
Distribution and spatial organization of groups of sperm
whales in relation to biological and environmental factors in
the South Pacific

by

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ABSTRACT

I studied the distribution, spatial organization and movements of groups of female and immature sperm whales (*Physeter macrocephalus*) in relation to chlorophyll concentration, amount of subsurface biomass, temperature gradients and underwater topography in the South Pacific. I examined the influence of these factors over a wide range of spatial scales (10 km - 1800 km) using a range of temporal resolutions (a few hours to 130 years), and assessed the importance of food resources in determining sperm whale distribution. Data were collected during a year-long survey around the South Pacific, and extracted from 19th century whaling logbooks and from satellite color observations. Principal component analyses and correlation analyses were used to assess the relationship between environmental measures and to relate them to sperm whale density. Groups were usually clustered over areas 10 to 70 km across, forming what I called "super-aggregations". The spatial scale of these super-aggregations seems to reflect closely the spatial scale of prey patches (inferred by indirect evidences). These super-aggregation were clumped in "concentrations" (about 550 km across), characterized by high sub-surface biomass and high underwater relief. When the data were averaged over a large temporal scale (8-130 years), sperm whales were generally found in upwelling and high chlorophyll concentration zones over spatial scales of 200 to 1800 km. An investigation of defecation rates suggested that movement patterns of groups of sperm whales were related to feeding success: groups with low feeding success tended to travel in straight lines, while groups with high feeding success tended to zigzag over areas roughly 40-60 km across. I conclude that the distribution, spatial organization and movements of groups of sperm whales are closely related to the distribution of food resources over spatial scales of a few tens of km to a few thousand km.

LIST OF ABBREVIATIONS AND SYMBOLS USED

χ^2	Chi-square statistic
°C	Degrees Celsius
CZCS	Coastal Zone Color Scanner
ETP	Equatorial Tropical Pacific
g	Gram
GPS	Global Positioning System
h	Hour
Hz	Hertz
IWC	International Whaling Commission
kg	Kilogram
KHz	Kilohertz
km	Kilometer
M	Million
m	Meter
mg	Milligram
ms	millisecond
PC	Principal Component
PCA	Principal Component Analyses
r_s	Spearman coefficient of correlation

s	Second
s.d.	Standard deviation
SE	Standard error
SST	Sea Surface Temperature
XBT	Expendable bathythermograph

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Whitehead, H. and Jaquet, N. (1996). Are the charts of Maury and Townsend good indicators of sperm whale distribution and seasonality? *Rep. Int. Whal. Commn* 46 : 643-647.

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CHAPTER 1

GENERAL INTRODUCTION

1.1. The sperm whale

Sperm whales (*Physeter macrocephalus*), the largest of the toothed whales, have a more extensive global distribution than any other marine mammal, rivaled in this respect only by the killer whale (*Orcinus orca*). They range through all oceans of the world from the equator to the edges of the pack ice (Rice, 1989). Sperm whales are pelagic and are seldom found in waters less than 1000 m deep.

They are the most sexually dimorphic of all cetacean species: physically mature males can reach 18 meters and weigh 50 to 57 tons, while physically mature females are only 10 to 12 meters long and weigh from 18 to 24 tons (Best, 1979). They also show a considerable sexual segregation in distribution and social organization. The females and their offspring are mostly found in warm water between 40°N and 40°S; although in the North Pacific females can regularly be found as far north as 50°N (Rice, 1989). The females live in family units of about a dozen individuals which stay together for at least several years. These permanent units may associate with one another for periods of about a week (Whitehead *et al.*, 1991) to form what is commonly called the "nursery group". Males have a less cohesive social organization and are generally found in colder waters (Caldwell *et al.*, 1966). The young males leave the family unit when they are between 4 to 10 years old and form "bachelor" schools usually in temperate waters (Best, 1979). As they grow older and larger, the males are progressively observed in smaller groups and at higher latitudes. The largest mature males are found singly or in pairs in polar waters. At least some of these socially mature

males migrate back to the tropical waters to mate with the females, but the details of these migrations are not well understood (Best, 1979).

The peak of the breeding season seems to occur between October and December in the Southern Hemisphere and between April and June in the Northern Hemisphere (Best *et al.*, 1984). Males and females are born at the same size (approximately 4 meters), but the growth rates start to differ significantly at around 9 years old (Best, 1970). Females reach sexual maturity at approximately 9 years old (Best, 1979) and males at about 18-20 years old (Oshumi, 1977); although they do not seem to effectively reproduce before age 25 (Best *et al.*, 1984). The gestation period of sperm whales is thought to be 14-16 months, the lactation period 1 to 2 years and the resting period 1 year (Best *et al.*, 1984). Therefore, it has been estimated that a mature female gives birth to one calf every 4-5 years.

Sperm whales are exceptional divers. Norris and Harvey (1972) recorded a dive to 2500 m and indirect evidence suggests that adult males may dive to over 3200 m (Clarke, 1977). Dives lasting 60 to 90 minutes have been reported by many observers (e.g. Rice, 1989). Watkins *et al.* (1985) reported a group of 5 sperm whales that remained under water for at least 138 minutes. However, recent studies of undisturbed sperm whales show that they usually dive to about 400 to 800 m for about 40 minutes followed by 10 minutes at the surface (Gordon, 1987; Papastavrou *et al.*, 1989).

The majority of the sperm whale's diet consists of meso- and bathypelagic cephalopods, in particular, the deep-sea squid belonging to the families Histioteuthidae, Gonatidae, Onychoteuthidae and Octopoteuthidae. In some

regions however, Ommastrephidae, Cranchiidae and Architeuthidae represent, by weight, the bulk of the diet (Clarke, 1980; Kawakami, 1980; Smith, 1992). The importance of fish in sperm whale diet is generally small except in the northeastern part of the North Pacific, New Zealand (Gaskin and Cawthorn, 1967) and Iceland-Greenland (Martin and Clarke, 1986). Thus, sperm whale diet varies considerably between regions.

Sperm whales ingest approximately 400 kg to 1 ton of squid a day, most of which range in size from 500 g to 1.2 kg (Clarke *et al.*, 1993). However, it is not uncommon to find giant squid up to 10 m in length in a sperm whale's stomach (Clarke, 1985). Mature males generally feed on larger squid and thus dive deeper than females, as most species of cephalopods descend to greater depth as they grow (Clarke and Lu, 1974; Lu and Clarke, 1975; Roper and Young, 1975; Clarke, 1980). The majority of squid eaten by sperm whales are ammoniacal, slow, and neutrally buoyant, and only a small proportion are muscular, fast, and negatively buoyant (Clarke *et al.*, 1993). Because of the ability of these deep-living squid to escape nets and trawls (Clarke, 1977; Clarke, 1985; Vecchione and Roper, 1991), and because of the difficulty detecting them using acoustic methods (Starr and Thorne, *in press*), much of our actual knowledge about them comes from analysis of sperm whale stomach contents (see Clarke, 1985).

Sperm whale vocalizations consist almost exclusively of clicks which can be used in at least four different ways: usual clicks, slow clicks, codas and creaks (Backus and Schevill, 1966; Weilgart and Whitehead, 1988). Clicks are broadband pulses with significant energy from below 100 Hz to about 30 kHz. In good oceanographic conditions they can be heard through hydrophones at ranges of

up to 10 km (Watkins, 1980). Usual clicks are mainly emitted while sperm whales are foraging. They consist of series of 1 to 3 clicks per second, each click lasting 2-24 ms (Goold and Jones, 1995). Slow clicks seem to be only produced by mature males and consist of 1 click every 5 to 7 seconds (Weilgart and Whitehead, 1988). Codas are composed of short patterned series of 3 to about 40 clicks lasting 0.5 to 1.5 seconds (Watkins and Schevill, 1977). Codas are mainly heard when whales are socializing, when most individuals are clumped close together at the surface moving slowly (Whitehead and Weilgart, 1991). Creaks are defined as rapid burst of clicks with repetition rates of up to 200 s⁻¹ (Gordon, 1987; Goold and Jones, 1995).

1.2 Incentives to study sperm whale distribution

Understanding sperm whale distribution and the factors controlling it is by no means a recent concern: it has been a major objective for the past two centuries. If very little is known about the subject, it is not a result of a lack of interest, but rather a consequence of the difficulties in studying this species.

During the Yankee whaling period (1761-1924), there was considerable interest in determining the oceanographic factors influencing sperm whale distribution. Knowing where the whales were meant less time at sea and larger profits (Melville, 1851). For about 160 years, whalers searched for the favorite haunts of sperm whales, frequently exchanging information about catches and sightings (Whitehead and Hope, 1991). "Gamming" was an important part of the life on the vessels, and the whalers seemed to take every opportunity to "speak to" one another. The accuracy of the information that was exchanged between whalers is

uncertain. However, exploration and information exchange meant that by the 1840's the whalers had discovered all the major sperm whaling grounds between 40°N and 40°S.

During the first half of this century, sperm whales were only lightly hunted, and therefore very little investigation was made of their distribution. In the 1950's, due to the drastic reduction of most baleen whale stocks, sperm whales again became a major target for whalers. During the 1960's and the 70's, sperm whales were, numerically and by weight, the most important single species in the world's whale catch (Best, 1979). Therefore, to be able to exploit the population in a sustainable and rational way, it became critical to obtain a good knowledge of the limits of the distribution and dispersion of sperm whales (Best, 1969).

In the past decade, the incentives to study sperm whale distribution and the factors controlling their distribution have changed from efficient exploitation to conservation and academic interest. Moreover, there are increasing concerns that banning hunting (IWC whaling moratorium, 1985) may not be sufficient if habitat is being destroyed. Therefore, studies of the factors which make habitat viable for sperm whales are essential.

1.3. Problems and limitations

To date, investigations of the factors controlling sperm whale distribution have been inconclusive. Berzin (1971) suggested that the three principal reasons for this are: the absence of knowledge concerning their main prey species, their predominantly deep water mode of life, and the long food chain with which they are associated.

The most obvious first step when investigating the distribution of a predator and the factors affecting its distribution, is to study the distribution of its principal prey. However, methods of effectively sampling deep-living squid have not yet been developed. Clarke (1985) showed that even the largest nets very seldom catch cephalopods in the size range of the sperm whale's prey. He also demonstrated that the species composition in trawls is completely different from that found in sperm whale stomachs. Therefore, much of the very little which is known about the distribution of the deep living cephalopods comes from studies of sperm whale stomach contents (Clarke, 1980, 1985; Nemoto *et al.*, 1985, 1988). Consequently, these data cannot be used for the purpose of studying sperm whale distribution without circular reasoning.

Because it is difficult to study the distribution of the sperm whale's prey, the next obvious step would be to investigate variation in overall biomass at the depth at which they feed. However, there is practically no information on variation in biomass at depths of several hundred meters, and no immediate possibility for direct observations. Therefore, the only possibility is to observe biomass near the surface and extrapolate to what could be happening at greater depth.

Vinogradov (1955) postulated that the development of a deep water fauna is related to the productivity and the amount of biomass in the surface layer, coupled with vertical migrations (mainly diurnal) of deep water animals toward the surface layers. Au *et al.* (1990) also stressed that certain surface observations could be good indicators of deep water biomass. They postulated that sea surface temperature reflects oceanographic process in general, and that measurement of the temperature at sighting localities is helpful in understanding the effects of the environment upon cetaceans. Similarly, Viale (1991) assumed

that surface thermal fronts reflect advective movements which may be associated with productivity at depth. It has also been shown that remotely sensed pigment concentrations, which have been recorded from the surface layer only (less than a fifth of the euphotic zone) can provide clues to the deep carbon flux (Deuser *et al.*, 1990).

However, the validity of using surface observations when trying to understand phenomena occurring at depth is controversial. Berzin (1971), using data from several exploratory voyages, demonstrated "the futility of seeking a relationship between the distribution of sperm whale and the hydrology of the surface water." Volkov and Moroz (1977) agreed with Berzin, and pointed out that, for example, the presence of a convergence zone at the surface does not mean that there is still a convergence zone 500 meters below. As the isopycnic surfaces are frequently inclined, there can be a considerable shift of the position of the zone in space with increased depth, and it may even be possible that, at a certain depth, convergence zones can be displaced by divergence zones.

Sperm whales are near the top of a very long food chain. It follows from what was discussed above that it is nearly impossible to investigate the distribution of any of the links which are fairly close to the sperm whale. Instead, it seems that the only links which can be studied are the ones at the base of the food chain, the zoo- and phytoplankton which mainly inhabit the surface layers.

Another approach would be to investigate factors likely to increase prey concentration or availability. For example, Selzer and Payne (1988) found that the distribution of white sided (*Lagenorhynchus acutus*) and common dolphins (*Delphinus delphis*) were correlated with high bottom relief, and they

hypothesized that some environmental conditions which concentrate prey may secondarily affect the distribution of cetacea. Concentration of prey is likely to increase foraging efficiency of sperm whales, and so they would be expected to aggregate in areas with high cephalopod density. Therefore, it may also be relevant to investigate oceanographic factors (e.g. bottom topography, presence of convergence zones, depth and gradient of the thermocline) which are known to influence prey availability and concentration (Uda, 1959; Angel, 1968; Green, 1967; Sutcliffe and Brodie, 1977; Bakun and Csirke, in press).

The last problem which occurs when examining sperm whale distribution is related to their pelagic mode of life and to the impossibility of making an instantaneous record of all the whales over a whole ocean at any one time. It is difficult to know whether a lack of sightings is due to absence of whales or absence of observers, or similarly, whether a concentration of sightings represents a real concentration of whales or a concentration of effort (Kenney & Winn, 1986).

1.4. A review of studies on sperm whale distribution

During the 19th century, whalers noticed that sperm whales were not uniformly distributed throughout the oceans but were abundant in certain areas or "grounds" (Rice, 1989). As early as 1840, Bennett (1840) found that sperm whales were numerous where there were powerful currents or where currents flowed in opposite directions. Correlations between sperm whale density and oceanic fronts were already being suggested by the whalers. Therefore, thermometers were often used to search for a new whaling ground, and a

sudden change in sea surface temperature was an indication of a promising area (Ashley, 1926).

Most of the knowledge about sperm whale distribution gained during the Yankee whaling period is summarized in Townsend's (1935) charts. Townsend undertook the colossal work of plotting 36,909 sperm whale catches from the logbooks of Yankee whalers (1761-1920) on world charts. They show concentrations of kills coincident with areas of upwelling, such as that along the equator, along the west coast of South America and South Africa, off California, etc. But they also show some concentrations of whales in the Sargasso Sea, and around the Hawaiian and Azores islands, areas which are believed to be of poor primary productivity. The charts also suggest extensive southward movements of sperm whales at the onset of the northern winter and a reverse movement at the onset of the northern summer. However, these migrations might be at least partially an artifact as whalers could not hunt successfully in high latitudes during the winter. B. Kahn (pers. comm.) found that 19th century whalers generally used areas with mean wind strengths between Beaufort scale 2.5 and 5 (8 - 38 km/h). Therefore, it is possible that these apparent migrations are partly the consequence of whalers fishing in summer at high latitudes and all year round in equatorial waters.

In the late 1940's, as the sperm whaling industry expanded, it was felt that more needed to be known about sperm whale migrations and home ranges. To achieve this objective, the campaign of marking sperm whales with "Discovery" tags was set up. Tagging was mainly conducted from 1950 to 1975, with the largest effort in the Northwest Pacific (Ohsumi and Masaki, 1977). During the program approximately 4,400 whales were tagged in the North Pacific and 1,250 in the Southern Hemisphere. However, the recovery rate was only between 3 to

5%, with a total of 274 marks recovered for both areas (Ivashin, 1981). No broad conclusions could be drawn from so few recovered tags, but these recoveries provided direct evidence that some whales do occasionally undertake extensive north-south movements. The maximum distance recorded for the movement of a marked male was 7,593 km and 3,704 km for a female (Best, 1969; 1979). Approximate measurements of straight line movement between marking and recapture produce an average figure of 1,574 km for males and 689 km for females (Best, 1979). Ohsumi and Masaki (1977) also showed that males undertake extensive migrations while females were mainly recovered in the same area. However, Wada (1980), who added the recovery of Soviet tags to Ohsumi and Masaki's analyses, found that the site fidelity of the female was not as complete as first thought.

During modern whaling, with the expansion of the use of the factory ships, large males inhabiting temperate and polar waters became more available to whalers. Being so much larger, adult males were also more profitable. This resulted in a switch in the main whaling target. It follows that much of the knowledge gained during this period on sperm whale distribution and on the factors controlling their distribution concerned large males. Most of the data were collected concurrently with whaling. However, so as to increase efficiency of the whaling, and to ensure that the factory ships headed for the most profitable grounds, several cruises were dedicated to survey only (Clarke, 1962). Airplane surveys were also used (Gambell, 1967).

Detailed studies of living sperm whales started in 1982 using newly developed non-lethal techniques (Whitehead and Gordon, 1986; Gordon, 1990). In contrast

to the studies using modern whaling data, this research was mainly focused on the females and their offspring (nursery groups).

Some of the work on sperm whale distribution was only descriptive with no tentative explanation of why they were aggregating in such areas or in such numbers. Oshumi and Masaki (1977), Oshumi *et al.* (1977) and Bannister and Mitchell (1980) gave accounts of whale sightings in the North Pacific and in Antarctica. Clarke (1962), Rice (1977), Berzin (1978) and Wade and Gerodette (1993) reported sperm whale sightings during extensive cruises in the Eastern Equatorial Pacific. Also, several recent studies have described sperm whale distribution in the Gulf of Mexico (Collum and Fritts, 1985; Brandon and Fargion, 1993; Sparks *et al.*, 1993).

In parallel to this, much work has gone into trying to understand the factors controlling sperm whale distribution and spatial organization. Clarke (1956) showed that even though sperm whales are often considered to frequent the open ocean far from land, they seem to be especially attracted to oceanic islands, where the continental shelf is narrow and the slope very steep. Nineteenth century whalers had already noticed this, and they suggested that food was more plentiful off oceanic islands (Wilkes, 1845; Maury, 1874). Clarke (1956) postulated that the upthrust of volcanic peaks presumably causes some vertical mixing which breaks down discontinuity layers and allows a local increase in organic production.

Several other studies showed that sperm whales not only frequent the open ocean, but are also a common species off the edge of the continental shelf. It was postulated that the main reason for this is that upwelling enhances

productivity in these areas. Off the west coast of South America, Clarke (1962) showed that sperm whales are found on the eastern border of the Humbolt Current and that there is a longitudinal segregation between males and females, the males being found closer to shore and in colder water. Best (1969) found that there is a discontinuity of distribution in the South Atlantic with few whales being found in the middle of the ocean. He postulated that if most sperm whales are found at the edge of the continental shelf, it is because oceanographic factors promote the abundance of cephalopods in these regions. Similarly, Bannister (1968) attributed the concentration of sperm whales along the edge of the continental shelf off Western Australia to an abundant food supply. Along the east coast of the United States, Kenney and Winn (1987) noticed that sperm whales were a common shelf edge species. However, unexpectedly, they demonstrated that the density of sperm whales was not higher in submarine canyons, which are believed to be regions of increased productivity, than along any other parts of the continental shelf. Whitehead *et al.* (1992) investigated sperm whale distribution along the Scotian Shelf edge. Contrary to Kenney and Winn (1987), they showed that although sperm whales were found all along the shelf, they were much more abundant in a large submarine canyon known as "the Gully". This canyon is characterized by high productivity resulting from important nutrient fluxes due to internal waves (Sandstrom and Elliott, 1989; Sandstrom and Oakey, 1995). In the Mediterranean Sea, Notarbartolo di Sciara *et al.* (1993) also demonstrated that sperm whales are a common shelf edge species. On the other hand, Hope and Whitehead (1991) showed that, during the Yankee whaling period, sperm whales were as abundant several hundred miles away from shore as they were close to the Galápagos Islands. Similarly, Nemoto

et al. (1988) argue that, in Antarctica, sperm whales are widespread throughout the deep pelagic ocean.

