Zooplankton in the Ligurian Sea: Part II. Exploration of their physical and biological forcing functions during summer 2000

JOSEPH D. WARREN[1,5]*, DAVID A. DEMER[2], DUNCAN E. MCGEHEE[3], ROSSELLA DI MENTO[4] AND J. FABRIZIO BORSANI[4]

[1]WOODS HOLE OCEANOGRAPHIC INSTITUTION, WOODS HOLE, MA 02543, USA, [2]SOUTHWEST FISHERIES SCIENCE CENTER, 8604 LA JOLLA SHORES DRIVE, LA JOLLA, CA 92037, USA, [3]BAE SYSTEMS, 4669 MURPHY CANYON ROAD, SAN DIEGO, CA 92123, USA AND [4]ISTITUTO CENTRALE PER LA RICERCA SCIENTIFICA E TECNOLOGICA APPLICATA AL MARE, VIA DI CASALOTTI 300, 00166, ROME, ITALY

[5]PRESENT ADDRESS: SOUTHAMPTON COLLEGE, LONG ISLAND UNIVERSITY, 239 MONTAUK HIGHWAY, SOUTHAMPTON, NY 11968, USA

*CORRESPONDING AUTHOR: joe.warren@liu.edu

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A survey of the biological and physical oceanography of the Ligurian Sea was conducted in the late summer of 2000. Forty-one stations were sampled for nutrients, oxygen, fluorescence and hydrographic information. Acoustic backscatter measurements were used to estimate abundance of small (<5 mm) zooplankton biovolume versus depth and the distribution of northern krill, Meganyctiphanes norvegica. Net-tow and underwater video data were collected to identify the zooplankton present. These data were used to analyze the Ligurian Sea ecosystem for physical and biological linkages that control zooplankton abundance and distribution. Results are compared with those from a similar study conducted in 1999. Hydrographic sampling showed a dome of dense water in the southwestern middle of the basin. The highest chlorophyll a (Chl a) concentrations were measured in this area, while small zooplankton biovolume was evenly distributed throughout the survey. Integrated values of Chl a and small zooplankton biovolume in 2000 were greater than in 1999. Meganyctiphanes norvegica, siphonophores and salps were the dominant components of the macrozooplankton population in the upper 200 m. In the sampled depth strata, siphonophore abundance did not change during the day, while M. norvegica were only caught at night. Acoustic backscatter data show that higher densities of M. norvegica occurred in deeper water and in the western and southwestern areas of the Ligurian Sea.

INTRODUCTION

In order to study the impact of anthropogenic sources of underwater sound on marine mammals, the unperturbed behavior of the animals must be known. One of the most important natural forces affecting baleen whales is the availability and distribution of krill, their primary food source (Orsi Relini *et al.*, 1994; Panigada *et al.*, 1999). To characterize the lower-trophic level ecosystem of the Ligurian Sea, multidisciplinary studies were conducted during the late summers of 1999 and 2000.

The Ligurian Sea is home to several marine mammal species, with both baleen and toothed whales commonly observed (Forcada *et al.*, 1995; Panigada *et al.*, 1999). In this region of the Mediterranean Sea, they feed upon northern krill (*Meganyctiphanes norvegica*), squid and small fish. These prey species are sustained by a highly productive upwelling region which is driven by the currents feeding into the Ligurian Sea. The surface currents create a counterclockwise gyre that draws nutrient-rich water toward the surface as a result of Ekman pumping (Pinca and Dallot, 1995; Millot, 1999). This increases the primary production of the region which, in turn, sustains the populations of the higher-trophic levels.

Results from the 1999 study (McGehee *et al.*, 2004) support this basic description of the ecosystem. From 0 to 500 m, the water column had a simple two-layer

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physical structure with a warm, mixed layer sitting atop a cool, deep layer. The thickness of the surface layer was a function of geographic location, thinnest in the center of the Ligurian Basin and thicker near the shelf. The highest concentrations of chlorophyll *a* (Chl *a*) were found in the center of the Ligurian Basin, above a dome of upwelled, higher-density water. Several possible mechanisms to explain the differences in the distribution of phytoplankton and small and large zooplankton have been proposed including advection of the small zooplankton by surface currents and migratory behavior of the large zooplankton (McGehee *et al.*, 2004). This study seeks to determine the extent to which biological and physical factors affect the distribution of the zooplankton population.

METHOD

To better study the lower-trophic level ecosystem, the survey region and the sensor suite were expanded for the 2000 survey. In addition to the measurements made in 1999 [water-column profiles of temperature, salinity, density, fluorescence; acoustic backscatter from a Tracor Acoustic Profiling System (TAPS) and a 120 kHz echo sounder; and a ring net for sampling small zooplankton], measurements made during the 2000 survey include meteorological information, acoustic backscatter from a 38 kHz echosounder, profiles of oxygen and nutrient distributions and sampling of the macrozooplankton community using a large net system for sampling the macrozooplankton community. All of these systems were deployed from the Italian Naval vessel *Ammiraglio Magnaghi* from 21 August through 8 September 2000.

