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The relationship between summer aggregation of fin whales and satellite-derived environmental conditions in the northwestern Mediterranean Sea

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Abstract

Few studies have tried to explain the summer distribution pattern of fin whales (*Balaenoptera physalus*) in the northwestern Mediterranean Sea, an area characterized with heterogeneous and transient hydrobiological features. Satellite imagery was used to gain knowledge on primary biomass over large time and space scales and to process environmental variables of significance to the problem of fin whale distribution.

Fin whale distribution was obtained from survey data and expressed into sightings per unit of effort. Net primary production (g C/m^2/day), NPP, can be estimated with a model by processing remote-sensed measurements of chlorophyll concentration, provided by SeaWIFS DAAC. NPP was integrated over different temporal scales, related to primary production cycles in the area. Additional variables were derived from sea surface temperature (AVHRR/NOAA sensors).

Multiple cross-correlation coefficients were calculated between these environmental parameters and the fin whale summer distribution from 1998 to 2002. A predictive model, the potential grouping index, was developed from this statistical approach.

This study improves our understanding of the variability of fin whale distribution in summer. While food availability at a particular time and place is a function of environmental conditions in the previous months, this study provides evidence that whales adapt their movements and group size directly to food availability rather than to instantaneous environmental conditions.

Keywords: Fin whale; Summer distribution; SeaWIFS remote sensing; Primary production; Mediterranean Sea

1. Introduction

Fin whales (*Balaenoptera physalus*) aggregate in the northwestern Mediterranean Sea from spring to the end of summer (Notarbartolo Di Sciara et al., 2003). The summer grouping is still to be understood, but is assumed to be related to primary biomass because the euphausiid *Meganyctiphanes norvegica*, its main prey, (Orsi Relini et al., 1994), is partly phytophageous during spring and summer (Casanova, 1974). This area of the Mediterranean is of interest as it is a marine mammal sanctuary subject to disturbance by maritime traffic.

The study was made possible by satellite remote sensing which enabled efficient long-term monitoring of the area. Satellite studies on the Gulf Stream and the California Current have shown links between ocean currents and the distribution of cetaceans (Brown & Winn, 1989; Jaquet et al., 1996; Smith et al., 1986; Waring et al., 1993). By comparison, the Mediterranean Sea is composed of smaller permanent or temporary hydrological structures, forming a complex environment with marked seasonal and annual variability (Taupier-Letage & Millot, 1986). Links between marine populations and environmental parameters can be difficult to identify: for example, no annual bloom cycle has been described over the northwestern Mediterranean Sea.

Primary production can be estimated with a model by processing remote-sensed measurements of chlorophyll concentration, provided by SeaWIFS DAAC. The frequency and spatial coverage of satellite surveying enables monitor-

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ing of dynamic ecological processes such as spring blooms, and can be applied to forecasting the distribution of secondary or even tertiary organisms, including baleen whales.

2. Materials and methods

This study used sea surface color to estimate primary production, and correlated it with data on summer fin whale distribution in the northwestern Mediterranean. Remote-sensed sea surface temperature was also used. Environmental parameters were correlated with fin whale sighting rates from boat surveys for the period 1998–2002. Using field and satellite data for consecutive 8-day periods, multiple cross-correlation coefficients were calculated for 30 × 30 in. spatial cells. A predictive model was developed to locate and to count areas potentially favorable to whales, and this was tested to compare predicted and actual fin whale distribution during summer 2002.

2.1. Study site and scales

The area of study extended from 4°E to 13°E, and from 40°N to 43°30′ N, for depths greater than 500 m. Fin whale sighting rates and hydrological and biological measurements were based on 30 × 30 in. latitude/longitude spatial cells. These cells were grouped in geographical provinces (Fig. 1), which were defined by geographical and hydrological criteria such as currents position, upwelling process or specific wind stress area. For example, the Ligurian province is an area of cyclonic currents between Corsica and the mainland. The period of study was 1998–2002, as data for these years was available from the SeaWIFS image system and from cetacean surveys.

Satellite data was obtained from early March to the end of August. Whales were observed throughout the summer; efforts of whale sighting in the different years and in the different regions are listed in Table 1. Data was treated by 8-day period, because this corresponded to the satellite data delivery agreement and is of biological significance in phytoplankton blooms.