It is generally admitted that sperm whales are found in rich productive areas; however, Berzin (1971) postulated that they are abundant in downwelling zones instead of upwelling zones. He developed one of the earliest hypotheses about the oceanographic factors controlling sperm whale distribution, which has been later adopted by other authors. He explained that upwelled water, rich in nutrients, becomes progressively richer in phyto- and zooplankton as it is transported away from the upwelling area by the Ekman transport. Therefore, at the downwelling point, the water is rich in macrozooplankton, which in sinking provides suitable conditions for large deep water organisms such as deep-living squid and fishes. He also suggested that, in upwelling areas at several hundred meters deep, intense development of life must be repressed by oxygen deficiency. On the other hand, in places of sinking, oxygen reaches the deep layers at a maximal rate. So, Berzin concluded that at the depth of several hundred meters, the volume of food biomass for sperm whales per unit water volume will be greater in downwelling areas than in upwelling, and greater than in any other place at the same depth. Berzin cited the coincidence of sperm whale concentrations with the lines of the subtropical and subarctic convergence as evidence of this. Berzin noted that the formation of permanent concentrations of sperm whales in regions of sinking was confirmed by data from the Mozambican channel, northeast of Madagascar, off the southwestern tip of Australia, around New Zealand, east of Cape Olyutorski in the Bering Sea and in the eastern part of the Indian Ocean.

This hypothesis has been confirmed by the work of several authors. Gaskin (1968a, 1973) demonstrated that male sperm whales are common along the convergence areas of the subantarctic, and that concentrations of sperm whales tend to be associated with areas where warm and cold currents meet. During his many surveys, Ivashin (1978) also found that sperm whales were principally associated with convergence zones. Best (1979) analyzed the catch statistics from Antarctica between 40°S and 80°S, and there was a clear correlation between the incidence of sperm whales and the position of the subtropical convergence. Viale (1991) made several surveys in the Mediterranean sea and she states that sperm whales were associated with fronts and thermal discontinuities. Preliminary results of studies conducted around the Canary Islands showed that sperm whales are found in the cool border of fronts (André *et al.*, 1993).

On the other hand, several authors have also demonstrated that sperm whales are found in upwelling areas. Caldwell *et al.* (1966) stated that the equatorial divergence accounts for the grouping of sperm whales on the equator and supported the famous "season on the line" of the American Yankee whalers. Similarly, Gulland (1974) stressed the striking correlation between the distribution of sperm whale catches and the major upwelling areas. He hypothesized that the catches away from the major upwelling areas were mainly due to whaling ships passing through these areas on the way to and from their home ports rather than to real concentrations of whales. Corroborating these hypotheses, Smith and Whitehead (1993) noticed that around the Galápagos Islands, the feeding success of sperm whales was highly correlated with the strength of the upwelling, and that most of the whales were found west of Isabella Island where the

upwelling is most prominent. Papastavrou *et al.* (1989) found that sperm whales dive to the oxygen minimum layer, and gave several reasons why sperm whales would have an advantage by feeding in a low oxygen layer. This again agrees with the upwelling hypothesis as, according to Berzin (1971), places of upwelling are characterized by low oxygen concentration at depth, while places of downwelling are characterized by high oxygen concentration at depth.

Other studies have tried to use different parameters to explain sperm whale distribution. From surveys in the Gulf of Mexico, Davis *et al.* (1993) found that sperm whale density was significantly correlated with primary productivity. On the other hand, from work in the Eastern Tropical Pacific, Reilly *et al.* (1993) demonstrated that sperm whales were negatively correlated with primary production.

Ramirez and Urquizo (1985) showed that, off the west coast of South America, sperm whales were more abundant in areas of low sea surface temperature, and that during El Niño years, when the sea surface temperature is higher than normal, they migrated further south. Similarly, Whitehead *et al.* (1989) showed that around Galápagos, sperm whale feeding success was negatively correlated with sea surface temperature. Other studies stressed the importance of the temperature gradient as the principal factor regulating sperm whale density. Uda (1959) demonstrated that a temperature gradient of 5°C in the uppermost 100 meters provided optimal conditions for schooling of squids, and that a gradient either larger or smaller decreased the squid biomass. Around New Zealand, Gaskin (1973) effectively found that sperm whale distribution was highly correlated with a vertical temperature gradient of 5°C in the first 100 m.

As an example of the general style of these studies, consider the work of Volkov and Moroz (1977) who suggested that sperm whale distribution is related to areas of convergence. Figure 1.1, redrawn from Volkov and Moroz (1977), shows the association between sperm whale sightings and convergence zones in the Eastern Tropical Pacific Ocean. This figure confirms the existence of an apparent overall correlation between sperm whale distribution and downwelling areas. However, from this figure, it is only possible to conclude that a high density of sperm whale was found in an area characterized by a high density of convergence zones. It is impossible to assess whether sperm whales are more closely associated with downwelling or upwelling areas, and due to the coarse resolution of the study, it is impossible to detect the scale of the relationship.

1.5. The problem of scale

The above review shows that the results of the studies on sperm whale distribution are very confusing and seem to contain many contradictions. Despite numerous investigations, the factors which are influencing sperm whale distribution are not clearly defined, nor is it possible to single out any environmental parameter which could be used to predict their distribution.

An explanation for this confusion could be the poor definition of spatial and temporal scales and the use of only one scale in most studies. Table 1.1 lists each study with the spatial and temporal scale over which the data were averaged. It shows that, in some instances, there was no mention of scale, and that in the other cases, the scales used were so different that no meaningful comparison is possible. The problem of scale is a central problem in ecology,

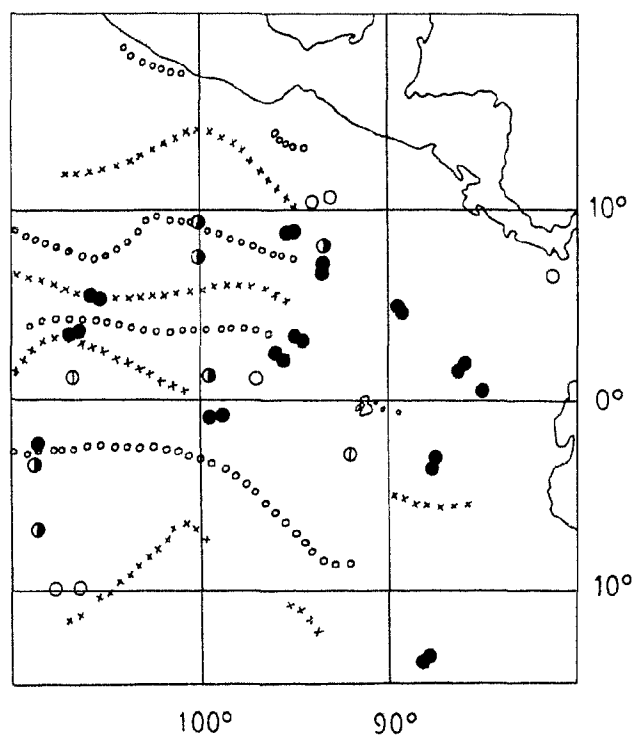


Fig. 1.1. Distribution of sperm whale sightings and divergence and convergence zones, redrawn from Volkov and Moroz (1977). \circ = 1 to 10 sperm whales, \odot = 10 to 20, \otimes = 20 to 50 and \bullet = more than 50. xxxxx = divergence zones (upwelling), and oooooo = convergence zones (downwelling).

Table 1.1 Spatial and temporal scales used in the studies on sperm whale distribution

References	Areas of observation	Spatial scales of the areas	Spatial scales. over which the data are averaged	Temporal scales. over which the data are averaged
André (1993)	Canary Islands	180 km / 180 km.	-	1 year
Ashley (1926)	-	-	-	-
Bannister & Mitchell (1980)	North Pacific	0° - 60° N & 110°W - 120° E	550 km / 550 km	159 years
Benett (1840)	-	-	-	-
Berzin (1971)	-	-	-	-
Best (1969)	South Africa	-	-	-
Best (1979)	Antarctic	40° S - 80° S	1,100 km / 1,100 km	8 years
Caldwell <i>et al.</i> (1966)	-	-	-	-
Clarke (1956)	Azores	-	-	-
Clarke (1962)	Peru-Chile Galápagos	3,400 km 5,000 km	-	15 days 22 days
Collum & Fritts (1985)	Gulf of Mexico	-	-	2 years
Davis <i>et al.</i> (1993)	Gulf of Mexico	continental slope	-	-
Gaskin (1967, 73)	Southwestern Pacific	30° S - 70° S & 150° E - 150° W	1,100 km / 1,100 km	Yankee whaling + 9 years
Gulland (1974)	World	-	-	-
Hope & Whitehead (1991)	Galápagos	10°/10° center around Galapagos	-	20 years
Ivashin (1978)	Pacific + South Hemisphere	-	-	-
Kenney & Winn (1987)	Northeast United States	35° N- 42° N & ~75-110 km over the shelf edge	37 km transect	3 years

Notarbartolo di Sciara (1993)	Mediterranean Sea	All around Italy	-	3 years
Oshumi & Masaki (1977)	North Pacific	25° N - 60° N & 120° W - 160° E	550 km / 550 km	21 years
Oshumi <i>et al.</i> (1977)	North Pacific Southern Hemis.	25° N - 60° N 120° W - 160° E & 30° S - 80° S	550 km / 550 km	9 years
Papastavrou <i>et al.</i> (1989)	Galápagos	2° S - 1° N & 90° W - 92° W	-	2 years
Ramirez & Urquiza (1985)	Peru	4° S - 10° S & the coast - 84° W	-	2 years
Reilly <i>et al.</i> (1993)	West Coast of USA	California current from Mexico to Oregon border	-	3 months
Rice (1977)	ETP	20° N - 10° S & 80° W - 110° W	1,100 km / 1,100 km	2 months
Smith & Whitehead (1993)	Galápagos	2° S - 1° N & 90° W - 92° W	-	5 years
Townsend (1935)	World	40° N to 40° S	--	159 years
Viale (1991)	Mediterranean Sea	-	-	3 years
Volkov & Moroz (1977)	ETP	80° W - 110° W & 15° S - 20° N	-	6 months
Wade & Gerodette (1993)	ETP	20° N - 10° S & 80° W - 140° W	-	4 years
Whitehead <i>et al.</i> (1992)	Scotian shelf	61° W - 57° W & 42° N - 45° N	55 km / 110 km	4 years

and the spatial and temporal variability of an ecosystem is one of its most important features (Steele, 1976). Therefore, it is almost meaningless to try to describe the variability and predictability of an environment without reference to the particular range of scales which are used for examining the processes (Levin, 1992).

However, there is no single natural scale at which ecological phenomena should be studied. Rose and Leggett (1990) stressed the importance of looking at predator-prey relations over a full range of scales. Failure to do so often leads to erroneous conclusions, as in the case of Fairweather *et al.* (1984) who showed that densities of whelks (*Morula marginalba*) were negatively correlated with those of barnacles (*Tesseropora rosea*). Later, in expanding the spatial scale, Fairweather (1988) found that the occurrence of these two species was highly positively correlated, and this last result completely changed the interpretation of their relationship. Similarly, Schneider and Piatt (1986), who studied the correlation between seabirds and schooling fish, found that the degree of association of marine birds with prey depended strongly on the spatial scale of the analysis. The association of murrelets (*Uria aalge*) with schooling fish was much stronger at scales of several km than at scales of several hundred of meters. This means that short transects would be unable to detect significant correlations. Schneider and Piatt (1986) argue that the lack of association between murrelets and fishes reported by Woodby (1984) was mainly because the correlation was tested at a single scale.

To interpret predator-prey correlations correctly in marine (and other) systems, it is necessary not only to use appropriate measurement scales, but also to

account for the physical dynamics of the system (Rose and Leggett, 1990). None of the literature cited in the above review of studies on sperm whale distribution takes into account the scale, temporal or spatial, at which the oceanographic processes (to which sperm whale density may be related) occur. The distance between divergence and convergence zones is never mentioned, and dissimilar conclusions may just be the consequence of the use of different spatial scales.

Therefore, it seems that an attempt to describe the spatial and temporal scales of the major oceanographic processes, which could be related to sperm whale distribution, may shed some light on the problem.

1.6. An attempt to describe spatial and temporal scales in oceanographic processes

Describing in full the spatial and temporal scales of the oceanographic processes related to sperm whale distribution is beyond the scope of this thesis. In addition, broad generalization is prevented by high geographical and seasonal variability. For example, several authors have given different descriptions of similar oceanographic phenomena. It is not clear whether these differences arise from studying the same entity from a different perspective or whether the geographic and temporal variations in oceanographic phenomenon are so great that separate ecosystem studies will each produce a unique description (Barber and Smith, 1981). However, it is still possible to give some general time and space scales for the major relevant processes, but examples from specific areas (mainly the Pacific Ocean) will be used.

Coastal upwelling is a mesoscale response to large scale wind driven processes. When winds favorable to upwelling occur, the ocean responds on a time scale of one to 10 days, a horizontal spatial scale of five to 100 km and recruits water from 40 to 80 m in depth (Barber and Smith, 1981).

The equatorial upwelling is driven by the trade winds and therefore follows a similar seasonal variability. The Coriolis force produces an Ekman transport perpendicular to the Equator (Mann and Lazier, 1991). This meridional flow is generally an order of magnitude slower than the westerly current (Vinogradov, 1981). The Pacific equatorial upwelling occurs within the South Equatorial current (flowing west), but the upwelled water originates in the Cromwell current, which is flowing in an opposite direction underneath the Equator (Wyrtki, 1967). Therefore, once upwelled, a parcel of water will be subject to two horizontal transports: a meridional one (away from the equator) and a zonal one (along the equator, going westward). In consequence, the locality of the highest nutrient concentration will be spatially separated from the locality of the highest chlorophyll concentration, which in turn will be separated from the highest concentration of herbivorous zooplankton and so on. Vinogradov (1981) estimated the time lag between the maximum chlorophyll concentration and the peak of fish and cephalopods densities to be approximately four months. This is in accord with Sette (1955) who demonstrated that the development of all trophic levels within a tropical marine community takes 50 to 150 days. In four months, a parcel of water will be transported approximately 1,800 to 2,600 km along the Equator and 260 to 460 km perpendicularly to the Equator (Vinogradov, 1981). As the equatorial upwelling is directly linked with the trade winds, it will be maximal around August - September and minimal around March (Barber, 1988).

However, due to the time lag between the peak of upwelling and the maximum nekton concentration, the maximum concentration of cephalopods would be expected to occur in periods of weak upwelling (Vinogradov, 1981).

Downwelling can be induced by two currents flowing in opposite directions (Le Fèvre, 1986). In the Pacific, the border between the South Equatorial current and the Equatorial countercurrent is situated at approximately 4°N (Wyrki, 1967). This is a major zone of downwelling and, due to the meridional transport from the Equator, it concentrates a high density of macrozooplankton and nekton. These organisms undertake diurnal vertical migration and so are subject to one horizontal current during the day and to an opposite one during the night. Therefore, once they are fully developed, macrozooplankton and micronekton stay in a zone of convergence (Vinogradov, 1981).

The year to year variation in the strength and productivity of the Pacific equatorial upwelling, and indirectly of the downwelling, is mainly due to the El Niño phenomenon. The El Niño is a natural, aperiodic, coupled ocean / atmosphere perturbation of the global heat budget that profoundly modifies the normal east-west asymmetry of both heat content and productivity in the Pacific basin (Barber and Kogelschatz, 1989). During an El Niño year, the eastern Pacific becomes progressively warmer and less productive in consequence of the thermocline becoming deeper. This anomaly lasts for about nine months in general. The recovery, or the cooling down of the East Pacific, is very quick and lasts less than a month (Barber, 1988).

Oceanic gyres are large anticyclonic cells which occupy most of the area between the equatorial divergence and the eastward mid-latitude currents. They

have a diameter of several thousand kilometers, and are virtually permanent. They mainly influence the top 500 meters of the area, and below that the gyres become much smaller (Blackburn, 1981). Oceanic gyres have been considered as completely oligotrophic with very low variation in primary productivity and concentration of standing stock. However, within a gyre, area variability can be enhanced by the presence of cold core rings. For example, at any time, the Sargasso sea contains about 10 cold-core rings (Mann and Lazier, 1991), covering up to 10% of the sea (Blackburn, 1981) which greatly enhance the mean productivity (Mann and Lazier, 1991). These rings originate from meanders of the Gulf Stream and contain continental slope water. They are a few hundred kilometers in diameter and approximately one kilometer deep. These parcels of water remain biologically rich for several months to two years (Blackburn, 1981). Therefore, presence of sperm whales within an ocean gyre would not necessarily mean that they are found in unproductive waters.

Flow of water across topographic features in the open sea produces a pattern of vertical circulation, including fronts and eddies, enhancing primary productivity. These phenomena have been detected on scales ranging from 1 m to approximately 110 km laterally and 1 m to 1 km in depth. They persist from a few hours to virtual permanence. Time and space scales seem to be related: for example, the most ephemeral fronts are usually the smallest (Owen, 1981).

The spatial and temporal scales of phytoplankton patches seem to be largely controlled by turbulence and mixing. However, biological events are also very important: grazing by herbivorous zooplankton will reduce or inhibit the formation of large patches of phytoplankton and so, for a phytoplankton bloom, it is necessary that there is also a lag in the onset of grazing (Steele, 1976). In going

up the food chain, the increased mobility of the organisms means that their spatial organization is less controlled by exterior physical factors like turbulence and mixing. However, they will generally be aggregated in places where their prey is highly concentrated.

Thus, it seems likely that nekton, including cephalopods, concentrate in areas of downwelling which are separated by 250 to 450 km from the main upwelling areas. The peak of their concentration would occur about four months after the peak of the upwelling and chlorophyll concentration. Therefore, studies having a resolution coarser than the usual distance between linked upwelling and downwelling cannot determine with which event sperm whale distribution is best associated.

1.7. Dolphin distribution and its controlling factors: A few examples

It has been shown that the factors controlling sperm whale distribution are difficult to study for a variety of reasons (cf. section 1.3.). However, most of the smaller species of odontocetes are also high on the food chain, and, therefore, studies of the factors determining their distribution may give some insight on the factors influencing sperm whale distribution and thus help in planning further research.

As dolphins are generally not commercially important, the relationship between dolphins and oceanographic features has not been studied for as long as that of large whales. However, in the last 30 years several attempts have been made to relate dolphin distribution to undersea topography (Hui, 1979 and 1985; Kenney

and Winn, 1986 and 1987; Evans, 1974; etc.), or to temperature parameters and convergence zones (Fraser, 1934; Uda and Dairokuno, 1958; Gaskin, 1968 b, Selzer and Payne, 1988; etc.). The concern about dolphin - tuna fisheries in the Eastern Tropical Pacific (ETP) has led much of the recent work on factors influencing dolphin distribution (Au and Perryman, 1985; Au *et al*, 1990; Polachek, 1987; Reilly, 1990; etc.).