The planned survey for 2000 expanded the tracklines to the southwest and northeast to provide greater coverage of the basin and continental shelf regions (Fig. 1). Most of the proposed stations were sampled with the exception of those along the two southeastern transects (E and F in Fig. 1a). Owing to rough weather, the ship made two port calls during the last week of the survey, which caused nine stations on these transects to be canceled. Additionally, station 35 was moved 4 km south due to a restricted zone. In total, 41 stations were occupied during the survey and under-way measurements of acoustic backscatter at 38 and 120 kHz, and meteorological data were collected over ~2600 km of trackline (Fig. 1b).

During the day, the ship would transit between stations, and then at night, it would retrace its path and resurvey as much of the trackline as possible. This method was used to obtain day and night measurements of acoustic backscatter to study the diurnal behavior of *M. norvegica*. Owing to the longer days and shorter nights in late summer in the northern hemisphere, it was not possible to revisit all the stations during the night.

Station sampling

At each station, a profile package was lowered at a nominal rate of 0.2 m s^{-1} from the surface to 150 m and 1 m s^{-1}

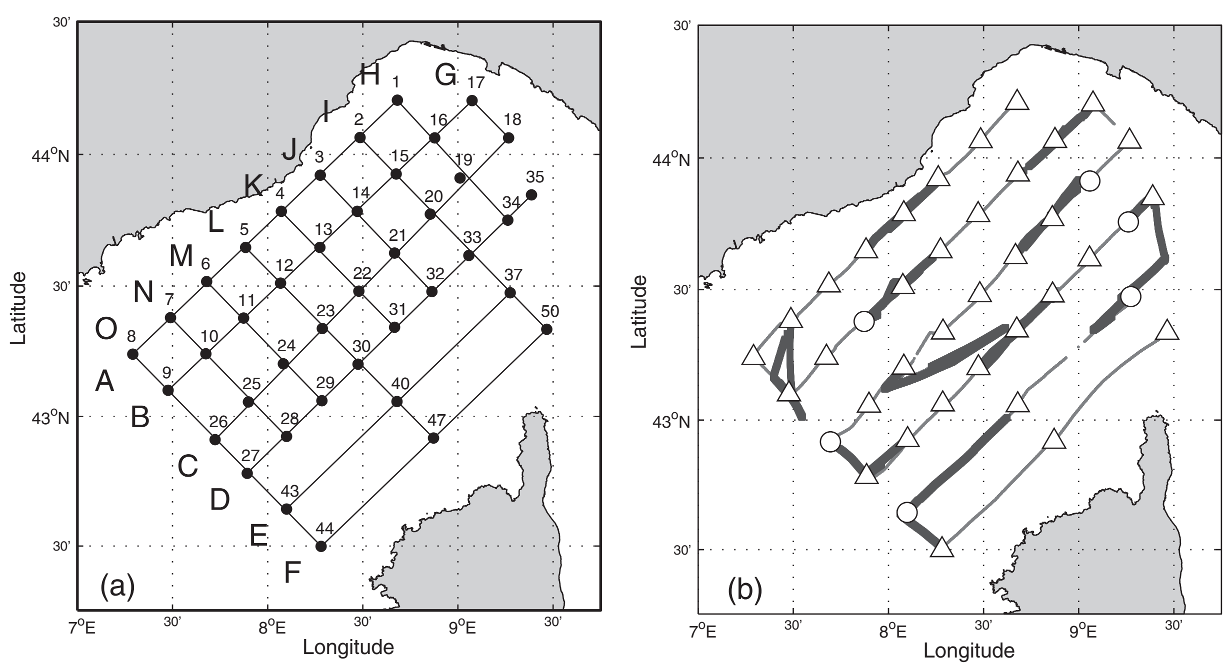

Fig. 1. Location of sampling stations. Transect letters and station numbers are given in panel (**a**). In panel (**b**), triangles indicate stations where the water column was sampled, while circles mark those stations were Isaacs–Kidd Mid-water Trawl (IKMT) net tows were also conducted. Day (thin) and night (wide) acoustic survey tracks are also shown.

from 150 to 600 m depth. All profiles were made during the day with the exception of station 43, which was occupied only at night. The profile package consisted of several instruments: a Seabird Model 19 CTD (conductivity, temperature and depth) with a Seabird 13 oxygen probe, a Wetlabs Wetstar fluorometer, TAPS and six 1.7 L Niskin bottles for collecting water samples. The CTD was provided by ICRAM (Istituto Centrale per la Ricerca scientifica e tecnologica Applicata al Mare) and calibrated before the cruise by SACLANT Centre. CTD and oxygen data were logged internally by the Seabird unit, while acoustic and fluorometer data were logged internally by the TAPS. At the end of each station, data were downloaded onto personal computers for analysis. All profile data were averaged in 1 m depth bins prior to analysis.

Water samples were collected for Chl *a* and nutrient analysis at 41 stations at four different depths: a surface sample (2–3 m), two samples that attempted to bracket the transition of the surface-mixed layer to deeper water (a subsurface sample between 30 and 40 m and a mid-water sample between 60 and 70 m) and a deep-water sample (400–500 m depth). Nine of the 164 water samples were not collected due to failure of the Niskin bottle-tripping mechanism. Samples were analysed for concentrations of Chl *a*, nitrite, nitrate, ammonia, total nitrogen, phosphate and silica dioxide.