2.2. Whale survey data

All survey trips used a 12-m boat and the same observer team. Sighting conditions were always good to excellent, with wind speed not exceeding Beaufort 3. Sampling was in random straight-line segments.

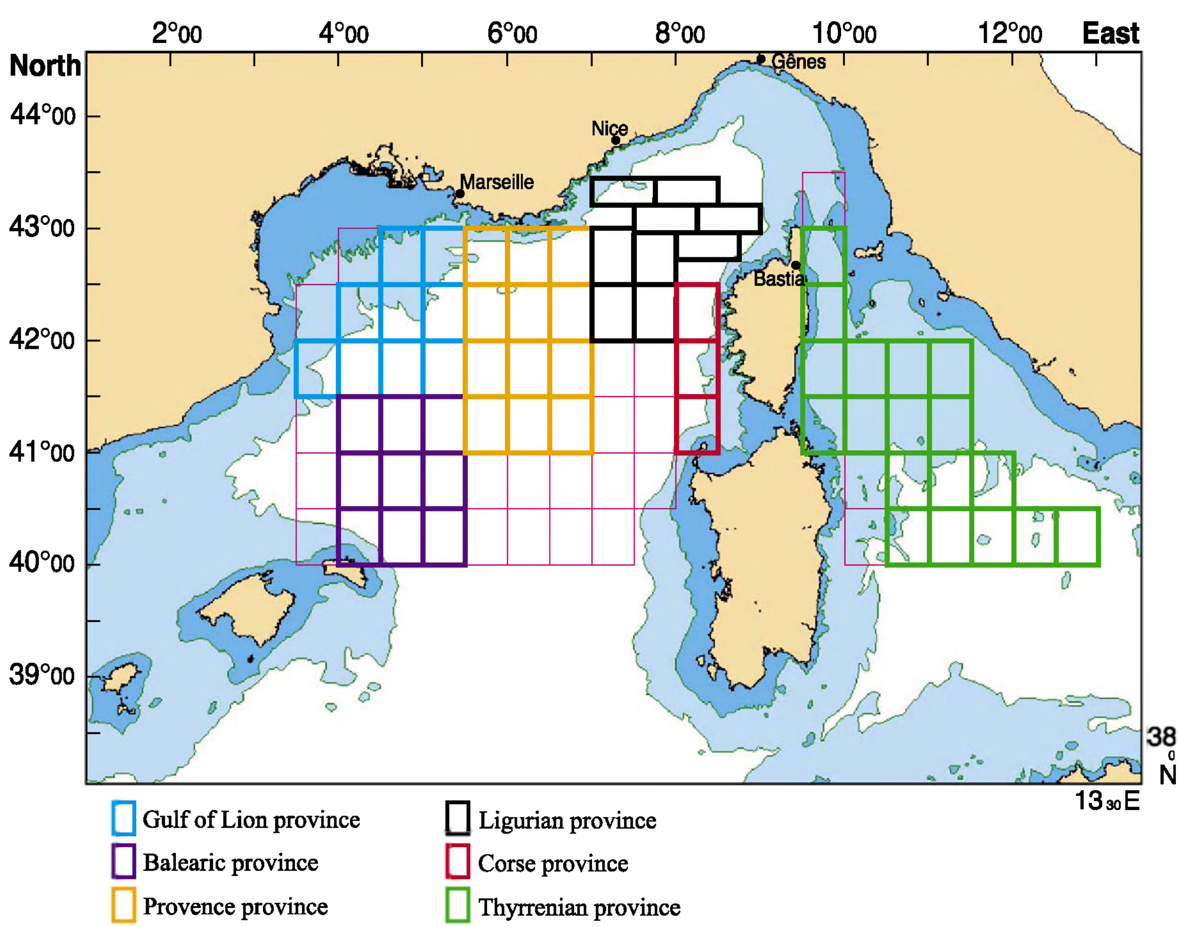

Fig. 1. The study area and the six provinces.