Hui (1979, 1985) used aerial surveys to describe the distribution of common dolphins (*Delphinus delphis*) and pilot whales (*Globicephala macrorhynchus*) along the coast of California. He surveyed about 370 km of coast, up to 185 km offshore over 8 consecutive years. As expected, he reported that both species were significantly more abundant over areas of high relief than over a flat bottom. He also found that this association was stronger for pilot whales, and he hypothesized that this is due to their narrow diet. He postulated that squids are more abundant and more available in high relief areas. This observation was supported by O'Dor *et al.* (1994) who tracked *Loligo forbesi* in the Azores, and found that they tend to stay close to sea-mounts. Selzer and Payne (1988) investigated the distribution of common and white sided dolphins (*Lagenorhynchus acutus*) on the continental slope off the northeastern United States from 35° to 45°N, between 1980 and 1985. They demonstrated that both species of dolphins occurred in regions of high sea floor relief but that their distribution was spatially segregated, except in situations of unusually high food supply. Kenney and Winn (1987), who worked in the same region, divided the area in 31 blocks about 36 km wide and surprisingly, showed that the cetacean biomass density was significantly lower in the vicinity of submarine canyons than in other areas of the shelf break.

Au and Perryman (1985) worked on dolphin distribution in the ETP and they demonstrated that during the winter, spotted dolphins (*Stenella attenuata*) and spinner dolphins (*Stenella longirostris*) were found in low salinity warm water with a shallow thermocline and relatively small annual variations in surface conditions. On the other hand, during the same study, common and striped dolphins (*Stenella coeruleoalba*) were found in cooler, more saline upwelling modified waters. Reilly (1990) expanded this study and found that, even if their summer distribution was different from their winter one, the habitat of these species of dolphins was still segregated. He also found that during the summer, striped dolphins were found in an intermediate habitat between spotted-spinner and common dolphins. He demonstrated that the high density of dolphins a few degrees north of the Equator coincides in location with a major convergence zone, the equatorial front. However, as the habitats of the species were not robustly separated using multivariate techniques and habitat characteristics, Reilly suggested that there were other processes, not directly related to physical habitat, which acted to separate dolphins species spatially.

Au *et al* (1990) demonstrated that dolphins (spotted, spinner, striped and common) are mainly encountered on the warm border of equatorial fronts. However, they postulated that as dolphins do not undertake extensive migrations, they are also sometimes found on the cool border of these fronts. They also showed that the association between dolphin distribution and convergence zones not only occurs on large scales like on the equatorial front or on the border between the Equatorial Countercurrent and the North Equatorial Current at about 10°N, but also over much smaller scales. They demonstrated

that, in the same area, sighting rate increased significantly on days characterized by strong surface temperature fluctuations.

In conclusion, the studies reviewed here showed that in general, dolphins are abundant in areas of enhanced primary productivity, like areas of high relief, and in convergence zones.

1.8. A few examples of studies of baleen whale distribution

Compared with odontocetes, baleen whales are on top of a much shorter food chain (for example, the typical food chain of Antarctic rorquals is diatoms to euphausiids to whales), and the knowledge of distribution and abundance of the baleen whales' main prey species is often extensive. Therefore, the major problems encountered while studying the factors controlling sperm whale distribution are less apparent when studying baleen whale distribution. This section gives a few examples illustrating our knowledge of the factors influencing baleen whale distribution.

Both sperm whales and baleen whales have been economically very important until recently. Therefore, for at least two centuries, there has been a considerable interest in describing their distribution and in determining the factors controlling it. As the food chain is so short, it has often been postulated that baleen whales aggregate in areas of upwelling (Berzin, 1971), or in areas of high primary productivity (Gulland, 1974). Volkov and Moroz (1977), who studied whale distribution in the Eastern Tropical Pacific (ETP), showed that the high abundance of baleen whales coincides with the main areas of upwelling, especially those around 7-10°N and the equatorial upwelling. They also showed

that baleen whales were not observed strictly along the axis of divergence but close to its northern or southern peripheries. Such distribution was explained by the meridional transport of the plankton from the location of the upwelling and therefore the presence of a maximum zooplankton biomass away from the axis of divergence.

Reilly and Thayer (1990) also showed a correlation between upwelling areas and blue whale distribution (*Balaenoptera musculus*) in the ETP. All of their sightings occurred in relatively cool upwelling modified waters, and 90% of them were situated along Baja California and in the vicinity of the Costa Rica Dome, which are among the most productive areas of the ETP (Love, 1972; Barber and Smith, 1981). Foerster and Thompson (1985) found similar results during their work on fin whale (*Balaenoptera physalus*) distribution in the Denmark Strait (24°W to 32°W and 62°N to 66°N). Fin whale distribution coincided almost exactly with the zooplankton distribution, which in turn matched the phytoplankton distribution. Therefore, most of the fin whales were found near the center of the upwelling zone, over a spatial scale of about 220 km by 110 km.

In most cases, the main prey item of baleen whales is better known and easier to study than the one of sperm whales, even if knowledge on the fine scale distribution of herring (important prey of minke, fin and humpback whales in the north Atlantic) is still lacking. It is therefore often possible to investigate the prey distribution and the predator distribution independently at different spatial scales. Then, any discrepancy in the match of the two distributions can be explained either by behavior or by factors responsible for concentration or availability of the prey. For example, Payne *et al.* (1985) showed that a good correlation between humpback whales (*Megaptera novaeangliae*) and sand eel distribution appeared

in the southern part of the Gulf of Maine but not on George's Bank. On George's Bank, sand eel are as abundant as in the southern part of the Gulf of Maine, but very few humpback whales were observed. The non-significant correlation between humpback whales and sand eel on George's Bank suggests that factors other than simply food concentration influence humpback distribution. Hain *et al.* (1982) showed that humpbacks use particular feeding strategies, which, to be efficient, need to be over a shelf floor with rugged relief. As George's Bank is characterized by a gently sloping continental shelf with no relief, the paucity of humpbacks on this bank can be explained by their particular feeding behavior.

Similarly, knowing the main prey distribution, ecology and standing crop allowed investigations of correlation between predator and prey over a wide range of temporal scales. Whitehead *et al.* (1980) presented evidence that, around Newfoundland, humpback whales change their geographic distribution over a temporal scale of a few days to a few weeks in response to change in capelin abundance. Whitehead and Carscadden (1985) suggested that estimates of capelin year class strength, predicted from abiotic variables, can be used to predict inshore whale abundance at least one year in advance.

In conclusion, these few examples show how knowing the distribution of the main prey species helps understanding the factors controlling whale distribution.

1.9. Objectives

This introduction demonstrates how ill defined spatial and temporal scales, and the lack of multi-scale observations, leads to confusion in describing the factors controlling sperm whale distribution. It also postulates that when scale and resolution are considered in the interpretation of results, apparent contradictions in published works may be resolved. Therefore, studying the factors influencing sperm whale distribution over a wide range of spatial and temporal scales should enhance our understanding of sperm whale habitat. Investigation of sperm whale movements and spatial organization over different spatial scales will also shed light on their habitat utilization. Thus, the objectives of this thesis are:

- To investigate relationships between the distribution of sperm whales and primary productivity over spatial scales ranging from 220 X 220 km to 1,780 X 1,780 km, using data averaged over a temporal scale of 8 to 130 years.
- To investigate sperm whale distribution in relation to underwater topography, temperature and thermocline parameters, chlorophyll concentration and measures of sub-surface biomass at spatial scales ranging from 150 to 1190 km, using survey data.
- To relate movement patterns of groups of sperm whales to their feeding success over spatial scales ranging from 9 km to 150 km.
- To investigate sperm whale spatial organization over spatial scales ranging from 10 to 5,000 km.

CHAPTER 2

COHERENCE BETWEEN 19TH CENTURY SPERM WHALE DISTRIBUTIONS, AND SATELLITE-DERIVED PIGMENTS IN THE TROPICAL PACIFIC

2.1. Introduction

Sperm whales play an important role in the pelagic marine food chain. With an estimated population size of about 1 to 1.9 million worldwide (Kanwisher and Ridgway, 1983; Rice, 1989) and a consumption rate on the order of 500 kg per individual per day (Clarke *et al.*, 1993), the annual intake of squid, the primary food source of sperm whales, is estimated to be ~ 150 - 300 M tons per year. By comparison, the total annual harvest of fish by humans is currently 101 M tons (FAO, 1993). The impact of sperm whales on the marine productive capacity, particularly in the open ocean, is therefore potentially strong where high concentrations of whales exist. Despite the potential importance of sperm whales in the marine food web, little is known of their ecology and distribution (cf. chapter 1). In particular, their expansive habitat limits our understanding of the distribution of sperm whales in relation to environmental variables over large spatial and temporal scales.

It has often been suggested that, given their large food requirements, sperm whale distributions should reflect the distribution of productive ocean environments (Townsend, 1935; Caldwell *et al.*, 1966; Bradford *et al.*, 1991, see also chapter 1). Gulland (1974) noticed the striking correlation between areas of upwelling and the main sperm whaling grounds as shown on charts of 19th century sperm whale catches. Similarly, Smith and Whitehead (1993) found that around the Galápagos Islands, sperm whales were more numerous and had greater feeding success west of Isla Isabella where upwelling and enhanced phytoplankton concentrations are most prominent (Feldman *et al.*, 1984).

However, other studies have stressed the coincidence of sperm whale concentrations with convergence zones (Gaskin, 1968a; 1973; Berzin, 1971; Volkov and Moroz, 1977; Viale, 1991; see also chapter 1), and thus postulated that sperm whales occur in downwelling areas.

This apparent contradiction concerning the factors controlling sperm whale distribution may be attributed to the differences in spatial and temporal scales used in these studies (see chapter 1). In an extensive literature search, Schneider (1994) did not find a single paper describing the relationship between whales and their potential prey at 2 or more spatial scales. As the factors controlling sperm whale distribution are likely to be scale dependent, a wide range of spatial and temporal scales have to be investigated to assess the relationship between sperm whale distribution and primary productivity. In addition, as spatial scales are closely linked to temporal scales (the largest structures being usually the most permanent, Stommel, 1963), the time scale of a predator-prey relationship needs also to be considered.

In this chapter, I investigate the relationship between the distribution of sperm whales and potentially productive ocean environment as indicated by surface pigment concentrations. As there is no recent extensive data set on the distribution of groups of female sperm whale (modern whaling was mainly concerned with males), the results of this study could also be extrapolated to give valuable information on the actual relationship between sperm whale density and primary productivity. Moreover, with easily accessible satellite images of ocean color, the existence of an association between chlorophyll concentration and sperm whale density, and the knowledge of the scales involved, could help us predict patterns of sperm whale distribution.

2.2. Methods

2.2.1. Sperm whale data

When considering a very wide range of spatial and temporal scales, sperm whale distribution is best described by catch and sighting data from the Yankee whaling industry, 1712 - 1925 (Best, 1983; Mitchell, 1983; Sherman, 1983; Shuster, 1983a). During this period, there were no restrictions on the hunt and no sanctuaries for the whales, so the whalers explored all oceans between 40°S and 40° N providing data over a very wide spatial range. Up to 565 ships cruised the oceans at any one time in search of sperm whales (Best, 1983) and their habit of "gamming" and sharing information about productive grounds made these whalers efficient exploiters of resources (Whitehead and Hope, 1991). Although whalers used primitive means of hunting whales, several hundreds of thousands of sperm whales were killed during this period (Shuster, 1983a), providing a very large data set on their distribution.

It has been estimated that a total of about 14,000 voyages were made by the Yankee sperm whalers between 1761 and 1924 (Shuster, 1983a), and that about 30% of the logbooks and private journals have survived (Sherman, 1965). Maury (1852) and Townsend (1935) extracted a large amount of data from these logbooks and their charts showing sperm whale distribution were used in the present study to evaluate the historical sperm whale distribution between 40°N and 40°S in the Pacific Ocean.

a) The Maury charts

Maury (1852) analyzed pre-1851 logbooks and compiled charts which give indications of effort in each area as well as kills and sightings. He divided the world into 5° by 5° squares, and for each square gave the total number of days spent by different vessels searching for whales during each calendar month, as well as the total number of sperm whales seen or killed during this month. The data therefore provides an indication of catch per unit effort.

b) The Townsend charts

Townsend (1935) analyzed the logbooks of 744 vessels making 1,665 voyages between 1761 and 1920 (mostly between 1820 and 1860). On each day that one or several sperm whales were killed, he plotted the position of the ship on a world chart. In total, he recorded the locations where 36,908 sperm whales were taken. As he used different colored marks for each 2-month period (December-January, February-March, April-May, June-July, August-September and October-November), the seasonality of the catches in different areas is clearly shown (Fig. 2.1).

The charts give no indication of the whaling effort. Therefore, the absence of catches in certain regions may not mean that no whales were found there, but may simply reflect little or no effort. Also, to avoid superimposing dots when several whales were killed at the same location, he plotted the dots beside another, sacrificing accuracy for readability.

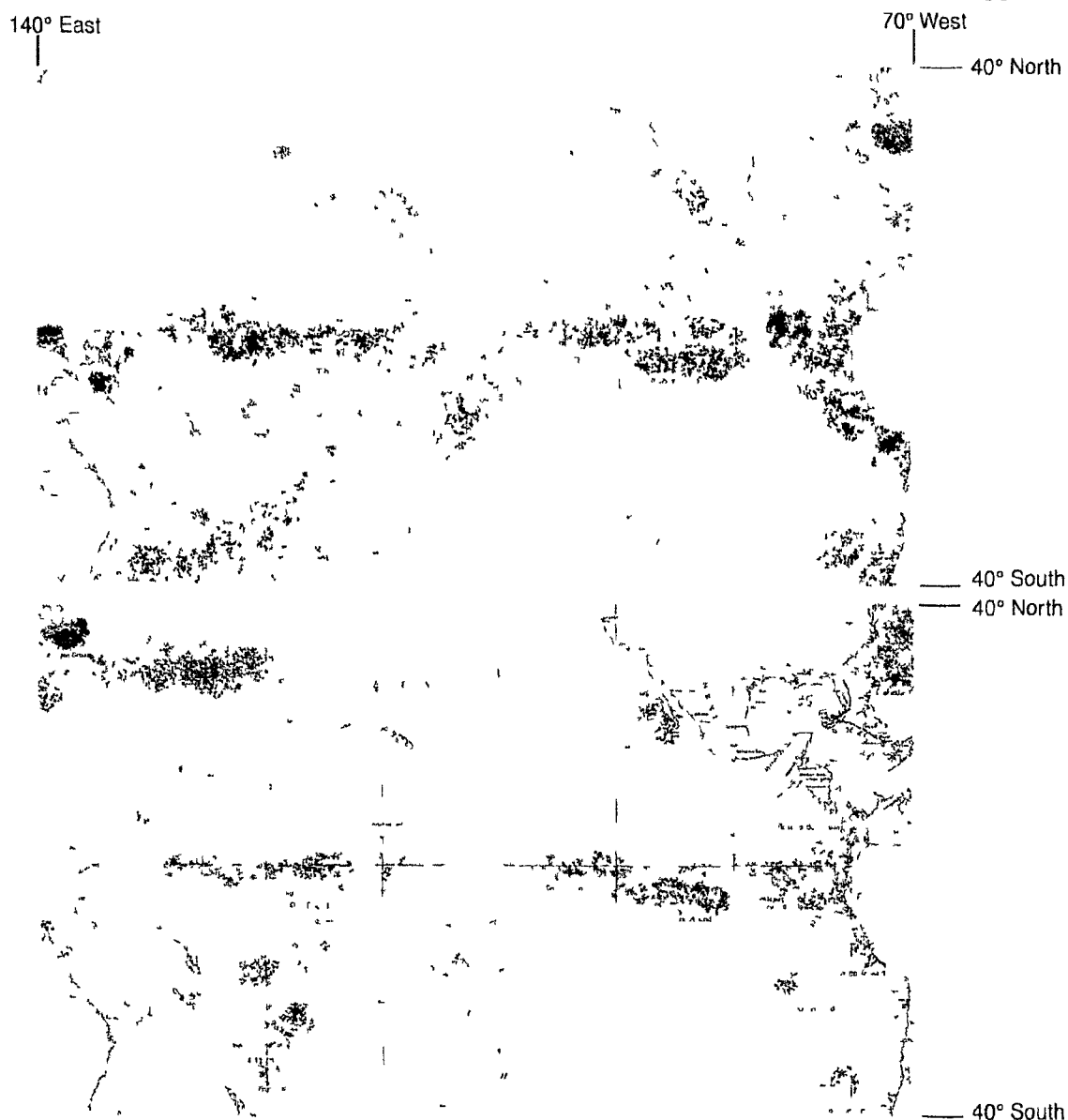


Fig. 2.1 Part of Townsend's (1935) charts showing the Pacific Ocean between 40°N and 40°S, the west coast of the American continents and the meridian 140° E. Each dot represent one or several sperm whales killed during one day by one vessel. The different colors represent different 2-month periods: brown=October-November, black=December-January, orange=February-March, green=April-May, blue=June-July, red=August-September. Reproduced with the permission of the New-York Zoological Society.

Whitehead and Jaquet (1996) used a simulation model to examine the relationships between total catch by Yankee whalers in an area, total catch per unit effort, and the pre-whaling spatial whale distribution. Both total catch and total catch per unit effort were highly correlated with the initial distribution but total catch was always better correlated than total catch per unit effort. Therefore, as the Townsend charts are more accurate and take into account more whaling voyages, they were used to describe sperm whale distribution in the present study. The Maury charts were only used to examine the differences in whaling effort over different parts of the Pacific Ocean.

2.2.2. Pigment data

To evaluate the distribution of sperm whales relative to surface pigment, satellite derived measurements of ocean color, which have given the first global view of the potential productivity of the oceans, are most appropriate (Feldman *et al.*, 1989; Lewis, 1989). The Coastal Zone Color Scanner (CZCS) onboard the NIMBUS-7 spacecraft was in operation from 1978 until 1986 (Brown *et al.*, 1985; Lewis, 1992; Yoder *et al.*, 1993). The sensor made observations of the spectral distribution of radiance emitted from the ocean surface as a result of selective absorption and backscattering of sunlight by particles and dissolved compounds in the sea. In the open ocean, removed from terrestrial influences, phytoplankton and their immediate breakdown products are the primary agents responsible for variation in ocean color as seen by satellite. The satellite radiances can therefore be used to compute the concentration of phytoplankton pigment in the upper ocean to an accuracy of 30% for these waters (Gordon *et al.*, 1988). Because the sensor was operated sporadically, and because of its inability to penetrate cloud

cover, coverage of the study region was not uniform in time or space. However, the data include over 26,037 valid individual observations over the study region and result in a representative view of the variability in the productive potential of the temperate and tropical Pacific Ocean. Data were extracted from the historical archive (Feldman *et al.*, 1989) and averaged spatially and temporally to match the finest scales resolved by the sperm whale distribution from Townsend (1935).

The estimated surface pigment concentrations define to first order the productive capability of the ocean environment (e.g. Eppley *et al.*, 1985). The exact relationship between pigment concentration, and local rates of primary productivity, remains an active area of research, and in general requires further ancillary data (such as solar radiation fluxes and surface temperature), and the fixing of locally appropriate parameters (Platt and Sathyendranath, 1988; Morel, 1991; Balch *et al.*, 1992; Longhurst *et al.*, 1995). However, the simple relationship between surface pigment and productivity defined by Eppley *et al.* (1985) appears to be valid when applied to more recently acquired data (J. Campbell, pers. comm.), and hence I have chosen to use the satellite surface pigment concentration as a good index of the potential productivity of the upper ocean over the range of scales investigated here.

2.3. The problem of wind speed and reliability of the Townsend's charts

It has been shown by simulation that Townsend's (1935) charts are a reliable source of information on sperm whale seasonal distribution only in areas where catch efficiency shows little seasonal change (Whitehead and Jaquet, 1996).