TAPS measures acoustic backscatter at six frequencies: 265 kHz, 450 kHz, 700 kHz, 1.1 MHz, 1.85 MHz and 3 MHz. The data were analyzed in a way similar to that in the 1999 survey (McGehee *et al.*, 2004). At these frequencies, acoustic backscattering strengths can be used to estimate the amount of small (<5 mm) zooplankton in the water column. Because of surface bubble clouds, only data from 15 to 150 m depth were used in this analysis. Acoustic volume backscatter data were converted to estimates of small zooplankton biovolume ($mm^3\ m^{-3}$) binned into different size classes by inverting a fluid-sphere scattering model using the non-negative least squares method (Lawson and Hanson, 1974; Holliday, 1977; Greenlaw and Johnson, 1983). Biovolume estimates were summed over all size classes. This method and the small sampling volume (5 L) of TAPS may cause the smallest (0–0.725 mm) and largest (2.475–3.0 mm) size classes of small zooplankton to be underestimated.

Two types of net tows were also conducted during the survey. A 0.5 m diameter ring net with 202 μm mesh was hauled vertically from 150 m depth to the surface and then again from 450 m to the surface. This sampling occurred at the station occupied closest to local noon and then repeated at the same location ~12 h later. Net samples were collected in this manner approximately every 2 days. As observed in 1999, the small zooplankton were dominated by small copepods (McGehee *et al.,* 2004). Zooplankton samples were also collected with a 2 m Isaacs–Kidd Mid-water Trawl (IKMT) fitted with a 505 μm mesh and a 16.5 cm diameter cod end. Day and nighttime IKMT net samples were collected at stations 11, 19, 26, 34 and 37 with a nighttime-only tow at station 43 (Fig. 1). Double-oblique tows to a maximum depth of ~200 m were completed in 30–40 min. Tow depths were estimated from wire-out and angle, while the volume filtered by the net was measured using a calibrated General Oceanic flow meter. Samples were processed within 2 h of collection, with mature euphausiids identified to species, counted and their length measured. Other zooplankton were identified to general taxonomic groups and enumerated.

Underwater video observations were made intermittently during the cruise using a color digital video camera in an underwater housing. The camera was lowered by hand over the side of the ship to depths of 50 m. A video monitor on the deck enabled real-time observations of the zooplankton present in the water column. These observations were used to identify animal taxa in order to validate the IKMT and acoustic transect data.

Transect sampling

In addition to the station sampling, acoustic and meteorological data were collected while underway. A WeatherPak 2000 meteorological system (Coastal Environmental Systems) was mounted amidship on the forward rail of the flying bridge of the vessel. Continuous measurements were made of air temperature, barometric pressure, relative humidity, wind speed and direction, photosynthetically available radiation, Greenwich Mean Time (GMT) and Global Positioning System (GPS) position of the vessel and logged to a laptop computer.

Two Simrad EY500 scientific echo sounders (38 kHz single-beam and 120 kHz split-beam) collected volume backscattering strengths throughout the water column while the ship was underway. The 120 kHz split-beam system also provided measurements of *in situ* target strengths. The 120 kHz split-beam transducer was attached to a v-fin and deployed from a boom extended from the starboard bow. At typical survey speeds of 12 km h^{-1}, the transducer resided at a depth of 5 m. GMT and geographic position from the ship's Trimble 4000 GPS were logged by the EY500 system onto a laptop computer. Data were post-processed using SonarData EchoView V2.0097. The 120 kHz echo sounder was calibrated prior to the cruise. The hull-mounted 38 kHz system was added to the instrument suite in 2000 to sample the deeper waters that *M. norvegica* reside in during the day. Owing to technical complications, the data were only used qualitatively to verify the behavior of the *M. norvegica*.

The 120 kHz system recorded mean volume backscattering strengths (S_v) in 0.03-m depth bins over a range of 250 m. Acoustic pulses of 1 kW with durations of 1 ms at 120 kHz were transmitted every second. These data were used to generate distribution maps using echo integration methods (Hewitt and Demer, 1993). Integrated volume backscattering coefficients [S_a; m^2 $(n.mi.)^{-2}$; MacLennan and Simmonds, 1992] attributed to *M. norvegica* were integrated over depths of 8–255 m and are believed to be proportional to estimates of areal krill density (numbers m^{-2}) (Demer *et al.*, 1999; Hewitt and Demer, 2000).

RESULTS

A large dome of dense, deep water was found in the southwestern portion of the survey grid (Fig. 2). This dome was large in size (~100 km in southwest–northeast extent at 100 m depth) and appears to extend outside of the study region to the west and south. The σ_t = 28.7 pycnocline marked the upper extent of the upwelled dome, which occurred at the same depth as the Chl *a* maximum measured by fluorescence profiles (Fig. 3).