Table 1
Summary of whale survey 1998–2002

	Effort (nautical miles)	Whales sighted
N Balearic	598	6
N Tyrrhenian	802	15
Ligurian	3760	127
Provence	1701	53
Gulf of Lions	579	60
Total northwestern	7440	261
1998	2247	35
1999	2395	71
2000	1229	22
2001	2165	89
2002	1238	44
Total western	9274	261

Effective effort (Wind Beaufort <4), numbers of whales are given in nautical miles by province and by year. Total effort by year is given for all western Mediterranean (no whales were seen south of 40°N).

The visual survey consisted of continuous naked-eye observation by groups of three observers in 2-h shifts. One observer stood in front of the mast, searching the $\pm 45°$ sector ahead while the other two observers scanned the 30° to 90° and $-30°$ to $-90°$ sectors on either side. The standard sampling unit was defined as 20-min observation. For each unit, the corresponding effort (distance covered during the period, about 3.7 km) and sighting data (number of whales sighted and school sizes) were recorded. This sampling unit corresponds with the unit used in the passive acoustic sampling which was carried out simultaneously for sperm whale tracking (Gannier et al., 2002). When fin whales were detected, the relevant parameters were recorded (bearing and distance from the boat, latitude and longitude, sea state), and the whales were usually approached to a distance of 100–200 m to determine the school size and structure, and to record behavior. A total of 13,625 km were surveyed, and 155 observations of whales were obtained, with 261 individuals counted. The whale distribution was quantified as a sighting rate for individuals ROR (whale/nautical mile of effort), for a time unit of 1 week. Average whale school sizes were computed, as school size can be an indicator of whale feeding success or food availability (Gannier, 2002; Giard et al., 2001).

2.3. Environmental parameters

Environmental parameters related to food availability were chosen, as summer is the main feeding period for fin whales (Orsi Relini et al., 1994).

2.3.1. Net primary production

Net primary production (NPP) was expressed in g C/m^2/day and estimated from satellite-derived pigments. Photosynthetically active radiation (PAR) was measured by SeaWIFS scanner, and sea surface temperature (SST) was measured by AVHRR scanner. These data were treated using the light-photosynthesis model of Behrenfeld and Falkowski (1997).

SeaWIFS products imported from the Goddard DAAC/NASA were spatially and temporally averaged (level 3 products, 8-day average) and mapped onto a uniform latitude/longitude projection. In these products, pixels correspond to bins having a size of 9×9 km^2 at the equator. SST products, obtained from the PO.DAAC/NASA, were used with the same spatial and temporal scales as the color data.

NPP describes local food availability better than does surface chlorophyll pigment concentration in the Mediterranean Sea, where the maximum chlorophyll concentration is subsurface (Joint & Groom, 2000). NPP was integrated over three temporal scales related to primary production processes, both short- and long-term: over 3 months from March to May (NPP1), over 5 months from March to July (NPP2), and over 3 weeks preceding each whale survey period sighting (NPP3).

2.3.2. Sea surface temperature

Two gradients were calculated from sea surface temperature. SST1 is a horizontal SST gradient, calculated as the temperature difference between two points in a cell 20 km apart, along the boat path. SST2 is the temperature gradient within each cell between two successive 8-day periods. This parameter was used as an indicator of wind effects on the vertical stratification or mixing through some 10 m depth. Water stratification may have effects on vertical migration of the prey species *M. norvegica*.

2.4. Analysis methods

Satellite images were displayed and analyzed using the WIM software (version 5.45, Kahru & Laksker, 2002). Survey results were superimposed on satellite images of the same period. Multiple cross-correlation coefficients between environmental parameters and summer distribution of whales were calculated (Snedecor & Cochran, 1957), by correlating all survey data and environmental data during the period 1998–2001.

Series were made by 8-day period to describe seasonal changes, by provinces to test geographical differences, and by year to test inter-annual variations.