Kahn (1991 and B. Kahn, pers. comm.) has suggested that, in the Indian Ocean, catch efficiency by the Yankee whalers decreased substantially when the mean monthly wind speed was above 25 km/h (force 4 on the Beaufort scale). Therefore, to investigate the relationship between sperm whale catch efficiency and wind speed, the number of catches reported on Townsend's (1935) charts in each 2° latitude by 2° longitude square (~220 km X 220 km) of an area of the Pacific (bounded by 40°N, 40°S, 140°E and the west coast of the American continents) were compared with mean bimonthly wind speed, extrapolated from the Marine Climatic Atlas of the World (Version 1.0, March 1992, Naval Oceanography Command Detachment, Asheville, NC 28801, USA). The wind speeds were given for 5° X 5° squares (~550 km X 550 km), so had to be extrapolated to 2° X 2° squares in order that they could be compared with the whale data. This resulted in a total of 10,475 reported kill positions over 14,929 bimonthly 2° X 2° squares. The mean catch per two month period and per 2° X 2° square was calculated for each wind speed from 9 to 41 km/h.

The mean catch rate at each wind speed is given in Fig. 2.2. Nine and 41 km/h were the minimum and maximum mean wind speeds in any square in any bimonthly period. The catch rate is very low at mean wind speed of 9 km/h and above 28 km/h, but is reasonably constant from about 11 to 22 km/h. Clearly, catch rates varied with mean wind speed. Although part of this could be due to fortuitous or environmentally caused correlation between whale density and mean wind speed, it is more plausible that the majority of the effect is due to changing catch efficiency with weather conditions : whalers showed little success with very light winds (11 km/h), presumably because their ships did not sail well, and with stronger winds (>26 km/h) when rough conditions would have made

sighting and catching more difficult. It is likely that the trends in Fig. 2.2 are exaggerating the relationship between catch efficiency and mean wind strength, as whalers will have avoided areas where catch efficiency was low. This compounding effect means that it is not possible to quantitatively estimate the effects of mean wind strength on catch efficiency.

However, it is certain that catch efficiency decreases at high wind speeds, and as Townsend's charts are only reliable when the catch efficiency is more or less constant, only the areas and the months where the mean monthly wind speed was below 24 km/h were used for this study.

2.4. Data analyses

The tropical and temperate Pacific (between the American coast and 140°E, and between 40°N and 40°S) was first divided into 2° latitude by 2° longitude (~220 km by ~220 km) squares. As the position of a Yankee whaling ship was generally assessed only once a day, and as the dots on the Townsend's (1935) charts were drawn one beside the other when their true positions overlapped, it was felt that any scale smaller than 220 km would be unreliable. For each square, the total number of whale kills marked on Townsend's (1935) charts was counted, and the mean annual pigment concentration was calculated using Coastal Zone Color Scanner (CZCS) data. To increase the spatial scale, squares were combined to form 4° by 4° squares (440 X ~440 km), 8° by 8° (890 X ~890 km) and 16° by 16° squares (1,780 X ~1,780 km). Similarly, the total number of whales killed in each square for each 2-month period (February-March, April-May, June-July, August-September, October-November and December-January)

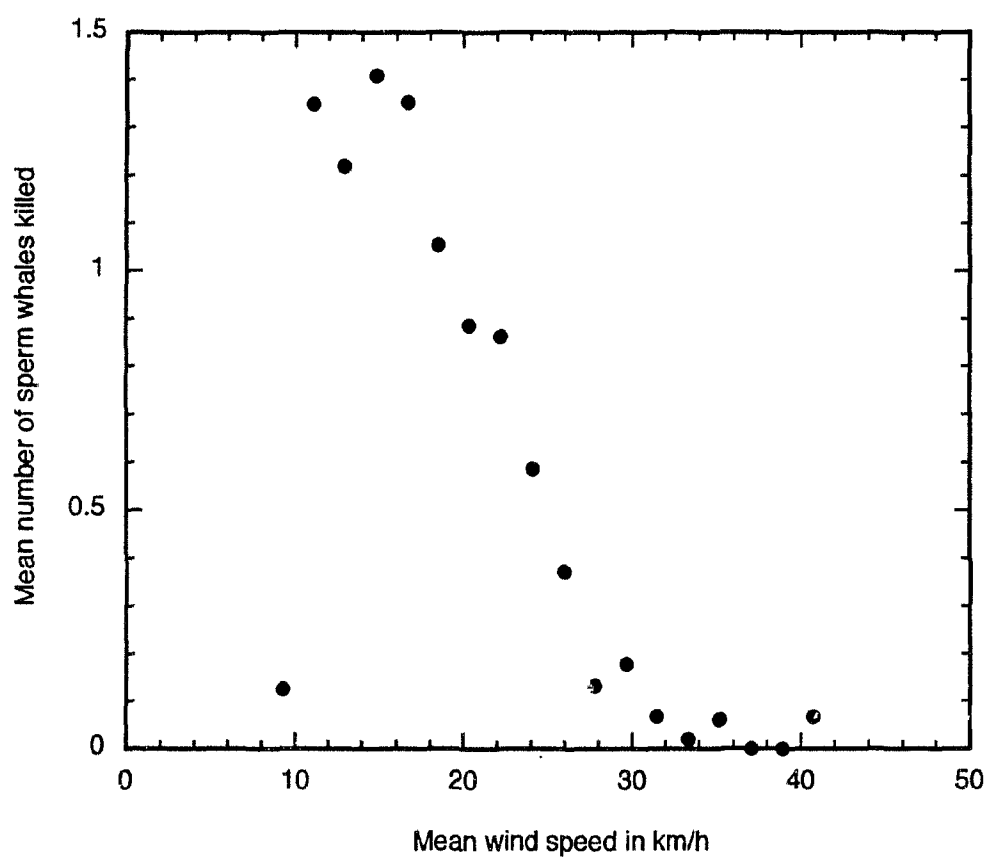


Fig. 2.2. Mean number of sperm whale killed per $2^\circ \times 2^\circ$ square and per bimonthly period (as marked on Townsend's charts) for different wind speed.

was counted, and the mean pigment concentration for each square and for each bimonthly period was likewise determined.

It has been shown for several species of baleen whales, that during breeding and/or calving season, the whales are found in waters which are less productive but more suitable for breeding and/or calving (Gaskin, 1982). If sperm whales follow a similar pattern, as the peak of the breeding and calving season occurs at different times in northern and southern hemispheres (Best *et al.*, 1984), a high correlation between sperm whale density and chlorophyll concentration might be present in one hemisphere, in contrast to a low correlation in the other hemisphere during a breeding or calving season. Therefore, for every 2-month period, the data were also separated by hemisphere (Northern hemisphere=0°-40°N; Southern hemisphere=0°-40°S), and the number of whales killed in each square for each 2-month period and for each hemisphere, as well as the mean pigment concentration for each square, period and hemisphere, was calculated.

As none of the variables were normally distributed, and as transformations (logarithm and square roots) succeeded in normalizing only the pigment concentrations over the largest spatial scales (Kolmogorov-Smirnov tests), non-parametric statistical methods were used to investigate the relationship between sperm whale distribution and chlorophyll concentration. Spearman coefficients of correlation (r_s) were calculated between whale kills and chlorophyll concentrations at all spatial scales. Both variables showed some autocorrelation between squares, and transformations (value difference between two squares) failed to remove the autocorrelations (ACF plots) but reduced it to one to two lags. However, as I was more interested in finding patterns and consistencies

than in rigorously testing hypotheses, I did not reduce the data set to remove the autocorrelations. Therefore, no significance test results are given here, but values of $r_s > 0.25$ or < -0.25 were taken as indicators of a relationship.

2.5. Results

For the whole study area, there were 2,560 squares of $220 \times \sim 220$ km, and a total of 10,475 dots on Townsend's (1935) charts, each representing the position where one or several sperm whales were taken in any one day (Fig. 2.3.A). The overall mean surface pigment concentration was 0.1 mg/m^3 , but the variability was very high ($\text{s.d.} = 0.1 \text{ mg/m}^3$). The highest pigment values were found in the upwelling area off Peru where chlorophyll concentration often exceeded 0.6 mg/m^3 . Along the equator, the pigment concentration was high between 80° and 100°W with many values between 0.2 and 0.5 mg/m^3 ; from 100°W to the date line, the chlorophyll values were around 0.1 mg/m^3 ; and lowest values, from 0.05 to 0.1 mg/m^3 , were found in the western Pacific. The Costa Rica Dome, some areas in the Japan grounds, the California upwelling and the Tasman Sea were also characterized by high values of pigment (Fig. 2.3.B and 2.4.).

The Spearman correlation coefficients between overall, time-averaged sperm whale kills and pigment concentrations are substantially positive over every spatial scale (Fig. 2.5.). The coefficient of correlation increases with increasing spatial scale up to $890 \times \sim 890$ km and then decreases slightly, suggesting that the maximum correlation between sperm whale catches and pigment concentration occurred at a spatial scale of approximately $900 \text{ km by } 900 \text{ km}$ (Fig. 2.5.).

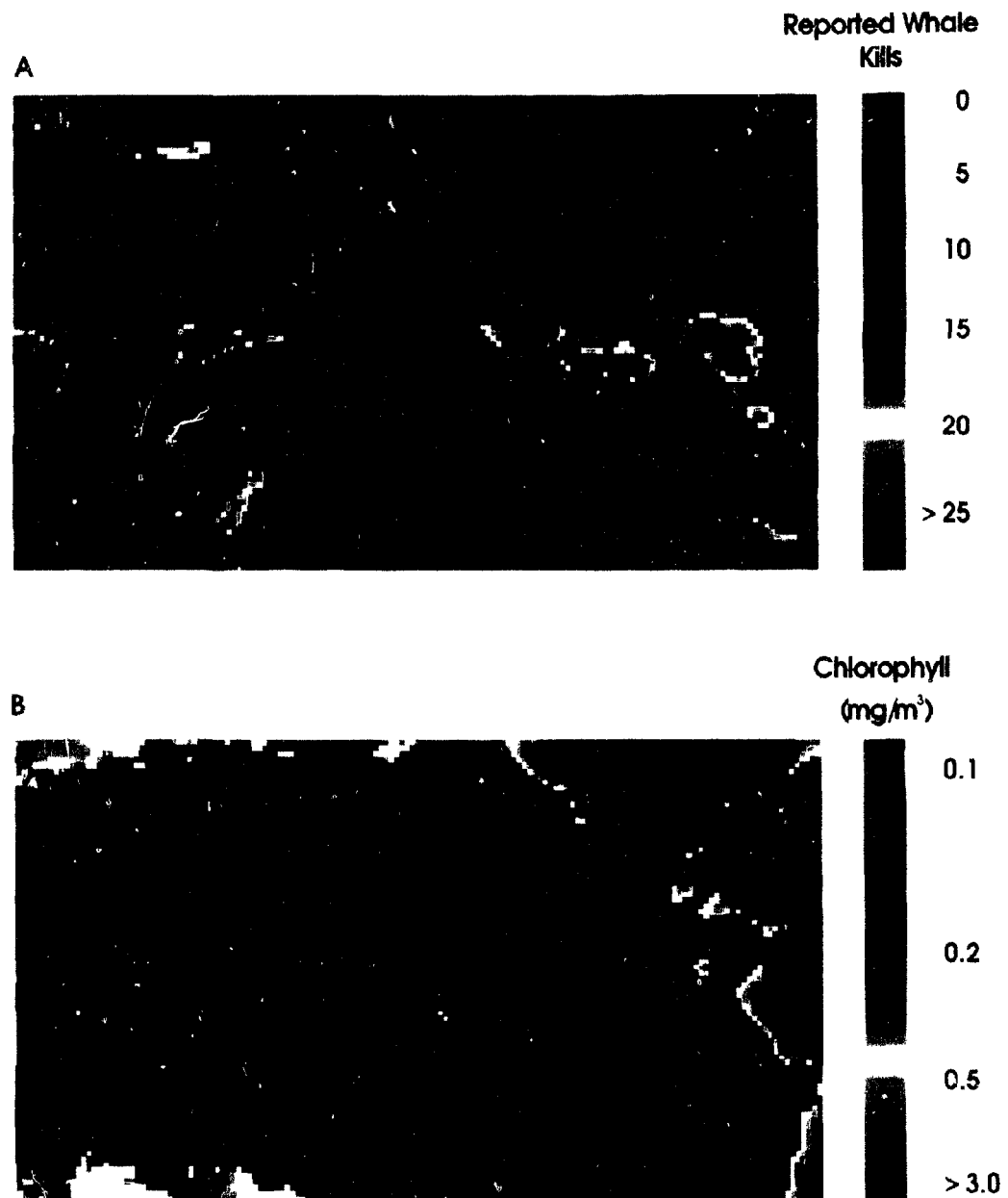


Fig. 2.3. (A) Sperm whale catches derived from the 19th century whaling records. (B) Composite image of ocean phytoplankton pigment concentration derived from Coastal Zone Color Scanner data acquired between November 1978 and June 1986.

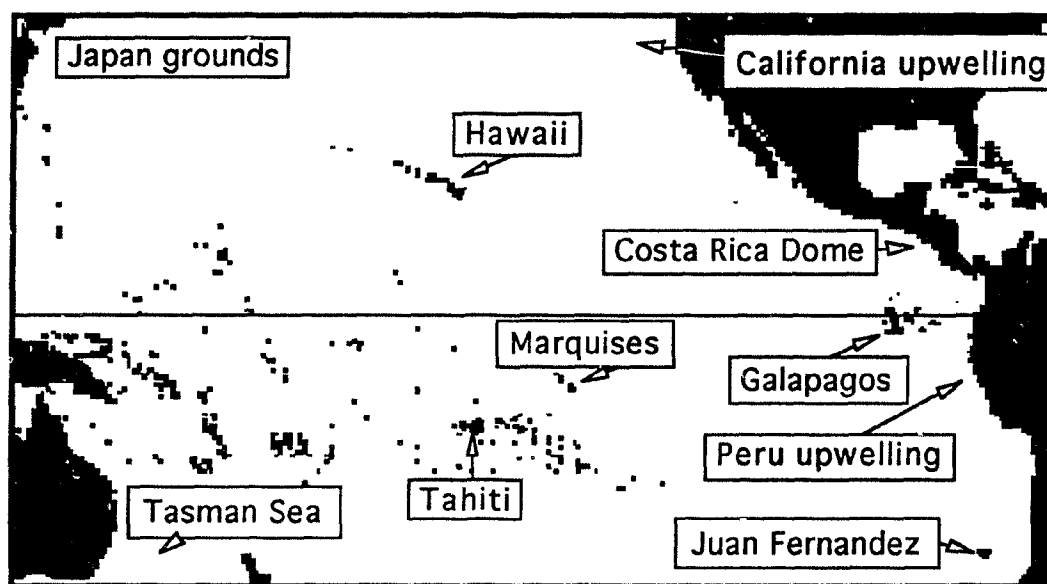


Fig. 2.4. Map of the study area and location of distinctive features and islands.

These analyses indicate that, at least in the Pacific, and averaged over a large temporal scale, sperm whales were generally found in areas of high chlorophyll concentration. However, some areas, like those off Tahiti, are characterized by a low productivity (pigment concentrations $<0.05 \text{ mg/m}^3$) but still support a rather high catch of whales (Fig. 2.3. and 2.4.). Also, both the Costa Rica Dome and the Californian upwelling are known for their high productivity but only very few sperm whales were ever killed in these areas (Fig. 2.3. and 2.4.). The Maury charts show that much effort was expended in Polynesia: in the four $5^\circ/5^\circ$ squares comprising Tahiti and the Marqueses, a mean of 564 days were spent searching for sperm whales in each square. On the other hand 301 days were spent in the $5^\circ/5^\circ$ square of the Costa Rica Dome and only a mean of 150 days in the four squares off California (fig. 2.4.).

For spatial scales greater than $220 \times \sim 220 \text{ km}$, time-resolved sperm whale catches and pigment concentration also show a substantial positive correlation for most 2-month periods (Fig. 2.6.). The correlation coefficients are low for a spatial scale of $220 \text{ km} \times \sim 220 \text{ km}$, but generally increase with increasing spatial scale similarly to those for the annual mean (cf. Fig. 2.5.). At all spatial scales, the values of r_s are generally higher for 4-month periods than for 2-month periods, but the pattern is very similar (Fig. 2.7.).

Figure 2.8. shows the Spearman correlations between sperm whale kills and pigment concentration when each hemisphere is treated separately. To avoid confusion, only the spatial scale of $890 \times \sim 890 \text{ km}$ is presented on this figure as it was the scale at which the correlation between sperm whale density and primary productivity was maximum; it is therefore the scale at which there is the

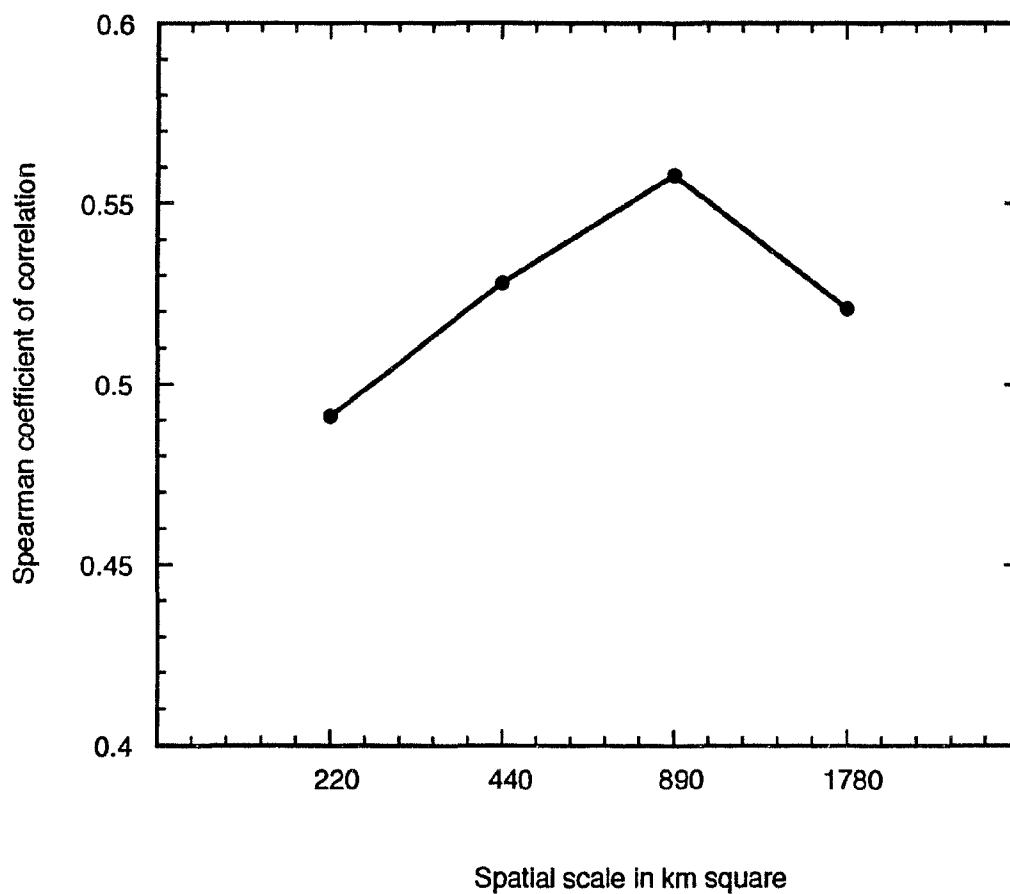


Fig. 2.5. Spearman coefficient of correlation between sperm whale kills and chlorophyll concentration over spatial scales ranging from 220 km X ~220 km to 1780 km X ~1780 km. The data were averaged over 12-month periods.