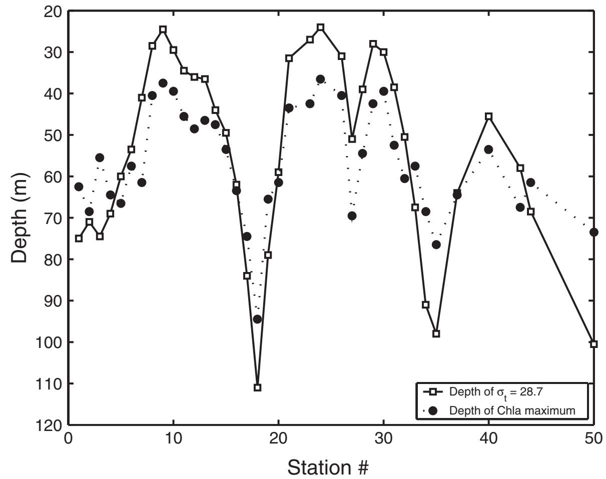

Fig. 3. Comparison of the depth of the peak in the chlorophyll *a* (Chl *a*) profile with the depth of the σ_t = 28.7 pycnocline. The σ_t = 28.7 marks the upper extent of the upwelled dome of dense water. The 1999 study of this region used the σ_t = 29 isopycnal as an indicator of the top of this dome which ranged between 40 and 70 m depth for much of the survey region. In 2000, however, the σ_t = 29 isopycnal was found much deeper, ranging in depth from 50 to 250 m.

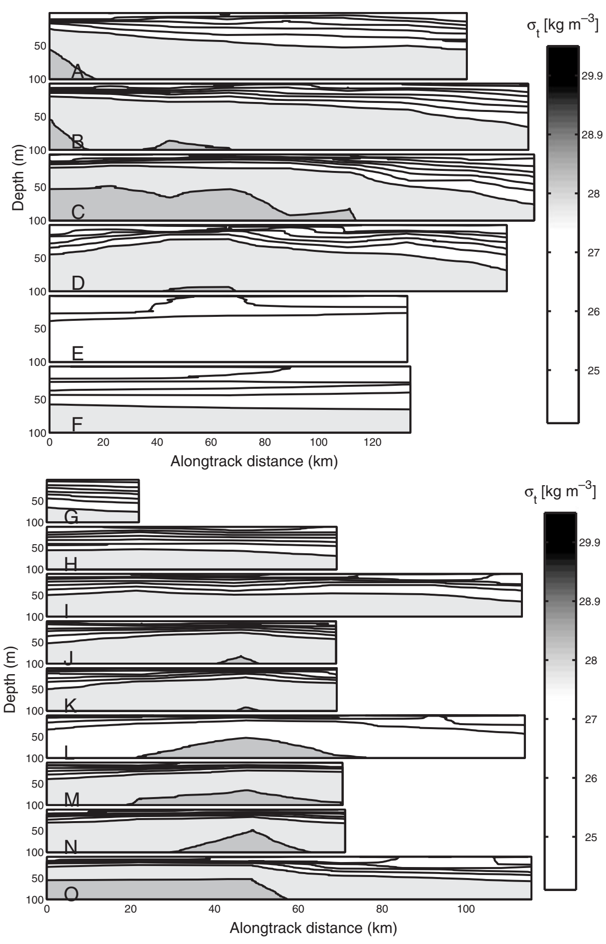

Fig. 2. Density transects of the upper 100 m from CTD station data. Transects A–F are southwestern to northeastern in direction, while G–O are northwestern to southeastern. A region of upwelled dense water can be seen in the southwestern portion of the survey area (transects A–D and L–O).

Subsurface maximum of both oxygen and Chl *a* concentration was between 30 and 70 m in depth throughout the survey region (Figs 4 and 5). The oxygen maximum was slightly shallower (5–10 m) than the Chl *a* maximum. The profiles of these two parameters show evidence of the upwelling in the southwest portion of the study region. Similarly, integrated Chl *a* concentrations from water samples are maximum in the southwest portion of the study area (Fig. 6).

Nutrient samples from four water depths at each station show that the deep waters (>400 m) were high in nitrate, nitrite, phosphate, ammonia and silica dioxide (Fig. 7). Surface waters (down to 40 m depth) for the entire region were nitrite and nitrate depleted, but samples from 60 m deep had elevated levels of nutrients in the southwest survey area. Phosphate samples followed a similar trend, although one station in the north also had high concentrations at 60 m depth. Chemical concentrations indicative of biological activity (ammonia excreted by zooplankton and silica dioxide concentrations) were fairly uniform both vertically and spatially throughout the study site, with ammonia showing a slight decrease with depth and silica dioxide demonstrating a stronger depth dependence.

Small zooplankton biovolume was distributed more uniformly than either nutrient or Chl *a* concentrations (Fig. 8). Biovolume profiles exhibited subsurface maximum at various depths, but most commonly peaks occurred