The role of each parameter in the variability of ROR was estimated from the correlation coefficient (partial correlation). Significance was tested with the Fisher–Snedecor test. Correlation results were used to predict fin whale grouping as a "Potential Grouping Index" (PGI), which was calculated as the most probable linear combination of the five environmental factors:

$$PGI = a\ NPP1 + b\ NPP2 + c\ NPP3 + d\ SST1 + e\ SST2$$

The value of this expression, describing the 1998–2001 period, was calculated and tested for 2002 environmental and whale distribution data. PGI scores were calculated for surveyed cells and were also applied to non-surveyed cells

Table 2
Yearly correlation coefficient between fin whale/nm (ROR) and environmental parameters

Year	Mean NPP	Coefficient of partial correlation					Contribution to explain ROR variability	*df*
		NPP1	NPP2	NPP3	SST1	SST2		
1998	33.9	0.224	− 0.024	0.485	0.373	0.2657	SST1: 25.6%; NNP3: 46.4%	30
2001	36.1	0.178	0.34	0.196	0.484	0.104	SST1: 50.2%; NPP3: 15.2%	58
1999	48.5	0.334	0.311	0.144	0.317	− 0.178	NPP1: 44.5%	41
2000	46.1	0.178	0.386	0.457	0.067	0.112	NPP2 + NPP3: 76.5%	65
2002	44.7	0.489	0.502	0.3489	0.6613	− 0.095	NPP2: 31%; NPP3: 55%	47

Mean NPP: mean daily primary production, March–August (22 weeks), g C/m^2/day.

in each province, in an attempt to identify areas with environmental characteristics similar to those where many groups of fin whales were sighted.

We also attempted to determine a relationship between the whale school structure, i.e. the average number of whales per group, and the availability of favorable areas, as given by the number of cells featuring a high PGI. Mean school size was compared with the frequency of favorable areas RF, defined as the ratio of the number of whale-favorable cells to the total number of investigated cells, for every 8-day period, over the entire northwestern Mediterranean.

3. Results

3.1. Fin whale distribution and environmental parameters

Relationships between the fin whale distribution (ROR) and the five environmental parameters used were not immediately apparent when data from all dates and all areas were pooled. When the data were sorted, clearer relationships emerged and the contribution of each parameter to ROR variability could be estimated.

When the data were analyzed by year, the contribution of the different parameters was related to the annual level of primary production (Table 2). During years of low primary production (1998 and 2001), the whale sighting rate (ROR) is more closely related to short-term environmental processes. Local primary production (NPP3) and the zone of thermal front (SST1) together explained 72% of ROR variability in 1998 and 65.4% of its variability in 2001.

During the years of high primary productivity (1999 and 2000), the number of whales was related to long-term environmental processes (the spring bloom) as shown by both NPP1 and NPP2. In 2000, the bloom started at the beginning of April, a month later than in 1999, hence the low NPP1 and high NPP3. In 2000, 94.8% of the variability was explained by NPP2 and NPP3. In 1999, all parameters combined account for 77.2% of the variability of ROR, NPP1 alone accounting for 44.5%. The relationship between long-term processes and ROR included a delay of several weeks.

Long-term processes explained whale distribution at the beginning of the summer, but the relative importance of long- and short-term processes as predictors of whale distribution changed as the summer progressed (Table 3). From the end of June to mid-July, fin whale distribution was mainly correlated with parameters of spring primary production (during 20–27 July, NPP1 explained 37.1% and NPP2 explained 46.3% of ROR variability). However, by the end of July, four environmental parameter were significantly correlated (NPP1 and NPP2 explained 42%; NPP3 and SST1 explained 55.8% of ROR).

From the end of July to mid-August, short-term processes were more significant: for period 4–13 August, NPP3, SST1 and SST2 combined explained 72.4% of the variability of ROR. For period 13–20 August, the same of three-parameter combination explained 74.6% of ROR variability.

Analysis of the spring sighting data of 2001 also indicated that the relationship between environmental parameters and whale distribution changes during the spring and summer. In April and May 2001, whales were observed in thermal front areas (SST1 explained 35% of ROR variability). No immediate correlation with primary production parameters was apparent, although spring blooming had begun.

Table 3
Eight-day period correlation coefficient between fin whales/nm (ROR) and environmental parameters, 1998–2002

Period	Coefficient of partial correlation					Contribution to ROR variability	*df*
	NPP1	NPP2	NPP3	SST1	SST2		
2–30 April; 24–31 May	0.184	–	− 0.015	0.86	0.096	SST1: 35%	37
17–26 June	0.444	0.399	0.198	0.375	0.132	NPP1 + NPP2: 83.4%	25
20–27 July	0.532	0.527	0.582	0.426	− 0.038	NPP1 + NPP2: 42%; SST1 + NPP3: 55.8%	44
27 July–5 August	0.089	0.302	0.340	0.358	0.214	NPP3: 23.9%; SST1 + SST2: 44.4%	42
4–13 August	0.287	0.036	0.507	0.444	0.129	NPP3: 40.2%; SST1 + SST2: 32%	21
13–20 August[a]	0.430	0.421	0.466	0.206	0.249	NPP3: 27.5%; SST1 + SST2: 47.1%	22

[a] Survey includes only Ligurian and Provence coastal areas.