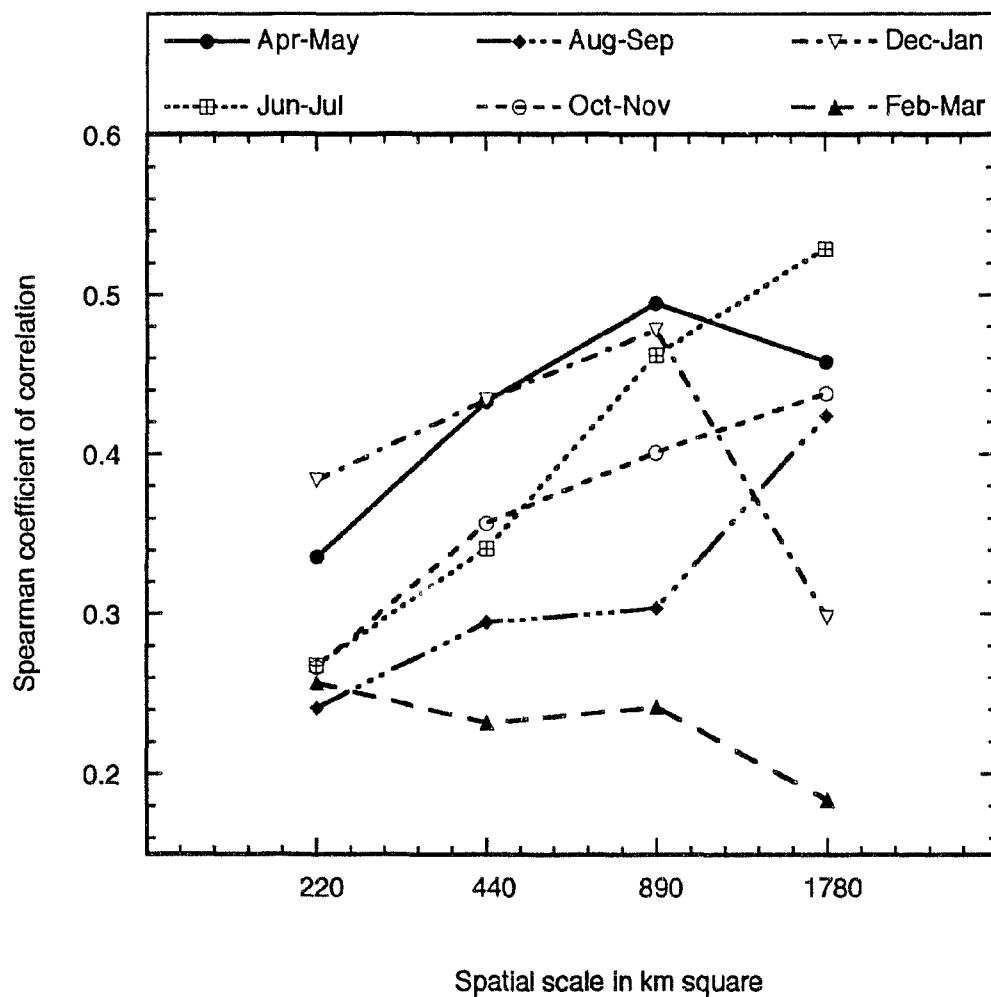


Fig. 2.6. Spearman coefficient of correlation between sperm whale kills and chlorophyll concentration over spatial scales ranging from 220 km X ~220 km to 1780 km X ~1780 km. The data were averaged over 2-month seasonal periods.

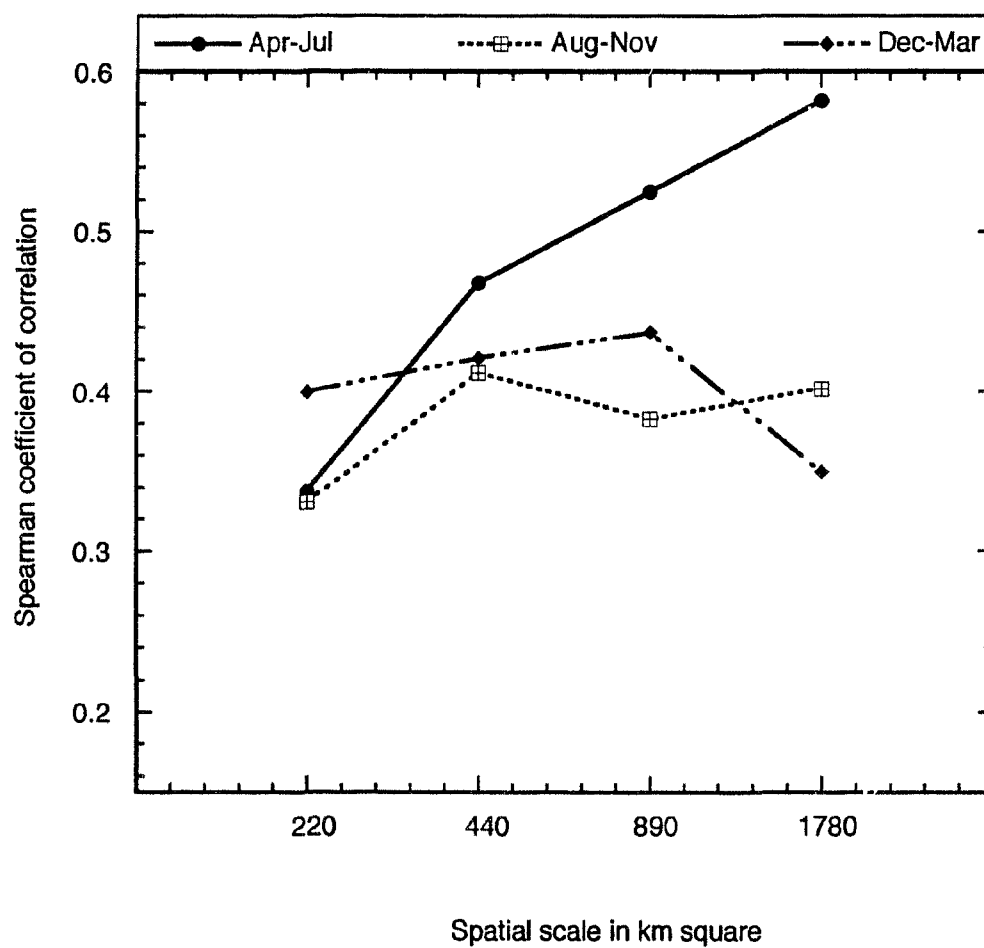


Fig. 2.7. Spearman coefficient of correlation between sperm whale kills and chlorophyll concentration over spatial scales ranging from 220 km X ~220 km to 1780 km X ~1780 km. The data were averaged over 4-month seasonal periods.

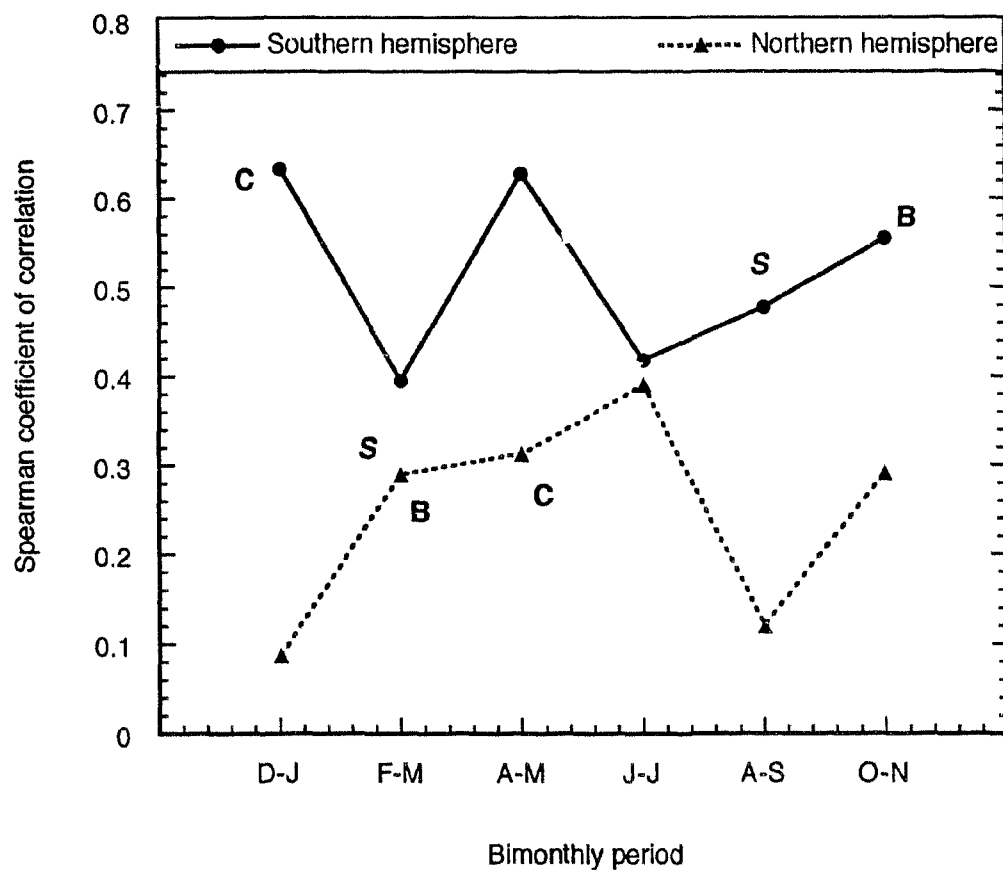


Fig. 2.8. Spearman coefficient of correlation between sperm whale kills and chlorophyll concentration for each hemisphere and for each 2-month period. B represents the peak of the breeding season, C the peak of the calving season and S the peak of the squid spawning season; (Caldwell *et al.*, 1966; Best *et al.*, 1984; O'Dor, 1992).

greatest likelihood of observing differences in the values of r_s due to breeding and/or calving requirements. This figure shows a high seasonal variability in the correlation between sperm whale catches and chlorophyll concentration, but for both hemispheres, there is not a lower correlation during the periods corresponding to the peak of the breeding and calving season than for other periods of the year. However, this figure also shows that, in general, the values of r_s are higher for the Southern hemisphere than for the Northern hemisphere. In the Northern hemisphere, a high number of whales were killed on the Japan ground, but this ground had to be removed from the analyses because of the prevailing high winds during half of the year. Moreover, as the Californian upwelling and the Costa Rica dome are both characterized by high chlorophyll concentration and by low sperm whale kills, it is not surprising to find a weaker correlation in the Northern hemisphere than in the Southern hemisphere.

2.5.1. Evaluation of biases

As the number of observations necessarily decreases with increasing spatial scale, the increase of r_s could simply reflect a relationship with the number of observations. To test this possibility, a bootstrap method was used, where files of respectively 50, 100, 150, 200, 300, 500, 700, 900, 1100 and 1300 observations were randomly extracted from the largest file (annual mean, spatial scale 220 km X ~220 km), and a Spearman correlation coefficient between pigment concentration and sperm whale catches was calculated for each of them. This revealed no increase of r_s with decreasing number of observations and no particular pattern.

Stronger correlations at larger scales could also be the result of the smoothing of high frequency variance. Because of stochastic effects, smaller numbers of kills per square at smaller spatial scales are not as good a measure of true whale abundance as are the larger numbers found at larger spatial scales. To test for this possible bias, I replaced each whale count by a randomly chosen count from the Poisson distribution whose mean was the original count, and recalculated a Spearman coefficient of correlation between sperm whale kills and pigment concentration. Ten such simulations were carried out at each spatial scale. The Spearman correlation coefficient was only biased downwards by 0.013 (standard error = 0.0021) at the 220 km scale, but there was no discernible bias (<0.01) at larger scales, suggesting again that the increase of r_s with increasing spatial scale is a real phenomenon.

Finally, to test how sensitive the pattern observed on Fig. 2.5. was to the location of the blocks, all the blocks were shifted by 220 km and a Spearman coefficient of correlation was calculated for the 3 larger spatial scales. I then shifted all the blocks by 440 km and by 890 km and recalculated a Spearman coefficient of correlation for the relevant spatial scales. In every cases, I always observed the same general pattern of increasing r_s with increasing spatial scale and only minor changes in r_s (± 0.01 -0.04). However, when the blocks were shifted, I did not find a diminution of r_s at the largest spatial scale (1780 km) suggesting that the peak observed on Fig. 2.5. at the 900 km spatial scale may depend on the blocks' location.

Therefore, I conclude that the increase of r_s with increasing spatial scale was not a methodological artifact, although the drop at 1780 km may not reflect reality.

2.6. Discussion

This study shows that, over large spatial and temporal scales, sperm whales are found in waters with higher chlorophyll concentration than adjacent waters; and that the coefficient of correlation between sperm whale catches and phytoplankton density generally increases with increasing spatial scale. Increasing coefficients of correlation between the distribution of a predator and the distribution of its prey with spatial scales have been observed in many studies involving marine birds and fish or zooplankton (Schneider, 1994). For example, in studying the distribution of macaroni penguins (*Eudyptes chrysolophus*) and Antarctic krill (*Euphausia superba*), Hunt *et al.* (1992) found an increase in r_s from 0.11 to 0.80 at spatial scales ranging from 2 km to 470 km. Patterns like the one shown on Fig. 2.5. have also been observed in other studies: the correlation between Antarctic fur seals (*Arctocephalus gazella*) and Antarctic krill shows an increase only until a spatial scale of 52 km and a decrease thereafter (Hunt *et al.*, 1992).

Several deviations occur in the relationship between sperm whale distribution and pigment density, and neither the low density of whales in the California upwelling and in the Costa Rica Dome nor the high catches around Tahiti are consistent with chlorophyll concentrations. These anomalies can partly be explained by the uneven amount of effort expended in different areas of the Pacific, as the whalers were constrained by the weather and by the need to resupply once or twice a year. A fair wind was a necessity for these vessels to sail; however, the California upwelling and the Costa Rica Dome are both

characterized by favorable winds during most of the year, and thus the low sperm whale catches cannot be explained by weather constraints.

During a typical voyage through the Pacific, the whalers usually sailed north along the west coast of South America, followed the equator pushed by the trade winds, went south to Tahiti to resupply, sailed back to the equator and followed it west before sailing north to the Japan Grounds in summer (Mitchell, 1983). During the boreal winter, the whalers usually returned to the equator via Hawaii. This circuit was sailed several times until the ship had been filled with oil. On their way home, the whalers often sailed through Tahiti, then south to meet the westerlies before going around Cape Horn (Mitchell, 1983). In the course of the nineteenth century, whalers tended to explore grounds further and further west, and occasionally to sail down the west coast of North America (Starbuck, 1878; Mitchell, 1983; Shuster, 1983b). Tahiti was therefore a very popular stop for the Yankee whalers, and this explains the high amount of effort in the region. However, if sperm whales were rare in the area, no amount of effort would permit high catches. Similarly, very little effort was expended along the California upwelling (a mean of only 150 days in each 5°/5° square), but if whales had been found in high concentration, it is very likely that the course of the voyages would have been changed to sail through these grounds.

Many species of muscular cephalopods spawn in unproductive tropical water; after hatching, the larvae drift with powerful western boundary currents to higher latitude feeding grounds and then the adults swim back to the spawning grounds a year later (Mann and Lazier, 1991; O'Dor, 1992). The spawning grounds are thus characterized by low chlorophyll concentration but very high biomass and could be very profitable for teuthophage species like sperm whales. Therefore, a

high density of sperm whales in apparently unproductive water could possibly be explained by a high density of spawning squids. However, except for a few species of commercially fished cephalopods, the location of the spawning grounds for most species remains unknown (O'Dor, 1992). Moreover, depending on the region considered, 53% to 78% of sperm whale diet consist of ammoniacal squids (Clarke, 1986), and very little is known of the life history of these cephalopods. It has often been suggested that this type of squid does not undertake extensive horizontal migrations, but shows an ontogenetic descent to cooler deeper waters (Roper and Young, 1975). Thus, to be able to assess whether sperm whales feed on spawning squids in unproductive water, much more would need to be known on meso- and bathypelagic cephalopod ecology and life cycles.

It seems therefore that, even if chlorophyll concentration is an important factor influencing sperm whale distribution over large spatial and temporal scales, other factors have to be considered in certain areas.

At spatial scales greater than 220 km X ~220 km, the Spearman coefficient of correlation between sperm whale kills and pigment concentration was substantially positive for every 2-month period except February-March, suggesting that throughout the year, sperm whales are found in areas of high chlorophyll concentration.

The coefficient of correlation between sperm whale catches and phytoplankton concentration is in general lower for a 2-month period than for a 4-month period, and both are lower than those of a 12-month period. This is consistent with the existence of a time lag between a peak in chlorophyll concentration and a peak in

sperm whale density. The present study cannot estimate the length of this time lag, as the data are averaged over long temporal scales (8-130 years), and as peak time of upwelling is likely to vary between years in many areas. However, this study suggests the existence of a time lag of at least 4 months. Sette (1955) estimated that a time lag of 75 to 150 days was required for the development of 3 trophic levels in a marine community, and Blackburn *et al.* (1970) suggested that the peak in density of primary carnivores (like some cephalopods or fishes) in equatorial regions lags behind the peak in chlorophyll concentration by about four months. Therefore, over very short time periods, there may be no correlation between sperm whale density and pigment concentration. This is consistent with predator-prey relationship theory: within the areas the size of a ground (500-2000 km), the density of sperm whales should reflect long-term mean prey density, but not necessarily prey density within a given year or a given season (Heinemann *et al.*, 1989). Similarly, Hunt (1990) and Piatt (1990) found that spatial association of birds with prey is episodic at small time scales but increase with increasing time resolution.

The increase of r_s with increasing spatial scales suggests that there is also a spatial lag between a peak in chlorophyll concentration and a peak in sperm whale catches. However, as the data are averaged over several years, and as it is likely that the exact location of upwelling (especially the equatorial upwelling) shifts slightly between years (Vinogradov, 1981), it is not possible to assess the size of the space lag. Vinogradov (1981) showed that there is about 280 to 460 km between associated up- and downwelling phenomena. Therefore, while this study suggests that sperm whales are found in large areas (~900 X ~900 km or larger) characterized by high primary productivity, within these areas sperm

whales could be more closely associated with downwelling phenomena than with the upwellings.

Unlike several species of baleen whale, sperm whales are not found in unproductive waters during the peak of the breeding and/or calving season. It has been postulated that the mysticete annual migrations evolved as a response to the need for warm water by newborn calves (Baker, 1978), although this is controversial as many small odontocetes live and give birth at high latitudes (Evans, 1990). Therefore, as female sperm whales stay all year round in waters warmer than 15°C (Rice, 1989), it is not unexpected to find that they do not seem to change their distribution to satisfy breeding and/or calving requirements. Similarly, for both hemispheres, the lowest values of r_s during two bimonthly periods cannot be attributed to the peak of the squid spawning season. However, too little is actually known of the life history of mesopelagic squid to rule out the possibility that sperm whales take advantage of the high cephalopod biomass occurring in spawning grounds at some times of the year.

2.7. Conclusion

This study suggests that, when averaged over large temporal scales, sperm whales are generally found in broad areas (~900 km X ~900 km or larger) characterized by high concentrations of chlorophyll. It also emphasizes the scale dependence in the aggregative response of sperm whales to pigment concentration both on a spatial and a temporal scale. In addition, this study demonstrates the potential of Yankee whaling data for investigating the factors controlling sperm whale distribution. Satellite observations of ocean color are

therefore useful for predicting likely areas of high sperm whale density. However, remote sensing can only be used as an indicator of sperm whale distribution over large spatial and temporal scales, as there is no relationship over small scales. Moreover, some "anomalies" in sperm whale distribution cannot be explained in terms of chlorophyll concentrations, implying that other factors (maybe squid spawning grounds) could be of significant importance in some regions.