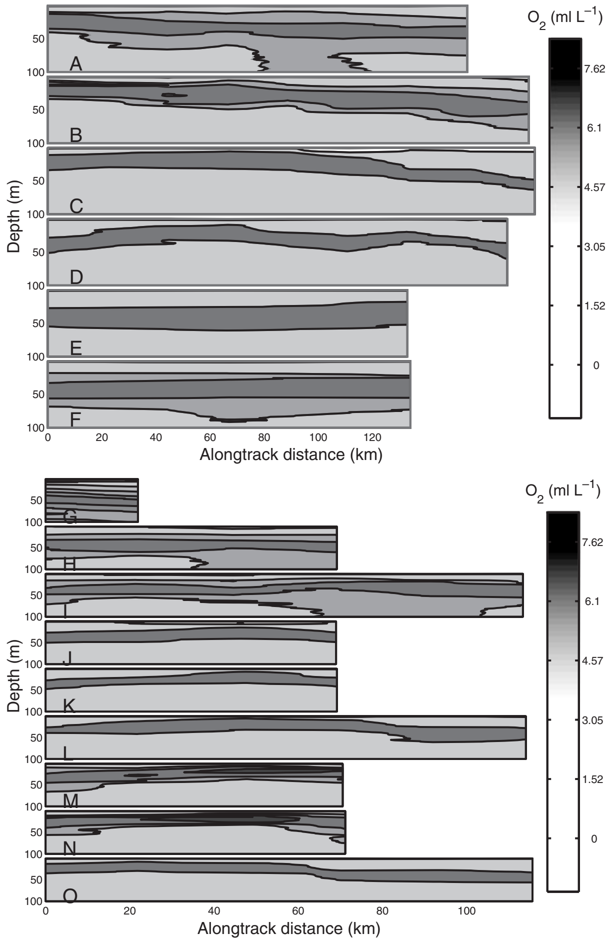

Fig. 4. Transects of dissolved oxygen concentration for the upper 100 m. Transects A–F are southwestern to northeastern in direction, while G–O are northwestern to southeastern. A subsurface maximum occurs throughout the study region at depths ranging from 20 to 60 m. The raising of the subsurface maximum in the left-most portion of transects A and B and the arched shape of several other transects (C, D, K, L, M and N) may be evidence of the upwelled dome of deep water.

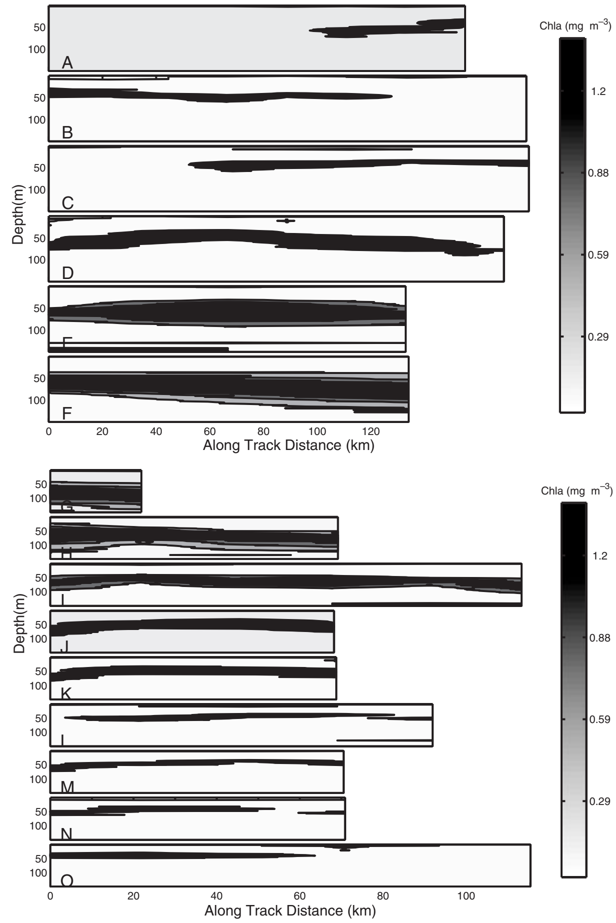

Fig. 5. Transects of chlorophyll *a* concentration (mg m^{-3}) as measured by fluorescence for the upper 150 m. Transects A–F are southwestern to northeastern in direction, while G–O are northwestern to southeastern. A subsurface maximum occurs throughout the study region at depths ranging from 40 to 80 m.

between 20 and 50 m (similar to Fig. 3 of McGehee *et al.*, 2004). Acoustic backscattering coefficients (S_a) at 120 kHz measured at night integrated from 255 m depth to the surface and averaged over 0.2 km bins were higher in the southern, central and western portions of the survey area (Fig. 8). On the basis of the IKMT net-tow data, the dominant scatterers were *M. norvegica*. Daytime acoustic survey results showed similar trends (elevated scattering in the western, central and southern regions); however, these data likely include scattering from other zooplankton such as salps and siphonophores. Values of S_a were comparable to those measured in 1999.

Krill, siphonophores and salps were the three most prevalent taxa found in the IKMT tows and the only zooplankton that occurred in numerical densities >0.1 animals m^{-3} (Fig. 9). Other animals found in densities >0.01 animals m^{-3} included panaeid shrimp, medusa, pteropods, amphipods and myctophids. Salp dispersion was uniform throughout the region and did not vary diurnally. Siphonophores were more common in shallower waters, but at night they were also found in deeper waters. *Meganyctiphanes norvegica* were only captured in the nighttime tows and were concentrated in the southwestern portion of the survey region. On the basis of length measurements of *M. norvegica*, the krill in this area were bimodally distributed, with the 1+ year class (mean length and standard deviation of 27.9 ± 4.9 mm) greatly dominating the recruits.