Table 4
Correlation coefficient for each province between fin whales/nm (ROR) and environmental parameters, 1998–2002

Province	Coefficient of partial correlation					Fisher estimation	Fisher statistic, $\alpha = 0.05$
	NPP1	NPP2	NPP3	SST1	SST2		
Ligurian	0.15	0.261	0.273	0.301	0.114	$F_{SST1} = 10.2$ $F_{NPP3} = 6.9$ $F_{NPP2} = 7.7$	$F_{\alpha} = 3.92$
Provence	0.217	0.176	0.289	0.394	− 0.005	$F_{SST1} = 3.35$	$F_{\alpha} = 2.08$
Tyrrhenian	0.509	0.524	− 0.104	0.327	− 0.097	$F_{NPP1} = 8.24$ $F_{NPP2} = 8.95$	$F_{\alpha} = 2.09$
Gulf Lions	0.176	− 0.01	0.204	0.166	− 0.032	$F < F_{\alpha}$	$F_{\alpha} = 2.307$
Balearic Is.	0.256	0.06	0.306	− 0.02	− 0.856		

Hence, fin whale summer distribution was correlated with spring primary production including a time lag of a few weeks, but gradually became more correlated with short-term processes such as production peaks linked to thermal fronts.

The study area was initially divided into provinces according to hydrological characteristics. Data analysis by province indicates that fin whale distribution also depends on local environmental factors (Table 4). In the western provinces (Balearic and Gulf of Lions), a significant Fisher–Snedecor correlation of ROR with short-term production was found ($F_{NPP3} = 37.3$ and $F_{0.05} = 5.32$), probably related to the repetitive short-term blooms and frequent Mistral wind events. In the Tyrrhenian Sea, relationships with early spring production (NPP1 and NPP2) and the thermal front were observed. This front is related to local upwelling east of Bonifacio, which produces strong surface thermal gradients.

In Provence and Ligurian provinces, there were also relationships with long-term processes—early spring production (for Ligurian province, $F_{NPP2} = 7.7$ and $F_{0.05} = 3.92$)—and with short-term processes (for Ligurian province, $F_{SST1} = 10.19$ and $F_{NPP3} = 6.9$). Furthermore, short-term blooming seems to be related to repetitive blooms after the first spring production, especially in the Ligurian province. These and other observations show that the hydrological characteristics specific to a province could often be used as a predictor of whale presence.

3.2. Prediction of favorable areas for fin whale aggregation

The 1998–2001 data gave a PGI varying from 29.9 to 68.3. Fin whales were frequent for a PGI>55 (Fig. 2). For smaller values, whale sighting rates were close to 0 whale/nm. The correlation coefficient r between PGI and ROR was 0.55 ($df = 188$). The observed value of t_{ROR} ($= 7.49$) exceeded the 95% confidence limit level ($t\alpha/2 = 1.97$), indicating a significant correlation of the fin whale sighting rate ROR with the PGI index. When the model was tested for 2002, the plot of PGI values (square points in Fig. 2) was similar to that of previous years, showing consistency of results across the years studied.

We also calculated PGI for a set of cells which were not surveyed by the boat. Cells with a PGI>55 were regarded as whale-favorable areas. During the 17th to 26th June 2000 period, whales aggregated in five areas (dots) with PGIs varying in the range 56–62 (Fig. 3a and b). The intense spring bloom of 2000 (shown green in Fig. 3b) explained these local values, as there was no evidence of high primary biomass or of thermal structure

