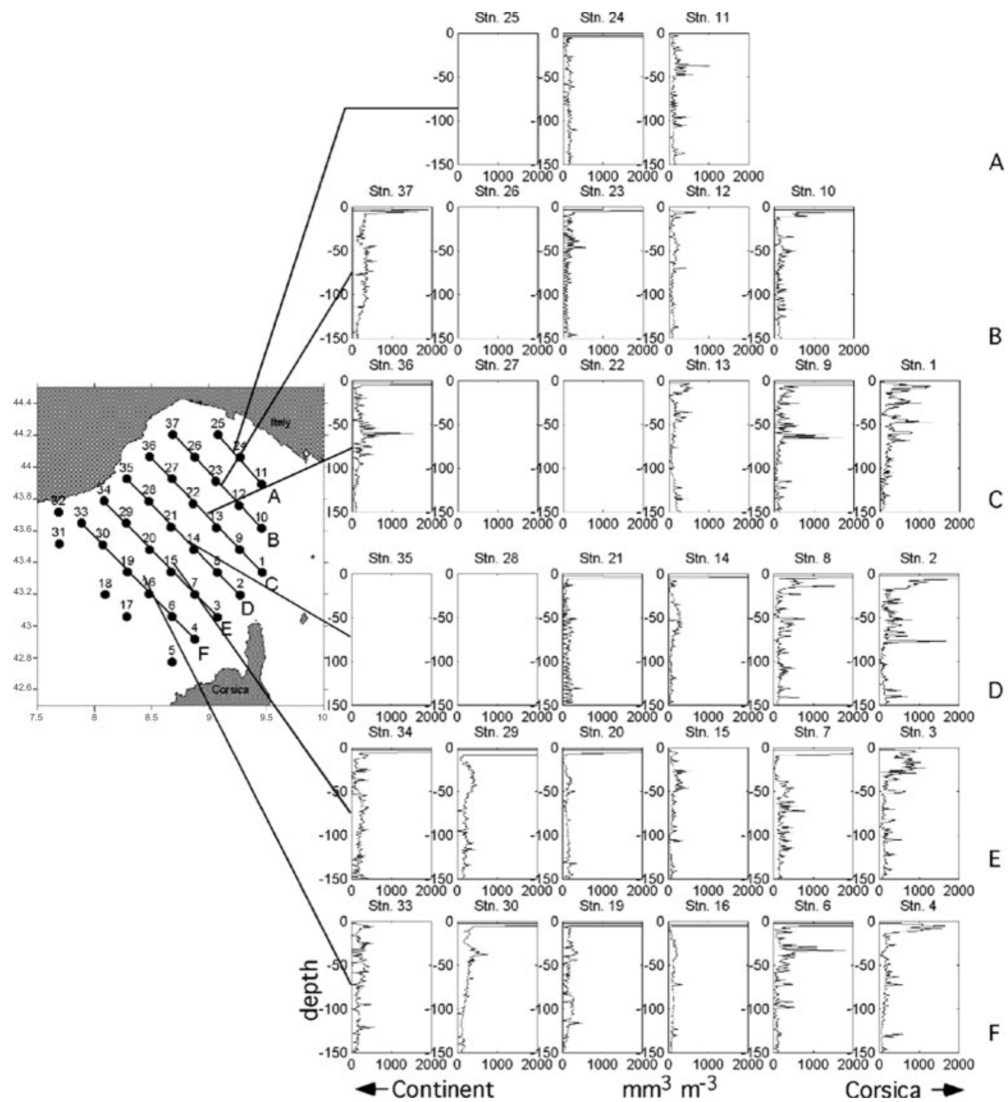

Fig. 6. Profiles of small [<3 mm equivalent spherical radius (ESR)] zooplankton biovolume ($mm^3\ m^{-3}$), measured by the Tracor Acoustic Profiling System (TAPS), from selected daytime stations. No biovolume data were collected at Stations 22, 25, 26, 27, 28 and 35. Very high values near the surface were most likely based on acoustic scattering from near-surface phenomena (e.g. bubbles, the surface and the ship) rather than from zooplankton.

by sources in the Algerian Basin and the Tyrrhenian Sea. Several researchers [e.g. (Boucher *et al.*, 1987; Sournia *et al.*, 1990; Pinca and Dallot, 1995)] have divided the Ligurian Sea into three zones: the peripheral zone, characterized by high currents; the central zone, characterized by low currents and possible upwelling; and the frontal zone, between the peripheral zone and the central zone, characterized by complex physical dynamics and high zooplankton diversity. Our observations generally support this view, although we did not find strong physical and biological distinctions between the peripheral zone and the frontal zone. In comparing our results to those of other researchers, it may be helpful to observe that Stations 1–4, 11, 24–26 and 31–37 were in the peripheral zone described by Sournia *et al.* (Sournia *et al.*, 1990), Stations 5–10, 12, 23 and 27–30 were in the frontal zone, and Stations 13–22 were in the central zone.