Typically, the late summer and early fall winds in this region are mistrals from the northwest; however, during this survey, meteorological data show that the winds (mean velocity was 5 m s^{-1}) were often (41% of observations) from the south or southwest. This change in wind direction could cause the surface waters to move toward the east and

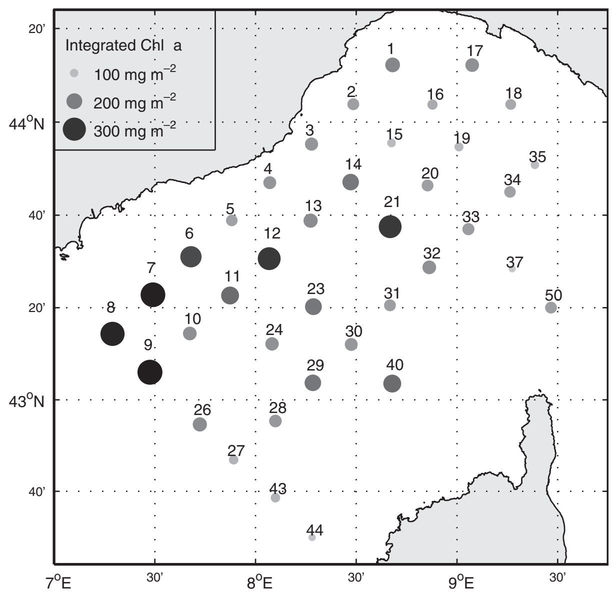

Fig. 6. Integrated levels of chlorophyll *a* (mg m^{-2}) from water samples collected at four depths for each station.

southeast, respectively, as a result of Ekman transport. Combining the effects of the observed winds with the general counterclockwise circulation leads to regions of smaller transport (in the northeast study area) and larger transport (in the southwest). Hydrographic data show that the center of the upwelling dome of water is in the southwestern portion of the study area (Fig. 2). This is consistent with the hypothesis that local wind-forcing transports surface water to the southeast and east.

DISCUSSION

The purpose of this study was to determine the distribution and abundance of krill (prey) in the Ligurian Sea, to aid researchers studying marine mammals (krill predators) in this region. Insight was also sought regarding the environmental factors controlling the populations and dynamics of the various trophic levels. Thus, more and different data sets were collected and analyzed relative to the 1999 survey (McGehee *et al.*, 2004).

The large zooplankton community of the Ligurian Sea in the late summer of 2000 was dominated by three different taxa: *M. norvegica*, siphonophores and salps. It is likely that the distribution of northern krill was related to the presence of nutrient-rich deep water being upwelled in the southwestern portion of the study area. The location of the center of the upwelling was due to both the circulation of the Ligurian Sea and local wind-forcing. Previous studies in this area (Pinca and Dallot, 1995; McGehee *et al.*, 2004) have observed this dome but with the center of the upwelling located in the middle of the Ligurian Sea gyre. Water samples indicated that this dome can provide an excess of nutrients to the photic zone at depths as shallow as 60 m. These additional nutrients supported increased concentrations of phytoplankton occurring at these depths. The distribution of Chl *a* (from both water samples and fluorometer measurements) and oxygen concentration show that the maximum levels of Chl *a* and dissolved oxygen were in a 10–20 m thick layer occurring between 20 and 80 m in depth which supports this hypothesis. Integrated Chl *a* concentrations were four times larger in 2000 than in 1999, with a maximum value of 322 mg m^{-2}.

However, the next step in the trophic pathway was not clear. Presumably, zooplankton would feed on the phytoplankton present, but the distribution of small zooplankton (as measured by the TAPS) and several of the larger zooplankton (salps and siphonophores as measured by net hauls) was not elevated in the southwestern area of the study and, instead, was generally uniform. Small biovolume values were twice as high as those found in 1999, with an average value of $8.7 \times 10^4 \pm 3.8 \times 10^4$ mm^3 m^{-2}. Unlike other zooplankton and also unlike the 1999 study, *M. norvegica* were found in higher concentrations (both by acoustic and by net-tow sampling) in the same area that had increased primary production. It is possible that either krill were the primary predators on the phytoplankton blooms that occurred as a result of the upwelling or the krill have consumed much of the small zooplankton which fed upon this bloom.

The first explanation may be possible due to the krill's stronger ability to actively migrate, which could allow them to minimize the effects of surface transport and remain in this highly productive region. Calculations based on August current speeds from Béthoux *et al.* (Béthoux *et al.*, 1982) suggest that the local residence time of surface water in the West Corsica/Tyrrhenian/Ligurian Current system is <1 month, while deeper waters with smaller current velocities would have longer residence times. It is possible that differences in vertical migration ability between small and large zooplankton combined with depth-varying current velocities could change the distribution of the zooplankton populations. However, this theory does not fully explain the difference in the distribution of large (krill) and small (copepods) zooplankton since both of these animals have been observed to migrate vertically in this region (Andersen *et al.*, 2001). The 1999 study found that *M. norvegica* were uniformly distributed throughout the basin, although the survey in 1999 was not as extensive as the 2000 survey so it may have not sampled regions of elevated krill abundance.