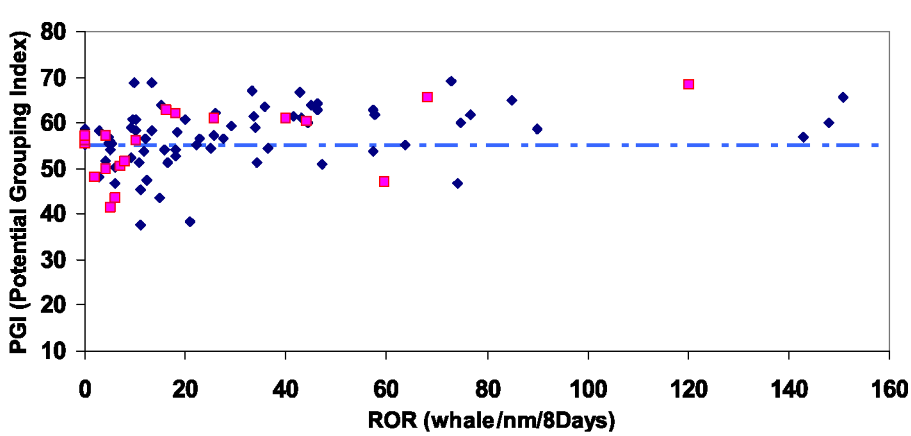

Fig. 2. Relation between number of fin whales observed/effort unit and PGI. Correlation coefficient $r = 0.55$, ◆ 1998–2001, ■ 2002, – below this limit, PGI < 55, number of whales = 0.