The Ligurian Sea was well stratified in August 1999 (Fig. 2). There was no evidence of shoaling isopycnals, as seen in the spring by Boucher *et al.* (Boucher *et al.*, 1987), nor was there any evidence of subducting layers of surface water. There was, however, a dome of dense water in the center of the basin, consistent with descriptions by Hela (Hela, 1963), Gostan and Nival (Gostan and Nival, 1967), Pinca and Dallot (Pinca and Dallot, 1995) and others. This dome was consistent with both a geostrophically driven counterclockwise current (the Ligurian Current) and central basin upwelling.

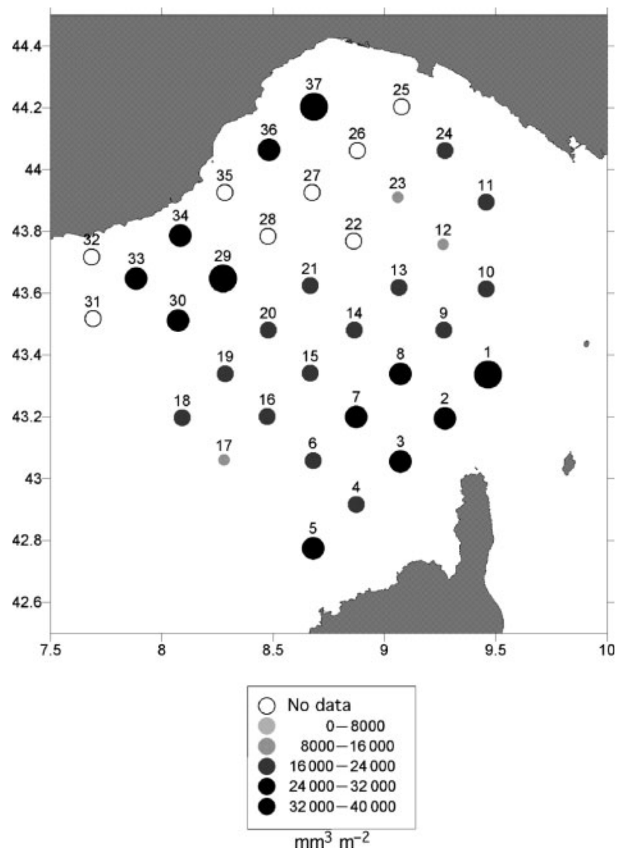

Fig. 7. Total small [<3 mm equivalent spherical radius (ESR)] zooplankton biovolume, integrated from 15 to 150 m depth.