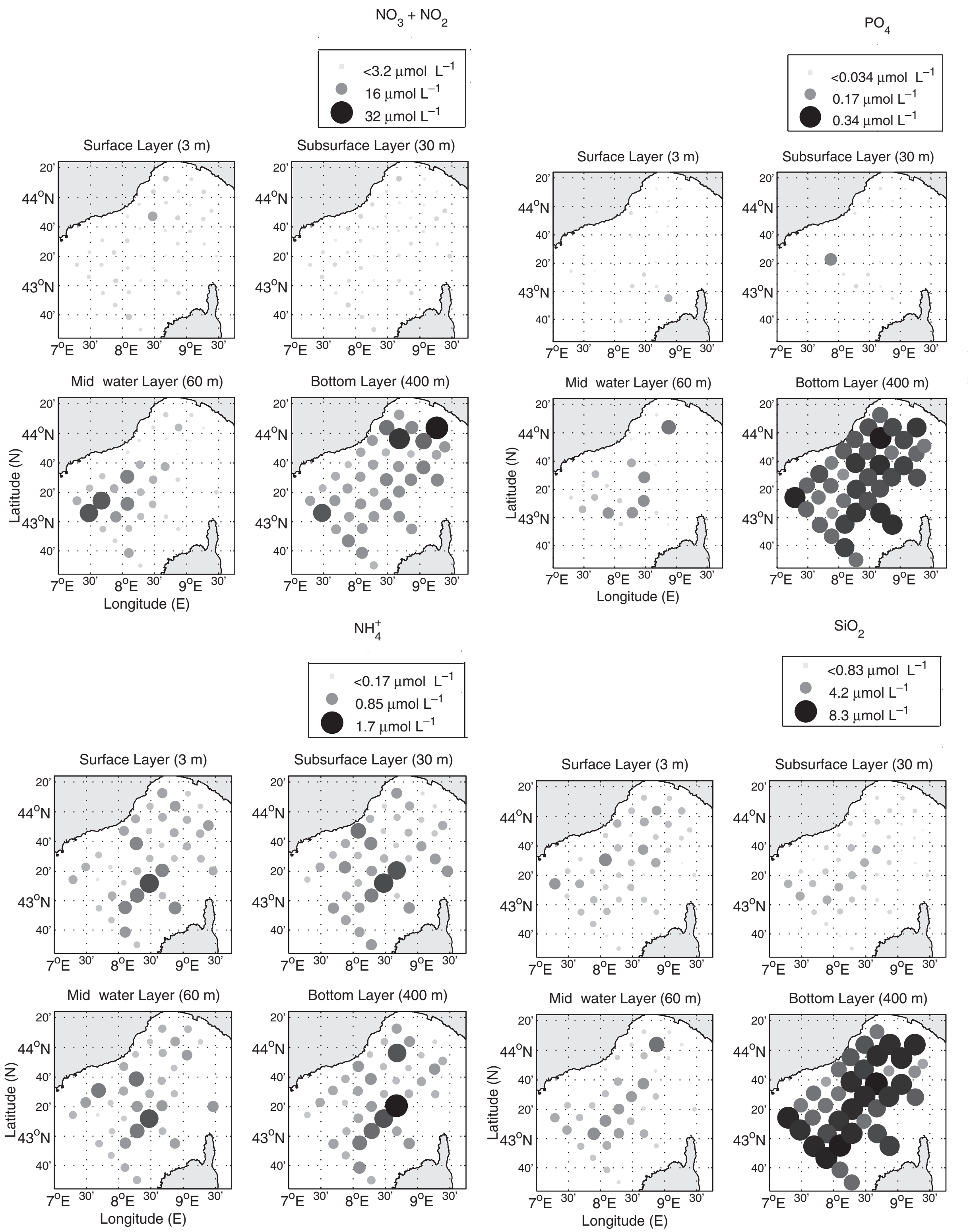

Fig. 7. Spatial and vertical concentrations of combined nitrate and nitrite, phosphate, ammonia and silica dioxide at four different depths [surface layer (3 m), subsurface layer (30 m), mid-water layer (60 m) and bottom layer (400 m)] from hydrographic water samples. Both nitrogen and phosphate are prevalent in the deep water and show higher concentrations at shallower depths in the southwestern portion of the survey. Spatial distributions of ammonia and silica dioxide are fairly uniform, although there are elevated concentrations in the middle of the survey area.