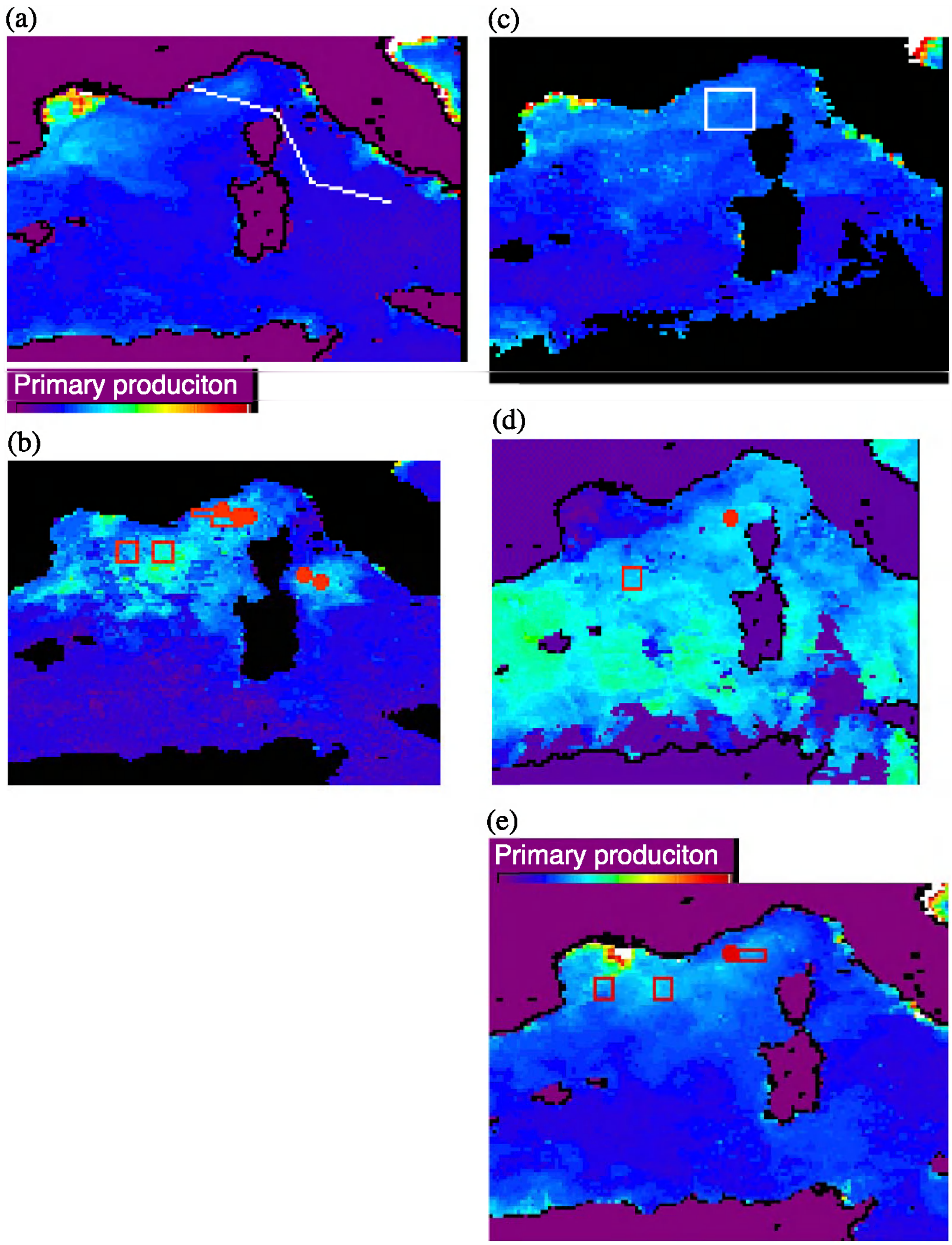

Fig. 3. Relationships between PGIs, fin whale distribution and environmental parameters. Left sets. (a) Distribution of net primary production (g C/m^2/8 days) 17–26 June 2000 (computed from SeaWIFS files). No oceanic structures are shown within the area surveyed by the boat during this period (white line). (b) Distribution of NPP1 (net primary production (g C/m^2), March–April 2000, SeaWIFS image). Red marks show whale aggregations (dots) and potential whale-favorable cells (squares) 17–26 June; they are located on high NPP1 areas. Right sets. (c) Distribution of net primary production (g C/m^2/8 days), 4–13 August 1999 (SeaWIFS image). White square shows area surveyed. A small production front was detected directly above the continental shelf, the northwestern side of the area surveyed encroaches on this production zone. (d) Distribution of sea surface temperature (SST), 4–13 August 1999 (AVHRR image). Red marks showed whale groupings (points) and potential cells (squares). The coastal zone was characterised by colder surface waters: its limit was marked by a thermal front at the 2000 m bathymetric line. (e) Distribution of NPP3 (net primary production in g C/m^2/3 weeks, 20 July–13 August 1999—SeaWIFS image). Red marks are whale groupings observed (dots) and other potentially whale-favorable cells (squares), 4–13 August. This image shows a phytoplankton bloom in the coastal zone, characterised on the AVHRR image by colder surface waters.

during the sea survey. Four other areas (squares in the picture) had also PGIs in excess of 55 because of the intense spring bloom (Fig. 3a); the boat did not surveyed these areas but according their PGIs, they should be supposed as whale-favorable as the five previous prospected areas.

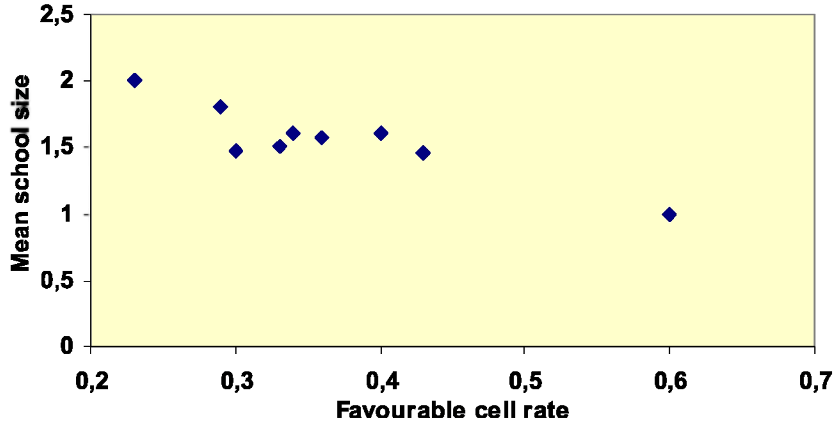

Fig. 4. Relation between the frequency of favorable spatial cells (RF) and the whale mean school size. RF = number of cells with PGI>55/total number of cells examined.

The August 1999 data (Fig. 3c) indicate that in late summer fin whales appeared to gather in areas affected by thermal structures (Fig. 3d) and short-term primary production NPP3 (Fig. 3e), as predicted by the model. During the study period, no biomass was detected in the surveyed area, but the thermal structure was marked.