CHAPTER 3

SCALE-DEPENDENT CORRELATION OF SPERM WHALE DISTRIBUTION WITH ENVIRONMENTAL FEATURES AND PRODUCTIVITY IN THE SOUTH PACIFIC

3.1. Introduction

Multiscale studies conducted on marine organisms have emphasized the importance of looking at a range of spatial scales (chapter 1). There is no single scale at which sperm whale distribution should be investigated: much is to be gained by studying how the relationship between sperm whale density and environmental parameters varies with scale (chapter 1).

This chapter investigates sperm whale distribution in relation to underwater topography, temperature and thermocline variables, chlorophyll concentration and measures of sub-surface biomass at four different spatial scales (148 km, 296 km; 592 km and 1185 km) with a temporal resolution of a few days. Scale-dependent correlations between sperm whale density and environmental features are examined and the importance of food resources in determining sperm whale habitat is discussed.

3.2. Methods

3.2.1. Field methods

Data were collected from a 12.5-meter, ocean-going cutter during a survey around the South Pacific in 1992-1993 (Fig. 3.1.). A total of 184 days were spent at sea. Sperm whales were located by listening every half hour through an omnidirectional hydrophone for their characteristic clicks (Backus and Schevill, 1966). Since the survey track was designed to go through all major 19th century sperm whaling grounds of the South Pacific (Fig. 2.1.), the sampling distribution

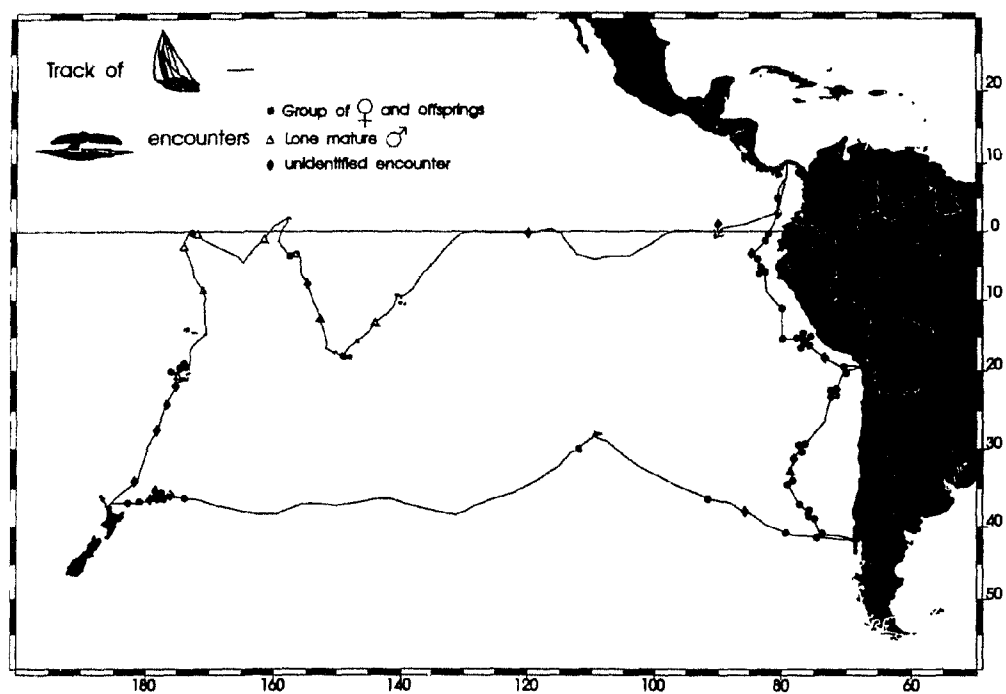


Fig. 3.1. Map of the South Pacific showing the track of the research vessel and all sperm whale encounters.

of searching effort was not random. Once located, the sperm whales were usually followed both acoustically and visually for periods ranging from a few hours to two and half days.

During the entire survey, biological and environmental data were collected regularly. Chlorophyll concentration was measured every day at 15:00 local time by a spectral radiometer (McLean and Lewis, 1991) and by a Secchi disk. The intensity and the thickness of scattering layers were recorded at three different depths every day at 15:00 local time using a Furuno CH 14 sonar (frequency: 60 KHz). The three depths were defined as follows: the surface layer, from 0 to 50 meters deep (~depth of the euphotic zone); the middle layer, from 50 to 300 meters deep; and the deep layer, from 300 to 600 meters deep (~depth at which sperm whales normally feed, Papastavrou *et al.*, 1989). To avoid diurnal solar heating effects, sea surface temperature was measured every day at 06:00 local time. Temperature profiles were determined every 550-700 km using expendable bathythermographs (XBT). The position of the boat was recorded every hour using a Trimble Transpak GPS.

In sailing around the South Pacific, the research vessel traveled through 4 main regions: 1) South American coast along the American Continent from Puerto Montt (42°S, 74°W) to Panama City (9°N, 79°W), to a longitude of 92°W; 2) Equatorial region along the Equator from 92°W to American Samoa (13°S, 170°W); 3) West Pacific region, west of 170°W; 4) South Pacific gyre between 170°W and 92°W, at a latitude of 30° to 40°S.

3.2.2. Data analyses

The track of the research vessel was divided into 148 km segments (= minimum distance traveled in one day). For each segment, the variables described in Table 3.1. were calculated.

Both the variable "density of whales" (*denswhal*) and the variable "number of encounters" (*nbrenc*) measured sperm whale density. However, as about half the time sperm whales were tracked once located, *denswhal* is biased in favor of the areas where the whales were followed. On the other hand, *nbrenc* is negatively biased in areas where whales were followed. Therefore, each analysis was carried out separately with the two sperm whale variables.

The Contour Index (*C.I.*) was calculated using the charts "Bathymetry of the North/South Pacific, Scripps Institution of Oceanography and Institute of Marine Resources, 1970". All segments were plotted on the charts, and the maximum and the minimum depth in a radius of half of the segment's length were used to calculate the *C.I.* according to Hui's formula (1979): $C.I. = 100 * [(maxdepth - mindepth) / maxdepth]$.

To increase the spatial scale, two segments were combined to make 296 km segments, and then 592- and 1185 km segments respectively. For each segment at each spatial scale all the variables listed in Table 3.1. were calculated.

Table 3.1. Description of the variables calculated for each segment

Variables	Description	Units
<i>Denswhal</i>	number of 1/2 hour listenings during which we heard or saw whales divided by the total number of 1/2 hour listenings	percentage
<i>Nbrenc</i>	number of times we encountered a "new" group of whales	-
<i>Chlconc</i>	Chlorophyll concentration	mg/m ³
<i>Intmax1</i>	Maximum intensity of the surface scattering layer (0-50 meters deep)	subjective scale from 0.00 to 4.00.
<i>Thick1</i>	Thickness of the surface scattering layer (0-50 meters deep)	m
<i>Intmax2</i>	Maximum intensity of the medium scattering layer (50-300 meters deep)	subjective scale from 0.00 to 4.00.
<i>Thick2</i>	Thickness of the medium scattering layer (50-300 meters deep)	m
<i>Intmax3</i>	Maximum intensity of the deep scattering layer (300-600 meters deep), subjective scale from 0.00 to 4.00	subjective scale from 0.00 to 4.00.
<i>Thick3</i>	Thickness of the deep scattering layer (300-600 meters deep), in meters	m
<i>SST</i>	Sea surface temperature	°C
<i>DiffinSST</i>	Difference in sea surface temperature between 2 consecutive segments	°C
<i>Δtmax</i>	Maximum difference in temperature between 2 consecutive measures (~ 65 cm) in the temperature profile	°C
<i>DepthΔt</i>	Depth of maximum difference in temperature between 2 consecutive measures (~ 65 cm) in the temperature profile, in meters; corresponds roughly to the mixed layer depth	m
<i>Gradient</i>	Gradient of temperature in the first 100 meters of depth	°C/100 m
<i>Meandept</i>	Mean ocean depth	m
<i>C.I.</i>	Contour index, define using Hui's (1979) formula, $C.I.=100*((maxdepth - mindepth)/maxdepth)$	-
<i>Distland</i>	Distance to the closest shore, including all oceanic islands	km

The relationships among the biological and environmental variables and between the environmental variables and the density of whales were first investigated using correlation analyses. None of the untransformed variables were normally distributed, and transformations (mainly square roots, logarithmic and arc-sines) succeeded only in rendering normal a few variables over the largest spatial scales (Kolmogoroff-Smirnoff tests). Therefore, non-parametric Spearman correlation coefficients (Sokal and Rohlf, 1981) were used. However, as the data were collected each day along a survey track, most variables showed considerable autocorrelation with lags ranging from 1 to 20 segments. Once again, transformations (value difference between two segments) failed to remove the autocorrelations (ACF plots), reducing it to a lag of about 6 segments (at the 148 km scale). As I was more interested in finding patterns and consistency in the patterns than in rigorously testing hypotheses, and as using only one segment out of six reduced the data set too drastically, all data were used for the correlation analyses but no significance test results are given. Correlation coefficients substantially greater than 0.25 or less than -0.25 were taken as indicators of a relationships.

As most of the environmental variables were strongly correlated, multivariate analyses were also used to investigate the relationship between sperm whale density and the environmental variables. Principal components analyses were performed on the correlation matrices of most of the environmental variables (if for a specified spatial scale a variable had too many missing points, it was deleted from the analysis). The resulting loadings provided a measure of association between each original variable and the resultant principal components. No multiple regression of sperm whale density on the various

factors was carried out, as the normality assumptions were still violated (plot of residual versus estimate show non-constant variance of the residual, Flury and Riedwyl, 1988). Therefore, non-parametric Spearman correlation coefficients were calculated between sperm whale density and the principal components over each spatial scale.

3.3. Results

During the survey around the South Pacific, we encountered sperm whales 70 times. Of these, 8 encounters were with single mature males, 47 with nursery groups (including about 20 females and immatures of both sexes), and in 15 cases, the type of aggregation encountered was unidentified (Fig. 3.1.). We listened 8,332 times for the characteristic clicks of sperm whale, and in 1,510 of these times whales were either seen or heard.

The track of the research vessel was divided into 264 segments of 148 km each. The summary statistics of the measurements of temperature parameters, chlorophyll concentration, surface, medium and deep biomass and bathymetry variables are shown in Table 3.2.

All statistical analyses were carried out using the 2 variables measuring sperm whale density (*denswhal* and *nbrenc*). But as they both gave similar results, only those using *denswhal* are presented here.

Table 3.2. Summary of statistics for environmental variables over a spatial scale of 148 km.

Variable	N. of cases	Min.	Max.	Mean	S.D.
<i>Chlconc</i>	149	0.06	8.72	0.46	0.86
<i>Intmax1</i>	173	0	4	2.06	1.42
<i>Thick1</i>	173	0	50	22.2	14.9
<i>Intmax2</i>	173	0	4	2.85	1.20
<i>Thick2</i>	173	0	250	130.1	59.3
<i>Intmax3</i>	173	0	4	1.15	1.38
<i>Thick3</i>	173	0	300	66.7	61.2
<i>SST</i>	171	15.2	29.5	23.6	3.75
<i>Δmax</i>	55	0.03	1.86	0.37	0.28
<i>DepthΔt</i>	55	11	180.2	69.3	43.4
<i>Gradient</i>	55	-0.7	11.96	5.60	3.54
<i>Meandepth</i>	258	500	6000	3612	1123
<i>C.I.</i>	264	0	100	35.9	35.2
<i>Distland</i>	264	4	2600	580	340

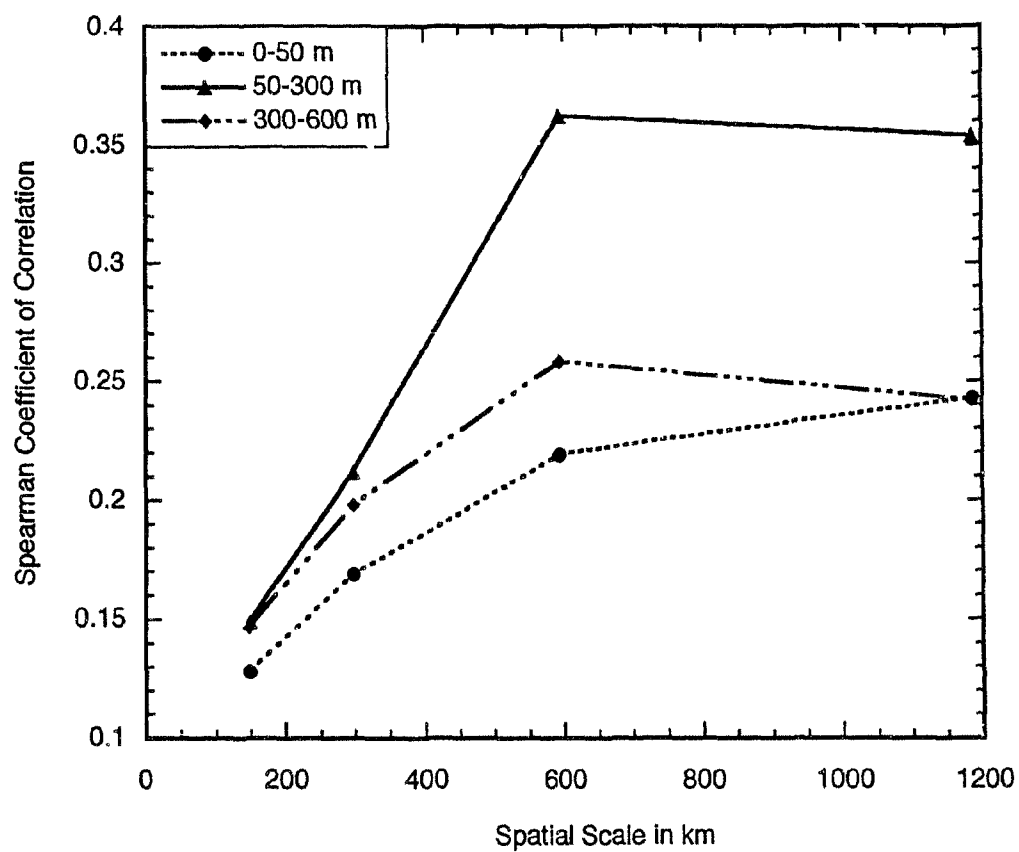


Fig. 3.2. Spearman coefficient of correlations between sperm whale density and maximum intensity of the scattering layer at three different depths over a range of spatial scales.

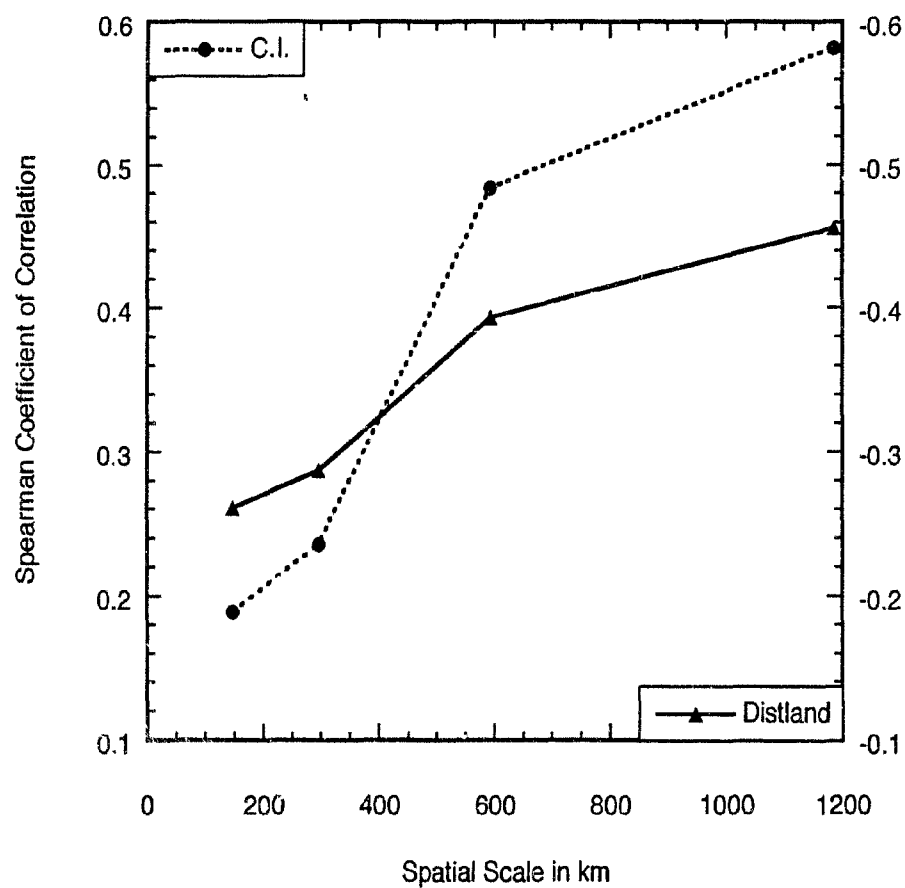


Fig. 3.3. Spearman coefficient of correlations between sperm whale density and contour index (C.I., positive correlations) and distance to the closest shore (negative correlations) over a range of spatial scales.

No correlations greater than 0.2, or less than -0.07, were found between sperm whale density and any temperature variable (sea surface temperature, difference in sea surface temperature between 2 adjacent segments, depth and intensity of the thermocline, gradient of temperature in the first hundred meters) at any spatial scale. Similarly, no correlations greater than 0.24 or less than -0.08 were found between sperm whale density and chlorophyll concentration, or between sperm whale density and the thickness or intensity of the surface scattering layer at any spatial scale. However, the Spearman correlation coefficients between sperm whale density and the intensity and thickness of the middle and deep scattering layers showed substantial positive correlations over spatial scales of 592 and 1185 km (Fig. 3.2.). There were also substantial positive correlations between sperm whale density and the contour index at the two largest scales. Substantial negative correlation between sperm whale density and the distance to the closest shore was also found only for the two largest scales (Fig. 3.3.).

As the Spearman coefficient of correlation could be dependent on the number of observations, the increase of its value with increasing spatial scale could therefore be an artifact resulting from smaller number of observations at larger spatial scales. To assess the relationship between the value of the coefficient of correlation and the number of observations, subsets of 20, 30, 40.....210 observations were randomly chosen from the largest file (148 km). Spearman coefficients of correlation analyses were carried out for each subset and for the five relevant variables (*intmax1*, *intmax2*, *intmax3*, *C.I.*, *distland*). The coefficient of correlation was plotted against the number of observations to investigate possible dependency. As the results showed no increase of r_s with decreasing number of observations, and no other consistent trend, it was concluded that the

patterns observed on Fig. 3.2. and 3.3. were not an artifact due to the methodology used.

The relationships within the environmental variables were further investigated by Principal Component Analyses (PCA). The three smallest spatial scales (148, 296 and 592 km segments) gave very similar principal components, with the component loadings being almost exactly the same. Therefore, only the results using the 148 km segments are presented in Table 3.3. The 1st principal component, explaining 31% of the variance, relates to high sub-surface biomass (mainly zooplankton and mesopelagic fish), as shown by the high loading of the 6 variables measured by the sonar. The 2nd principal component, explaining 20% of the variance, relates to a flat underwater topography, deep water and a great distance from shore. The 3rd principal component, explaining 16% of the variance, contrasts a low deep water biomass with a high chlorophyll concentration. The 1st component can be considered as an index of secondary productivity, the 2nd component, as an index of underwater topography and the 3rd component, as a contrast between deep secondary productivity and primary productivity. As the other principal components had eigenvalues less than 1.0 and explained only a small proportion of the variance, they were not investigated any further.

Table 3.3. Relationships between environmental variables over a spatial scale of 148 km, using principal components analysis.