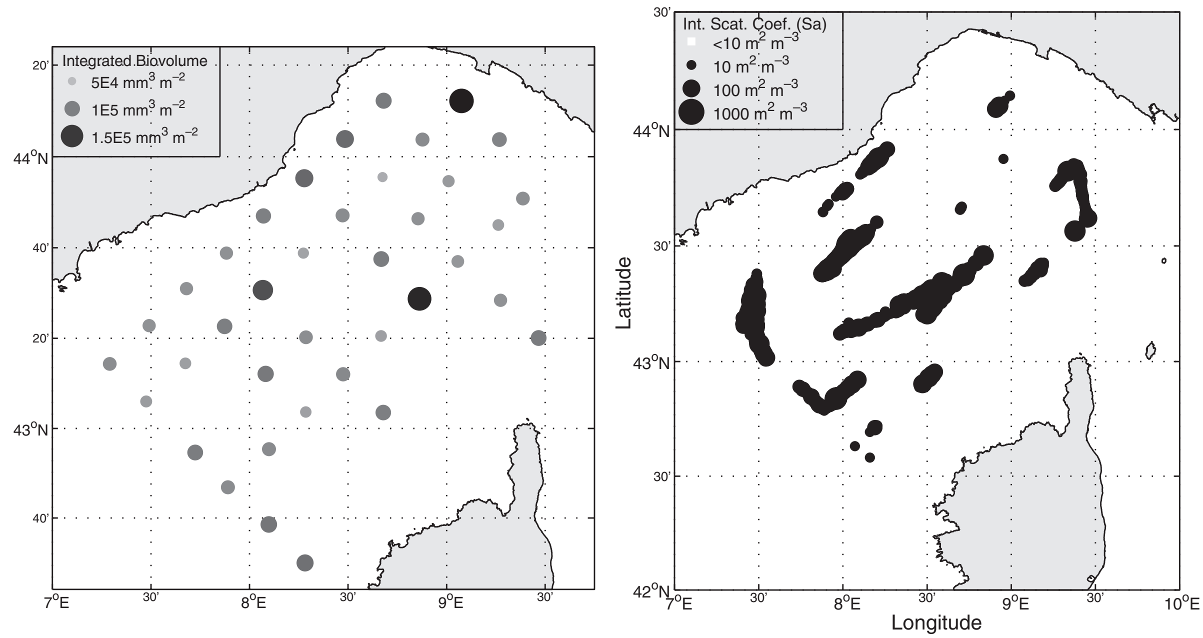

Fig. 8. Small (left) and large (right) zooplankton distributions as measured by acoustic systems. The small (<5 mm) zooplankton figure shows biovolume integrated from 15 to 150 m depth as measured by the Tracor Acoustic Profiling System (TAPS). The distribution of small zooplankton was fairly uniform in contrast to most of the other ecological parameters studied. The large (>5 mm) zooplankton figure shows nighttime acoustic backscattering coefficients integrated over the upper 100 m of the water column (S_a) at 120 kHz. Data collected at night show elevated concentrations of scatterers (dominated by *Meganyctiphanes norvegica*) in the southwestern survey area. Values of S_a are similar to those measured in 1999. Daytime S_a values were low likely due to *M. norvegica* migrating into deeper waters during the day.

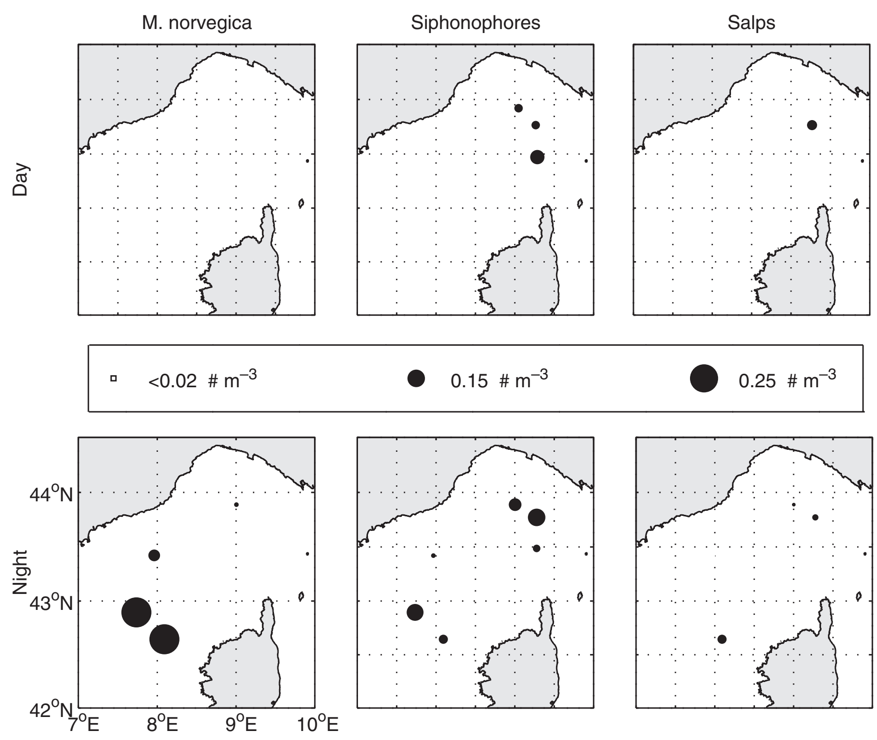

Fig. 9. Numerical density of the three main zooplankton taxa (*Meganyctiphanes norvegica*, siphonophores and salps) caught in an Isaacs–Kidd Mid-water Trawl (IKMT) to 200 m during the survey for both day and night tows. Krill exhibited diurnal migration and were caught in far greater numbers during night tows. Siphonophores also showed some evidence of migratory behavior, while salps were caught in similar concentrations regardless of the time of the net tow.

The results of this study indicate that the distribution of *M. norvegica* in the Ligurian Sea may be controlled by phytoplankton blooms resulting from upwelled nutrient-rich water. The location of this dome of bottom water is controlled by the general circulation of the sea but also affected by local winds. Future studies of lower-trophic ecosystems should include current or historical meteorological and physical oceanographic data sets in their analysis since these factors may provide insight into the distribution and abundance of the krill population.

Meganyctiphanes norvegica are omnivorous (e.g. Mauchline, 1960; Sameoto, 1980) and, thus, ideally suited for life in the Ligurian Sea, where central gyre upwelling guarantees continued primary productivity late into the summer. The euphausiids remain in the Ligurian Sea, even in the peripheral and frontal zones, by migrating down to low-current regimes. From this perspective, it is perhaps not surprising that we did not find a stronger pattern of distribution of these animals. It is also not surprising that they provide a stable food source for top predators. Forcada *et al.* (Forcada *et al.,* 1995), for example, point out that during their 1991 cetacean survey of the western Mediterranean, *all* detections of fin whales were made in the Liguro-Provençal Basin.

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