3.3. Relation between frequency of favorable areas for fin whales and mean school size

The mean school size was inversely correlated with the frequency RF of whale-favorable cells throughout the study period (Fig. 4). In August 2000, 60% of cells sampled had environmental conditions favorable to whales (RF = 0.6), and the mean school size was only about 1. By contrast, in July 1999, the rate of favorable cells (RF) was 0.23, and the mean school size was about 2.

4. Discussion

4.1. Relationships between whale distribution and environmental characteristics

Several studies have attempted to correlate mysticete distribution patterns with oceanographic parameters. Within the limits of the highly variable ecosystem of the northwestern Mediterranean Sea, we have shown that fin whale distribution could be a result of the development cycle of the first trophic levels. In years of high spring primary production (1999 and 2000), fin whale groupings were observed in cells of high and long-lasting production.

Warren et al. (submitted for publication) studying the biological and physical factors affecting the distribution of *M. norvegica* and other zooplankton in the Ligurian Sea in late summer 2000 explained that euphausiids are strong vertical migrators and are not exported by surface currents as are some smaller zooplankton. It is assumed that reproductive success (including juvenile development from late winter to late spring) strongly determines krill abundance and distribution (Casanova, 1974; Labat & Cuzin-roudy, 1996). Consequently, high recruitment of *M. norvegica* depends on the intensity of the local primary production in spring. Comparison of acoustic survey results on zooplankton, obtained in the Ligurian Sea on 2–13 August 1999 (McGehee et al., submitted for publication), and fin whale sightings within the same area and time show that fin whales aggregated within large zooplankton patches, which were located largely in areas where spring primary production peaked (our results).

In agreement with this finding, the years of low spring primary production (1998 and 2001) would be expected to produce a less successful cohort of new krill. For these years, summer distribution of fin whales was linked to short-term production and to thermal fronts. Even temporary thermal front zones, as in the Ligurian Sea, can be considered as areas of concentration of euphausiid juveniles and filter-feeders (Jacques, 1994). These biomass concentrations may constitute an alternative feeding resource for large organisms such as fin whales.

The seasonal relationship between fin whale distribution and environmental conditions may also indicate a link with food availability. During the April–May bloom, the second trophic level is composed of the adult euphausiids that remain from the previous year's cohort, and this year's larvae and juveniles (Labat & Cuzin-roudy, 1996). Euphausiid biomass was low, and fin whales were observed in association with large permanent frontal structures. From late June to mid-August, the grown euphausiids became attractive prey, and fin whale aggregations were in areas where spring primary production had already peaked and generated zooplankton recruitment. This relationship was observed in all the provinces studied.

At the end of summer, fin whale distribution was linked to frontal zones, close to coastal areas (Ligurian and Provençal provinces), or above the upwelling east of Bonifacio. These results suggest that fin whale grouping is linked to availability of prey which is in turn determined by primary production.

Spring and summer primary production was variable during the 5 years studied, and the size of fin whale groups was not constant. The linear relationship between the number of cells offering favorable environmental conditions and the mean size of whale groups provides evidence that whales adapt their movements to food availability, and group size is accordingly modified.

4.2. Advantages of the methods used

The study of a diurnally migrating zooplankton such as *M. norvegica* by conventional methods requires extensive survey work, and is consequently space- and time-limited. This is true to a lesser extent for a whale species such as *B. physalus*.

Satellite observation measures only chlorophyll pigments and surface temperature. There are time lags between chlorophyll peaks and zooplankton blooming peaks, and in turn between zooplankton peaks and observed fin whale aggregations. Continuous satellite measurement makes it possible to integrate information over time, giving a chronological description of the superficial waters. The development of a model to estimate primary production allows description of the environment in terms of global food resources, and the NPP presented here is an attempt to link these global resources to the feeding strategy of a predator.

5. Conclusion

This study improves our understanding of the variability of fin whale distribution in summer. While food availability at a particular time and place is a function of the environmental conditions of the previous months, this study provides evidence that whales adapt their movements and group size directly to food availability rather than to the immediate environmental conditions.

Remote sensing affords a new methodological approach where water masses can be monitored. Other predictors of fin whale distribution probably include wind conditions which influence prey patchiness, and vertical migration of prey species.

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