	Principal Components		
	1	2	3
Eigenvalues	3.132	1.970	1.614
% of total var.explained	31.320	19.703	16.139
<i>Intmax1</i>	0.74	0.28	0.30
<i>Thick1</i>	0.69	0.16	0.31
<i>Intmax2</i>	0.78	0.21	0.17
<i>Thick2</i>	0.59	0.33	0.41
<i>Intmax3</i>	0.57	0.14	-0.68
<i>Thick3</i>	0.56	0.24	-0.63
<i>Chlconc</i>	-0.17	0.03	0.59
<i>Meandepth</i>	-0.33	0.65	-0.06
<i>C.I.</i>	0.47	-0.77	-0.05
<i>Distland</i>	-0.38	0.79	-0.09

Three of the four regions described in the methods could be well separated on the basis of the first two principal components (Fig. 3.4.). Most of the segments belonging to the South American coast region have a positive value of the 1st principal component (PC), suggesting that this region is characterized by a high sub-surface biomass. The 2nd PC, being as often positive as negative, shows that both very uneven underwater topography and flat ocean floor occur in this region. The South Pacific gyre is characterized by a low sub-surface biomass and a flat ocean floor. The West Pacific region is mainly characterized by a very high relief.

Although the correlation between the first PC and sperm whale density is weak at a spatial scale of 148 km, the correlation coefficient increases with increasing spatial scale. At a scale of 592 km, there is a substantial positive correlation between amount of sub-surface biomass and sperm whale distribution (Fig. 3.5.). This suggests that whales are found in areas of high sub-surface biomass over a spatial scale of about 600 km or more. Similarly, the ocean floor topography (2nd PC) seems to have no influence on whale distribution over small spatial scales (148 and 296 km), but has an effect over spatial scales of at least 592 km. However, the third PC shows little or no correlation with sperm whale distribution over the three spatial scales. Therefore, over a scale of 148 km, and when the first 2 PCs are considered, there is no obvious difference between representations of the segments where sperm whales were or were not found (Fig. 3.4.).

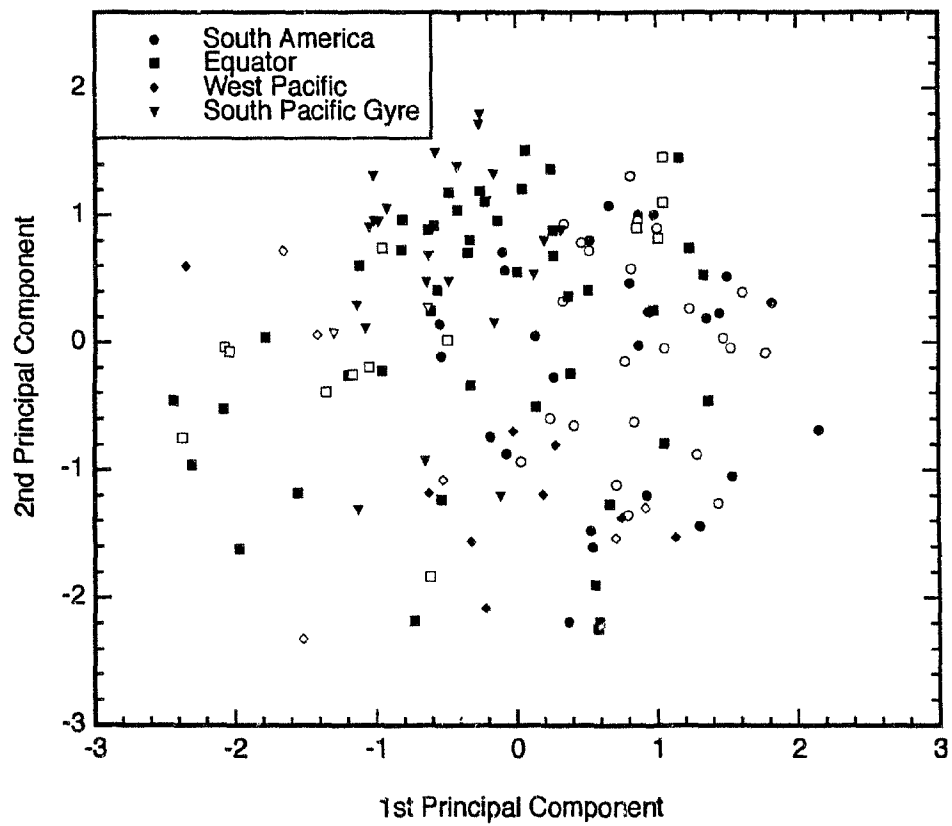


Fig. 3.4. Scores of the second principal component plotted against the first over a spatial scale of 148 km. The open symbols represent the segments where whales were either seen or heard.

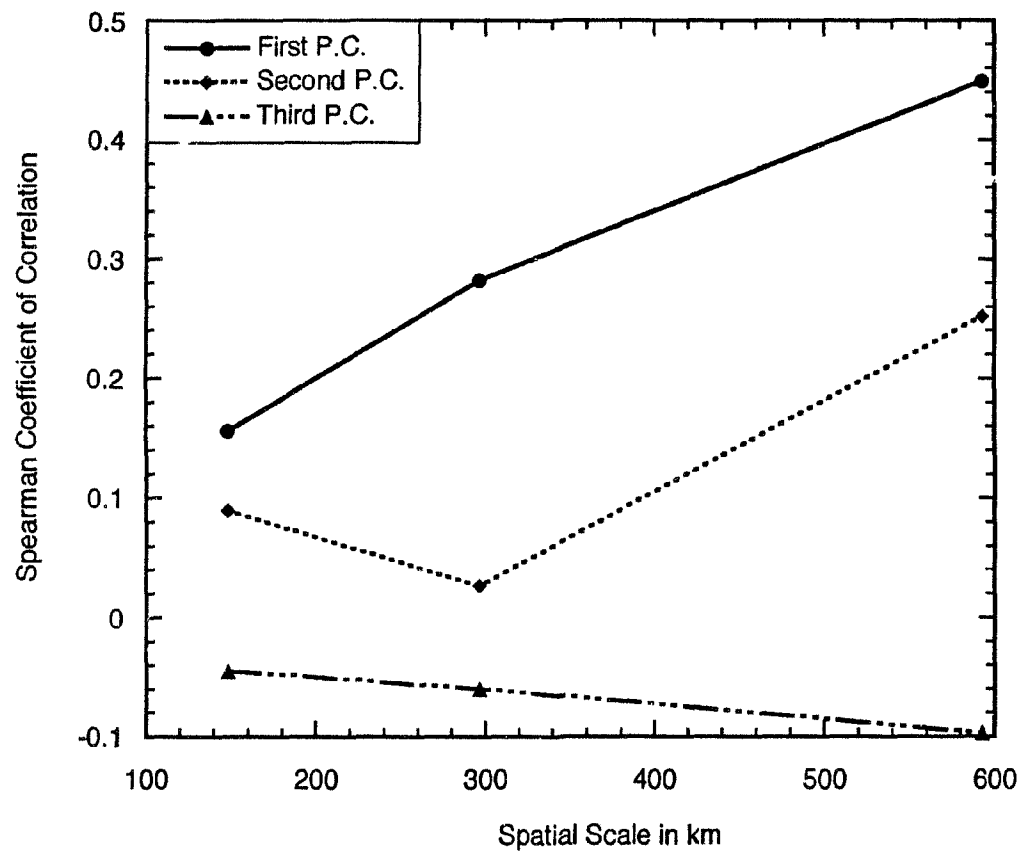


Fig. 3.5. Spearman coefficient of correlations between sperm whale density and the first three principal components of the environmental variables over a range of spatial scales.

For the 1185 km spatial scale, four PCs had large eigenvalues and were therefore considered (Table 3.4.). The first PC., which accounts for 26% of the variance, relates to a high surface and deep biomass, a high gradient of temperature in the first 100 meters and a low sea surface temperature. The second PC relates to a high surface and medium biomass, a high relief and a short distance to land. The third PC relates to a high deep biomass, a high relief and a short distance to land. The fourth PC relates to a weak and deep thermocline, a low sea surface temperature and little difference in temperature between consecutive segments. There is only a weak correlation between the 1st PC and sperm whale density, and no correlation between sperm whale density and the 4th PC (Table 3.4.). However, there is a substantial positive correlation between sperm whale density and the second and the third PC, suggesting that sperm whale distribution is correlated with a strong relief and a high subsurface biomass at a spatial scale of 1185 km.

3.4. Discussion

The sperm whale distribution that we observed in the South Pacific in 1992-93 has much in common with the distribution of the 19th century sperm whale catches (Fig. 2.1). High densities of sperm whales were found along the west coast of South America, "On the Line" between Christmas Island and the Phoenix Islands, along the Tonga archipelago and on the "Vasquez Ground". However, only a single sperm whale was heard on the "Offshore Ground" and on the "On the Line Ground" between the Galápagos and the Marquesas. This last

Table 3.4. Relationships between environmental variables using PCA; and value of the Spearman coefficient of correlation between the first four principal components and sperm whale density, over a spatial scale of 1185 km.

	Principal Components			
	1	2	3	4
Eigenvalues	3.954	3.061	2.163	1.757
% of tot. var. explained	26.36	20.40	14.42	11.72
<i>Intmax1</i>	0.587	0.632	-0.328	0.045
<i>Thick1</i>	0.517	0.658	-0.065	-0.121
<i>Intmax2</i>	0.482	0.732	-0.142	-0.071
<i>Thick2</i>	0.442	0.707	-0.286	0.055
<i>Intmax3</i>	0.731	-0.133	0.493	-0.178
<i>Thick3</i>	0.682	-0.027	0.573	-0.119
<i>Chlconc</i>	-0.203	0.335	-0.351	0.049
<i>SST</i>	-0.578	0.251	-0.077	-0.650
<i>DifinSST</i>	0.066	-0.215	0.150	-0.556
Δt_{max}	0.422	-0.094	0.199	-0.655
<i>Depth</i> Δt	0.497	-0.238	0.083	0.625
<i>Gradient</i>	0.800	-0.340	0.169	0.044
<i>CI</i>	-0.416	0.532	0.611	0.099
<i>Distland</i>	0.433	-0.579	-0.514	0.037
Value of r_s between: <i>denswhal</i> and each PC	0.156	0.461	0.454	0.055

result was very unexpected as high densities of sperm whales were known to inhabit this area year round during the last century (Maury, 1852; Townsend, 1935; Berzin, 1978; Shuster, 1983b). Since summer 1992 was highly productive in the Equatorial Pacific (R. T. Barber, comm. pers.), the El Niño Southern Oscillation cannot be an explanation for the paucity of whales. No obvious explanation could be found, and other surveys would be necessary to determine if the scarcity of sperm whales in this area is a real and constant phenomenon and, if so, to what cause it could be attributed.

Three of the four regions described in the methods were meaningfully segregated by the two first principal components (over spatial scales of 148-1185 km): high productivity in the East Pacific; low productivity and flat ocean floor within the gyre; high contour index and variable productivity in the West Pacific. The equatorial region was more difficult to characterize as there is a gradient of productivity from West to East and a gradient of sea surface temperature and of depth of the mixed layer from East to West.

The statistical analyses of the relationships between whale density and environmental features were very consistent: no substantial correlation at a spatial scale of 148 km, and an increased correlation with increasing spatial scale for every variable concerned. Moreover, correlation analyses and principal component analyses gave similar results. This suggests that the results are meaningful, and that the pattern can be interpreted even if no significance tests could be done due to strong autocorrelation, multiple correlation tests, and non-normality of the PCA variables.

Over large spatial scales (592-1185 km), sperm whales were found in regions of high relief and close to land. This is consistent with the work of Clarke (1956) who showed that sperm whales seem to be especially attracted to oceanic islands where volcanism has raised the land sheer from the depth. He postulated that the upthrust of volcanic peaks causes vertical mixing which breaks down discontinuity layers and allows a local increase in organic production. S. Gowans and S. Hooker (pers. comm.) failed to detect any correlation between sperm whale density and a high relief around the Galápagos Islands. However, they only used spatial scales of 18X18, 27X27 and 55X55 km, and the absence of correlation at such small scales is consistent with these results.

Several authors have noted an association between sperm whale density and areas of high primary productivity (Townsend, 1935; Caldwell *et al.*, 1966; Gulland, 1974). However, no attempts have been made to understand the scale of the relationship. In these results, chlorophyll concentration was not closely related to sperm whale distribution, at any spatial scale. Vinogradov (1981) demonstrated that the development of all trophic levels between phytoplankton and large squid takes approximately four months, and thus a peak in chlorophyll concentration is temporally and probably spatially separated from a peak in squid density. Therefore, it might be difficult to detect a relationship between sperm whale distribution and phytoplankton concentration without averaging the data over temporal scales of at least several months. This is consistent with the results of chapter 2.

This study shows that the amount of sub-surface biomass is closely related to sperm whale distribution. The correlation analyses suggest that sperm whale density is more closely related to the amount of biomass in the medium layer (50-

300 m) than to the amount of biomass in the deep layer (300-600 m), and that there is only a very weak correlation between sperm whale density and the amount of surface biomass (0-50 m). Most of the organisms forming the scattering layers undertake vertical diel migrations, and thus the depth of the scattering layers is strongly related to the time of day at which the observations are made. Therefore, if the observations had been made at another time of day or night, it is possible that sperm whale density would be more closely correlated with the deep or the surface layer than with the medium layer as in the present case. However, the principal component analyses do not discriminate between depth. The first PC (for 148, 296 and 592 km spatial scale) has high loading for every variable describing the amount of sub-surface biomass, regardless of the depth. At a spatial scale at 1185 km: both the 2nd and the 3rd PC have about the same correlation coefficient with sperm whale density, even though the 2nd represents a high surface and medium layer biomass while the 3rd represent a high deep layer biomass. The correlation between sperm whale density and sub-surface biomass is consistent with Berzin (1971) who postulated that sperm whales are found in areas with a high density of deep water fauna, and that the development of this fauna is optimum in downwelling regions. However, he gave no indication of the spatial scale involved. Our results, using both correlation analyses and PCA, indicate that the association between sperm whale density and amount of sub-surface biomass occurs only at spatial scales equal to or greater than about 600 km.

In contrast to the work of Gaskin (1973) and to Ramirez and Urquiza (1985), this study failed to detect the possible impact of the gradient of temperature and of the surface temperature on sperm whale distribution. Due to funding constraints,

only 55 XBT's were launched during the entire survey. It is likely that such a low number, in comparison to the large area investigated, was insufficient to detect anything but a very strong relationship. Since groups of female sperm whales are found at every latitude from 0° to 40° and in every ocean of the world, it is clear that they are found at a very wide range of sea surface temperatures (SST). Thus, to detect the possible influence of SST on sperm whale distribution, it would be important to investigate one rather homogenous region at a time, instead of the entire South Pacific. However, in the present study, the data were not sufficient to allow discrete analyses over each region.

Therefore, these results suggest that groups of female sperm whales are generally distributed within large areas (592 to 1185 km) characterized by high secondary productivity and steep underwater topography. The size of these areas may reflect the distance over which groups of female sperm whales move in search of food. This is consistent with the work of Dufault and Whitehead (1995), who compared individual identifications from fluke pictures of sperm whales taken during the South Pacific survey to the extensive fluke catalogue from the Galápagos Islands, and found that a whale was never seen more than 1100 km from the location where it has been first identified. Similarly, during the "Discovery" campaign of marking sperm whales, undertaken between 1950 and 1975, the mean distance between marking and capture for female sperm whales was 690 km (Best, 1979).

The absence of correlation between sperm whale density and environmental features or productivity over smaller spatial scales may indicate that factors other than food resources influence sperm whale distribution over these scales. However, feeding requirements could still have an important influence on sperm

whale distribution at smaller spatial scales, but may not have been detected for two main reasons. Firstly, there is a space lag between the position of large meso- and bathypelagic cephalopods and the location of zooplankton (Vinogradov, 1981). Therefore, if the distance between high biomass of zooplankton and high density of squids is larger than the spatial scale investigated, correlation analyses will show no association between sperm whale and secondary productivity, wrongly suggesting that food resources are of no importance over these scales. Secondly, due to their large size, sperm whales could fast or eat very little for periods of weeks without being affected (Brodie, 1975). Therefore, it may be advantageous for them to "commute" from one small area of very high cephalopod density to the next one, as soon as the first area is depleted. During their "commuting" they would still be foraging, but their feeding success would be much lower. Using defecation rate as a measure of feeding success (Smith and Whitehead, 1993), I found that feeding success was highly variable between encounters (cf. chapter 4). Thus, a certain proportion of whale encounters could have happened while groups were "commuting", which would explain the absence of correlation over small spatial scales.

CHAPTER 4

SMALL SCALE MOVEMENTS, DISTRIBUTION AND FEEDING SUCCESS OF SPERM WHALES IN THE PACIFIC OCEAN

4.1. Introduction

Habitat description and its utilization by an animal is central to the study of its ecology (Johnson, 1980). The two previous chapters, describing sperm whale habitat over spatial scales of hundreds to thousands of km, have shown that sperm whales are usually found in areas of high relief which are characterized by intense scattering layers. However, as the relationships between the distribution of a predator and the distribution of its prey are invariably scale-dependent (Schneider and Piatt, 1986, Horne and Schneider, 1994, see also chapter 1), the results of the previous chapters cannot be extrapolated to smaller scales. Investigating habitat utilization by sperm whales is a difficult task as they forage at depths of several hundred meters, severely reducing opportunities for direct observations. Therefore, knowledge concerning the environmental factors influencing sperm whale distribution over small spatial scales and the extent to which they are feeding in a particular habitat is still very limited.

In ecological studies relative movements of predators and prey are likely to affect how correlations between their distributions change with scale (Veit *et al.*, 1993). If the relationship between the distribution of a predator and the distribution of its prey is studied at too small a scale, coherence will seem to be absent as predators are seldom exactly aligned with prey. On the other hand, if the system is studied at too large a scale, little will be learned of the small scale relationships. Over small spatial scales, Rose and Leggett (1990) suggested that the best scale to choose is the one that corresponds to the patch size of aggregations of both predators and prey.

Relationships between predator and prey distributions over small spatial scales (1-10 km) have been conducted successfully on various marine species that forage at or near the surface. Woodley and Gaskin (1996) demonstrated that over a spatial scale of 5 km by 5 km, North Atlantic right whales (*Eubalaena glacialis*) were closely associated with copepod abundance. Veit *et al.* (1993) used a spatial scale of 1.8 km by 1.8 km to examine the relationship between pelagic predators (birds and fur seals) and Antarctic krill (*Euphausia superba*). They observed that the distributional patterns of predators were strongly influenced by the distribution of krill swarms. They also found an offset of a few km between a peak in krill density and peaks in some predator densities, suggesting that each predator specializes in a different part of the swarm, or that different species of predators avoid each other, or both. Schneider and Piatt (1986) showed a positive correlation between the distribution of piscivorous seabirds (*Uria algae* and *Fratercula arctica*) and schooling fish (primarily capelin *Mallotus villosus*) over a spatial scale of 2 to 6 km. In all these cases, both aggregations of prey and aggregation of predators could be observed directly, and the patch size measured.

On the other hand, sperm whales spend about 70% to 75% of their time at depths exceeding 400 m (Gordon, 1987; Papastavrou *et al.*, 1989; Watkins *et al.*, 1993), and so direct observations of sperm whales foraging are not possible. In addition, because of the ability of deep-living squid to escape trawls and nets (Clarke, 1977; Clarke, 1985; Vecchione and Foper, 1991), and because of the difficulty of observing them using acoustic methods (Starr and Thorne, in press), much of our knowledge of these cephalopods comes from studies of the stomach contents of sperm whales (Clarke, 1985; Nemoto *et al.*, 1985; Nemoto *et al.*,

1988). Therefore, it is not possible to directly relate sperm whale distribution to the distribution of its main prey item, nor to directly measure the size of a patch of squid.