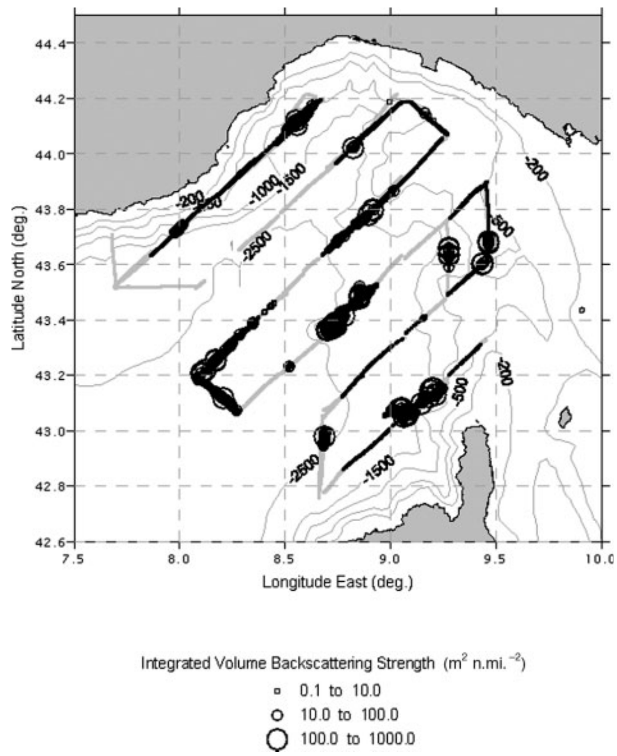

Fig. 8. Relative dispersion and abundance of *Meganyctiphanes norvegica* estimated by summing S_v from 5 to 155 m depth and averaging over 185.2 m distance bins. The resulting data (Sa: m^2 nm^{-2}) are interpreted as being proportional to areal krill density [numbers m^{-2} (Hewitt and Demer, 2000)]. Gray lines indicated daytime active acoustical survey effort; black lines denote additional nighttime effort.

There was a subsurface peak in vertical chlorophyll distribution at just about all the stations (Fig. 3). This peak was generally closer to the surface in the central zone than it was in the peripheral or frontal zones. This effect had also been observed by Baussant *et al.* (Baussant *et al.*, 1992) and Goffart *et al.* (Goffart *et al.*, 1995). The depth of the chlorophyll peak was closely associated with the $\sigma_t = 29.00$ kg m^{-3} isopycnal (Fig. 4). This had not been observed by either Baussant *et al.* (Baussant *et al.*, 1992) or Goffart *et al.* (Goffart *et al.*, 1995), although the former did note a degree of association between the $\sigma_t = 29.00$ kg m^{-3} isopycnal and the overall vertical distribution of chlorophyll (see their Fig. 8a).

One possibility for the close association between the chlorophyll peak and the $\sigma_t = 29.00$ kg m^{-3} isopycnal is that this isopycnal surface may represent the top surface of a nutrient-rich mass of intermediate water. Upwelling would then bring these nutrients close to the surface in the central zone, locally enhancing productivity. Total integrated chlorophyll was highest in the central zone (Fig. 5), consistent with the upwelling of nutrients near the surface in that area. However, a decrease of grazers in this area could also account for the observed chlorophyll distribution.

Small zooplankton were more abundant in the peripheral and frontal zones than in the central zone (Fig. 7), in agreement with observations made by Pinca and Dallot (Pinca and Dallot, 1995). *Meganyctiphanes norvegica* is often the most common euphausiid in the Corso-Ligurian basin (Franqueville, 1971; Wiebe and D'Abramo, 1972; Orsi Relini *et al.*, 1994; Andersen *et al.*, 1998). Tarling *et al.* (Tarling *et al.*, 2001) collected net samples in the Ligurian central zone which were dominated by *M. norvegica* and a pteropod species. On the basis of nighttime migratory data from Andersen *et al.* (Andersen *et al.*, 1998) for *M. norvegica*, and on the basis of our own experience with the acoustics of euphausiid swarms [e.g. (Demer and Hewitt, 1995)], we believe that many of the patches observed acoustically were *M. norvegica*. Large zooplankton were observed acoustically only at night, owing to their strong vertical migration. The nighttime distribution was extremely patchy, with patch size in the order of 10 vertical meters and 200 horizontal meters. These patches appeared at times to be associated with the peak in the chlorophyll distribution. There did not appear to be any connection between hydrographic zone and the nighttime distribution of large zooplankton (Fig. 8), nor between the distribution of large zooplankton and either chlorophyll or small zooplankton (Figs 5, 7 and 8).

In summary, the data presented in this study support several widely accepted hypotheses concerning the lower trophic levels of the Ligurian ecosystem. Warren *et al.* (Warren *et al.*, 2004) compare these observations to a similar but more extensive set of observations made in 2000.

ACKNOWLEDGEMENTS

The SOLMAR program was organized largely by Angela D'Amico from the Supreme Allied Commander, Atlantic (SACLANT) Undersea Research Centre. Funding was provided by the United States Office of Naval Research. The Italian Navy provided ship time aboard *Ammiraglio Magnaghi*. Equipment was provided by SACLANT (CTD and fluorometer), BAE SYSTEMS (TAPS), Rick Pieper at the Southern California Marine Institute (plankton net) and the United States Antarctic Marine Living Resources (echosounder). John Dawson analysed the plankton samples. Roberto Chiarabini, from the SACLANT Undersea Research Centre, maintained and operated all SACLANT equipment during the cruise. We express special thanks to the officers and crew of *Ammiraglio Magnaghi* for their expert seamanship and great efforts on our behalf.

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