However, it is likely that environmental variables influence the density of squid as well as the sizes of their patches. It has been postulated that a temperature gradient of about 5°C in the upper 100 m and the presence of oceanic fronts are important factors contributing to the concentration of squids (Uda, 1959). Therefore, the small-scale distributions of some species of teuthophagous predators have been studied in relation to environmental factors. For instance, Hui (1985) showed that pilot whales (*Globicephala macrorhynchus*) were encountered significantly more often in areas of high relief than in areas of low relief over a spatial scale of 11 km.

In the absence of direct observations, habitat utilization can be inferred from feeding success. Whitehead *et al.* (1989), Smith and Whitehead (1993) and Whitehead (1996) have shown that the defecation rate of a group of sperm whales (a measure which can easily be recorded in the field) gives a valid indication of their feeding success. If the small scale movement patterns of groups of whales are correlated with feeding success, it is then likely that the extent of a group's movements gives an indication of the size of a patch of prey and on the distances between the patches.

In this chapter, I relate movement patterns of groups of sperm whales to their feeding success to investigate foraging behavior, and to estimate the probable size of patches of prey and the distances between them. I also investigate relationships between the feeding success of a group of whales and an index of

underwater relief and the intensity of scattering layers. Finally I describe the environmental and biological characteristics of sperm whale habitat over small spatial scales by examining changes in environmental variables while sailing away from a group of whales.

4.2. Methods

4.2.1. Field methods

Data were collected from a 12.5 meter, ocean-going cutter during a survey around the South Pacific in 1992-1993 (Fig. 4.1.). Sperm whales were located by listening every half hour through an omnidirectional hydrophone for their characteristic clicks (Backus and Schevill, 1966). Weather permitting, the sperm whales were then followed both acoustically and visually for periods ranging from a few hours to two and half days (Whitehead and Gordon, 1986). A total of 626 hours were spent in visual or acoustic contact with groups of sperm whales.

When groups were nearby, photographs of flukes were taken in order to identify individuals (Arnbom, 1987). Due to the metabolic demands of deep-diving (Kooyman *et al.*, 1981), sperm whales are likely to defecate only at the surface. Therefore, the presence or absence of a defecation at the start of a dive was recorded to give an indication of feeding success (Whitehead *et al.*, 1989; Smith and Whitehead, 1993; Whitehead, 1996). Defecation rates (percentage of dives with defecation) were calculated for groups only when 15 or more slicks (slick=location of the fluke-up, visible for several minutes after the whale dove) were checked. As previous studies have shown a mean defecation rate of about 10% (Whitehead, 1996), 15 slicks was roughly the minimum which had to be

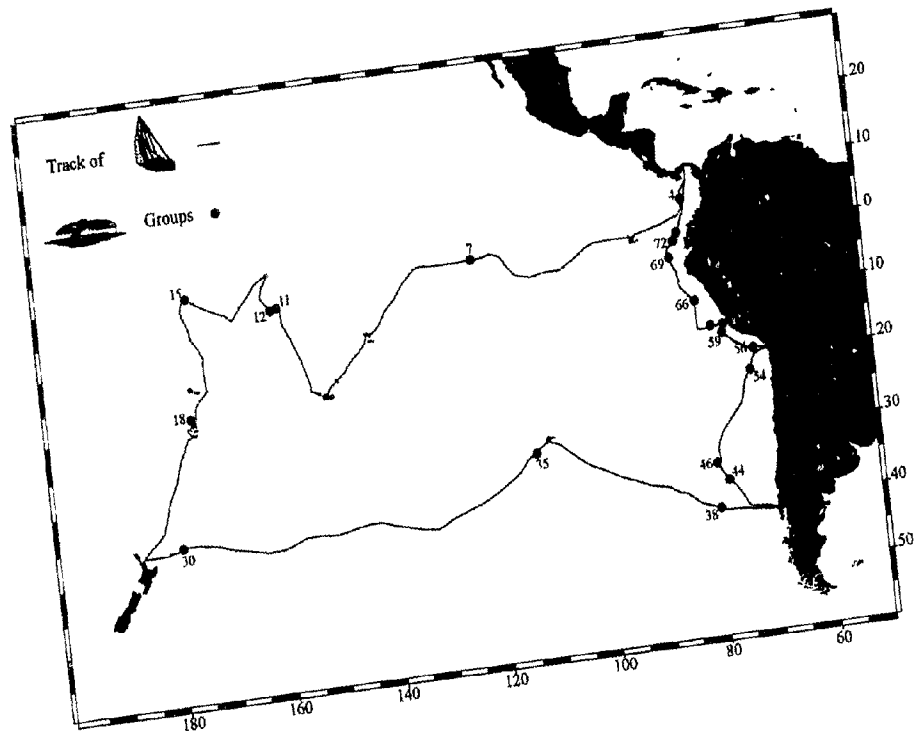


Fig. 4.1. Track of the research vessel with positions and identity numbers of groups of female and immature sperm whales which were followed for more than 8 hours and/or for which variations in chlorophyll concentration, intensity of scattering layers and sea surface temperature were measured while sailing away from the group.

checked in order to obtain a reasonably reliable difference between a low feeding success (0 slicks with defecations/15 slicks checked) and a high feeding success (2-4 slicks with defecations/15 slicks checked). During daylight, the proportion of time the whales were either foraging (animals spread out in small clusters and fluking up at the start of deep dives) or socializing (animals clustered closely together at the surface, moving very slowly) was recorded every hour (Whitehead and Weilgart, 1991). The position of the boat was also noted every hour using a Trimble Transpak GPS.

Environmental variables were measured each time a group was first encountered, then once a day at 15:00 local time, and once more before leaving the group. Whenever possible, environmental variables were also recorded every 9 km until 45 km while sailing away from a group, on a heading roughly perpendicular to their general heading (Fig. 4.2.). Chlorophyll concentration was estimated by a spectral radiometer (McLean and Lewis, 1991) for most of the survey, and by a Secchi disk when sailing away from a group. During half of the survey, chlorophyll concentration was recorded simultaneously by a spectral radiometer and a Secchi disk to assess the validity of the Secchi disk measurements. Secchi depth (in meters) was converted to chlorophyll concentration using the following formula:

$$\text{Chl} = 920 Z_{\text{sd}}^{-2.6}$$

where Z_{sd} is the Secchi depth in meters (Lewis *et al.* 1988).

The intensity of sub-surface scattering layers were recorded at three different depths using a Furuno CH 14 sonar (frequency: 60 kHz) as described in section 3.2.1. Sea surface temperature was recorded every 3 hours.

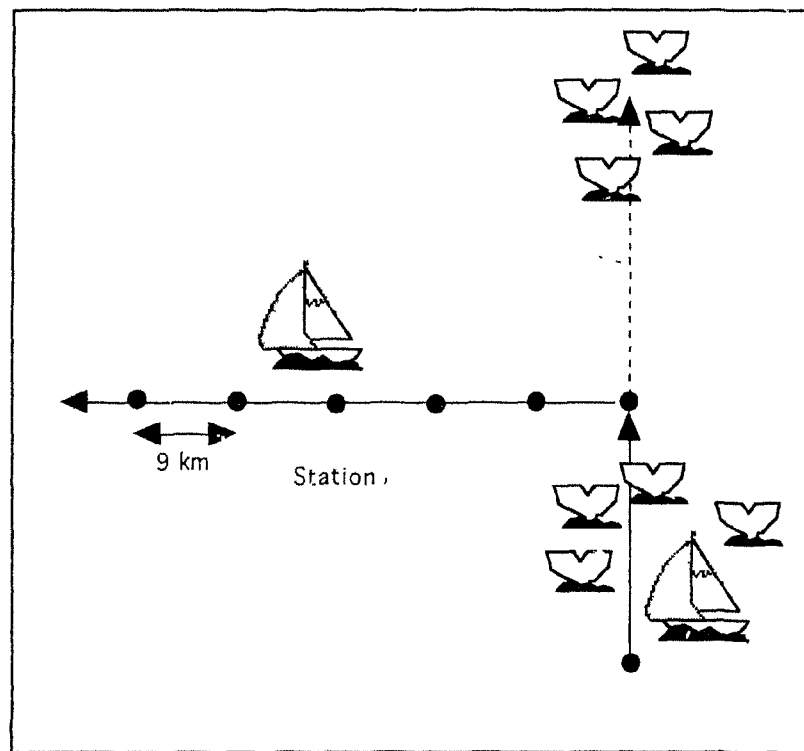


Fig. 4.2. Small scale observations while sailing away from a group of whales. At each "station" measurements of chlorophyll concentration, intensity of scattering layers at 3 different depths and sea surface temperature were made.

4.2.2. Data analyses

For each group which was followed for more than 8 consecutive hours, the means of all the variables listed in Table 1 were calculated during the period that the group was followed. The mean straight-line distance traveled by a group in 12 hours while being followed by the research vessel was expressed by *Straidis-12*; the mean real distance traveled by the group in 12 hours (counting all zigzags) was expressed by *Realdis-12*. The variable *zigzag* (*Realdis-12* divided by *Straidis-12*) gives an indication of the small scale movements of a group of sperm whales during the time it was followed. A high value (>1) means that the group was mainly moving back and forth over an area while a value of 1 means that the group was traveling in a straight line. The feeding success (*feedsucc*) was calculated from the defecation rate (see above). The lack of data on the time lag between ingestion and excretion in sperm whales presents a problem when attempting to determine feeding success over periods of hours. Studies of stomach contents (notably Clarke, 1980) suggested that digestion of cephalopod flesh takes place within hours of capture by the whale. Therefore, defecation rate is likely to give an indication of the feeding success during the past 12h (Smith and Whitehead, 1993). The Contour Index (*C.I.*) was calculated using the charts "Bathymetry of the North/South Pacific, Scripps Institution of Oceanography and Institute of Marine Resources, 1970". The track of a group of whales was plotted on the charts, and the maximum and the minimum depths in a radius of 70 km were used to calculate the *C.I.* according to Hui's formula (1979): $C.I. = 100 \times [(maxdepth - mindepth) / maxdepth]$. All variables except *zigzag* were roughly normally distributed or became roughly normally distributed after transformations (inverse and/or square roots).

Table 4.1. Description of the variables calculated for each group of whales. The variables in bold were also calculated from data obtained while sailing away from a group.

Variables	Description	Units
<i>Meanspeed</i>	Total distance traveled by a group while followed over the number of hours it was tracked	km/h
<i>Straidis-12</i>	Mean distance traveled in straight line during 12 hours	km
<i>Realdis-12</i>	Mean total distance traveled during 12 hours	km
<i>Zigzag</i>	Total distance traveled by a group between the position when first encountered and the position when left divided by the straight-line distance between these 2 positions	-
<i>Timefeed</i>	Proportion of daylight time during which most of the group is showing "foraging behavior"	percentage
<i>Feedsucc</i>	Number of fluke ups with defecation divided by total number of fluke ups checked	-
<i>Chlconc</i>	Chlorophyll concentration	mg/m ³
<i>Intmax1</i>	Maximum intensity of the surface scattering layer (0-50 m)	subjective scale from 0.0 to 4.0
<i>Intmax2</i>	Maximum intensity of the medium scattering layer (50-300 m)	subjective scale from 0.0 to 4.0
<i>Intmax3</i>	Maximum intensity of the deep scattering layer (300-600 m)	subjective scale from 0.0 to 4.0
<i>SST</i>	Sea surface temperature	°C
<i>Biotot</i>	Amount of sub-surface biomass (=Intmax1 X thickness of surface S.L. + Intmax2 X thickness of medium S.L. + Intmax3 X thickness of deep S.L.)	-
<i>C.I.</i>	Contour index, defined using Hui's (1979) formula, $C.I. = (100 \times ((\text{maxdepth} - \text{mindepth}) / \text{maxdepth}))$	-

To investigate the relationship between the feeding success and the small-scale movement of a group, a Spearman coefficient of correlation was calculated between *zigzag* and *feedsucc*. A positive correlation would mean that the whales moved back and forth over an area at times when feeding success was high, but traveled consistently in one direction when feeding success was low.

The spatial and temporal scales of sperm whale movements were investigated by calculating for each group the mean straight-line distance traveled in any 3 hours, then the mean straight-line distance traveled in any 6 hours, and so on until the total length of time a group was followed had been covered (maximum = 66 hours). For each group, the mean straight-line distance traveled over time intervals from 3 to 66 hours was then plotted against the time interval in hours. If a group is moving back and forth over a certain area, the mean straight-line distance covered by the group in any time interval can not be larger than the largest diameter of the area. On the other hand, if a group is moving in straight-line, the straight-line distance covered by the group will keep increasing with increasing time intervals (Fig. 4.3.). These small scale movements were then related to feeding success.

Differences in foraging behavior between groups of sperm whales having a high feeding success and groups having a low feeding success, and between groups moving in a straight-line and the ones zigzagging were investigated by correlation analyses. To examine whether the mean swimming speed was related to feeding success and/or to zigzag, Spearman coefficients of correlation were calculated between *meanspeed* and *feedsucc* and between *meanspeed*

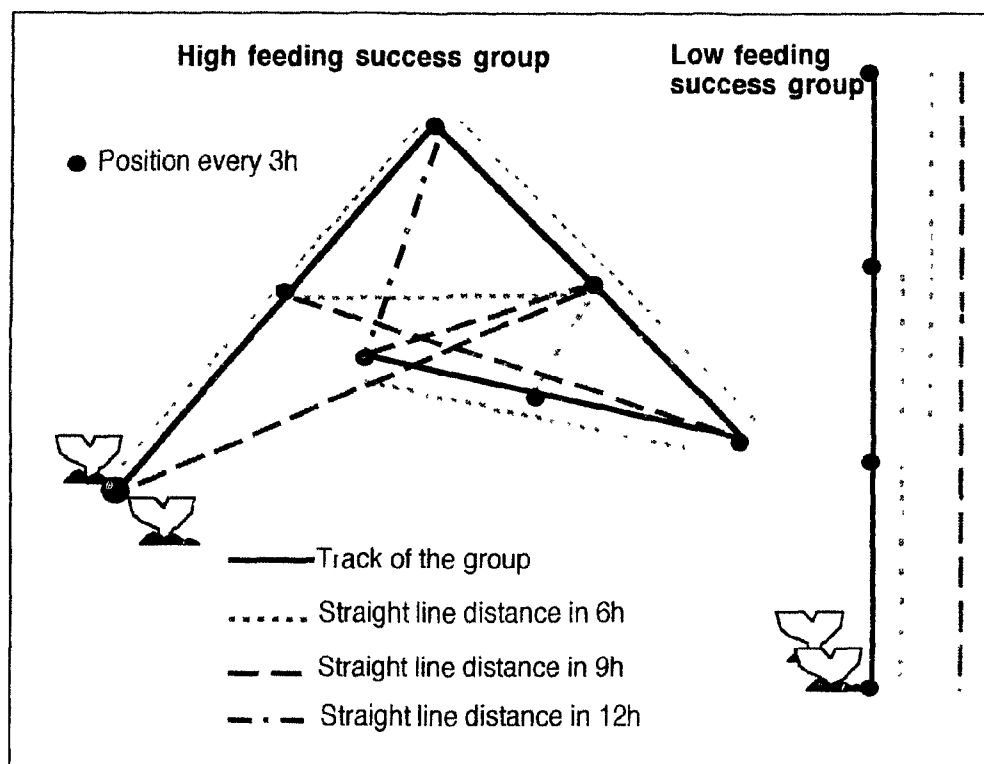


Fig. 4.3. Examples showing 2 groups, one with high feeding success zigzagging over an area, and one with low feeding success traveling in a straight-line. Each of the dash-lines represent a straight-line distance traveled in respectively 6h, 9h and 12h. Then, the mean straight-line distance cover in 6h by a group was calculated as the average of all the 6h segments.

and *zigzag*. Also, to examine whether the proportion of time a group spent foraging was related to feeding success or movement patterns, Spearman correlations were calculated between *timefeed* and *feedsucc* and between *timefeed* and *zigzag*.

The analyses in chapter 3 have shown that sperm whale distribution is related to amount of subsurface biomass and to contour index over spatial scales of about 500 – 1000 km. Therefore, to investigate how feeding success was related to productivity and environmental variables, Spearman coefficients of correlation were calculated between *feedsucc* and *biotot* (= a measure of the total amount of sub-surface biomass, calculated as the intensity of the surface scattering layer multiplied by its thickness, plus the intensity of the medium scattering layer multiplied by its thickness, plus the intensity of the deep scattering layer multiplied by its thickness) and between *feedsucc* and *C.I.*

Finally, to investigate whether there were consistent changes in environmental variables at different distances from groups, and so to give further indications of the possible sizes of prey patches, the values of some environmental variables (*Chlconc*, *intmax1*, *intmax2*, *intmax3*, *SST*) were recorded just before leaving a group of whales and then every 9 km until 45 km (Fig. 4.2.). For each variable and for each group, the difference between the values at each station (9, ..., 45 km) and the values just before leaving a group were calculated. Then, for each station, the mean value and the standard deviation of all the differences was calculated for each variable. The environmental data were collected for 17 groups, but measurements of chlorophyll concentration were recorded only for 10 groups, and scattering layer characteristics for 12 groups.

4.3. Results

Eighteen groups of female and immature sperm whales were followed for more than 8 hours (Fig. 4.1.); the maximum was 67 hours and the mean was 32 hours. The summary statistics of the measurements of all the variables recorded while following groups are presented in Table 4.2.

The mean speed (4.2 km/h, S.D.=0.7) was very consistent between groups. The total distance traveled through the water in 12 hours (mean=50.3 km/h, S.D.=9.0) was more consistent between groups of sperm whales than the distance covered in a straight line during 12h (mean=34.7 km/h, S.D.=12.9). Feeding success was significantly correlated with *zigzag* index ($r_s=0.729$, $p<0.05$), suggesting that, as hypothesized, sperm whales are feeding more when they are going back and forth over an area than when they are moving in a straight line.

For each group, the mean straight line distance traveled during periods of 3 hours to 66 hours is plotted on Fig.4.4 to 4.7. Fig 4.4 shows that, when the feeding success was low (<0.06 defecations/fluke-up), sperm whales tended to travel in a rather straight line without zigzagging, as indicated by the straight-line relationship between distance moved and time interval. The slope of these relationships is very similar among all these groups, suggesting a very similar mode of travel. None of the curves reach an asymptote indicating that none of the groups started backtracking while being followed. Therefore, as these groups traveled between 100 and 240 km, this suggests that the distance between "good quality" prey patches is in the order of at least 100 km. Fig. 4.6 shows the relationship between distance traveled and time intervals for the groups having a

Table 4.2. Summary of statistics for all variables recorded while following a group of sperm whales.

Variables	N. of cases	Min.	Max.	Mean	S.D.	Units
<i>Meanspeed</i>	18	2.5	5.4	4.2	0.7	km/h
<i>Straidis/12</i>	16	13.6	48.9	54.7	12.9	km
<i>Reeldis/12</i>	16	29.6	64.8	50.3	9.0	km
<i>Zigzag</i>	18	1.05	3.7	1.68	0.80	-
<i>Timefeed</i>	13	11	90	58.65	26.77	%
<i>Feedsuc</i>	11	0	0.325	0.084	0.09	-
<i>Chlconc</i>	18	0.1	8.72	0.95	2.06	mg/m ³
<i>Intmax1</i>	18	0	4	2.22	1.42	-
<i>Intmax2</i>	18	1	4	3.21	1.00	-
<i>Intmax3</i>	18	0	4	2.13	1.49	-
<i>Biotot</i>	18	150	1440	793.5	416.8	-
<i>SST</i>	18	17.2	28.8	24.27	3.25	°C
<i>C.I.</i>	18	0	93	55.32	32.51	-

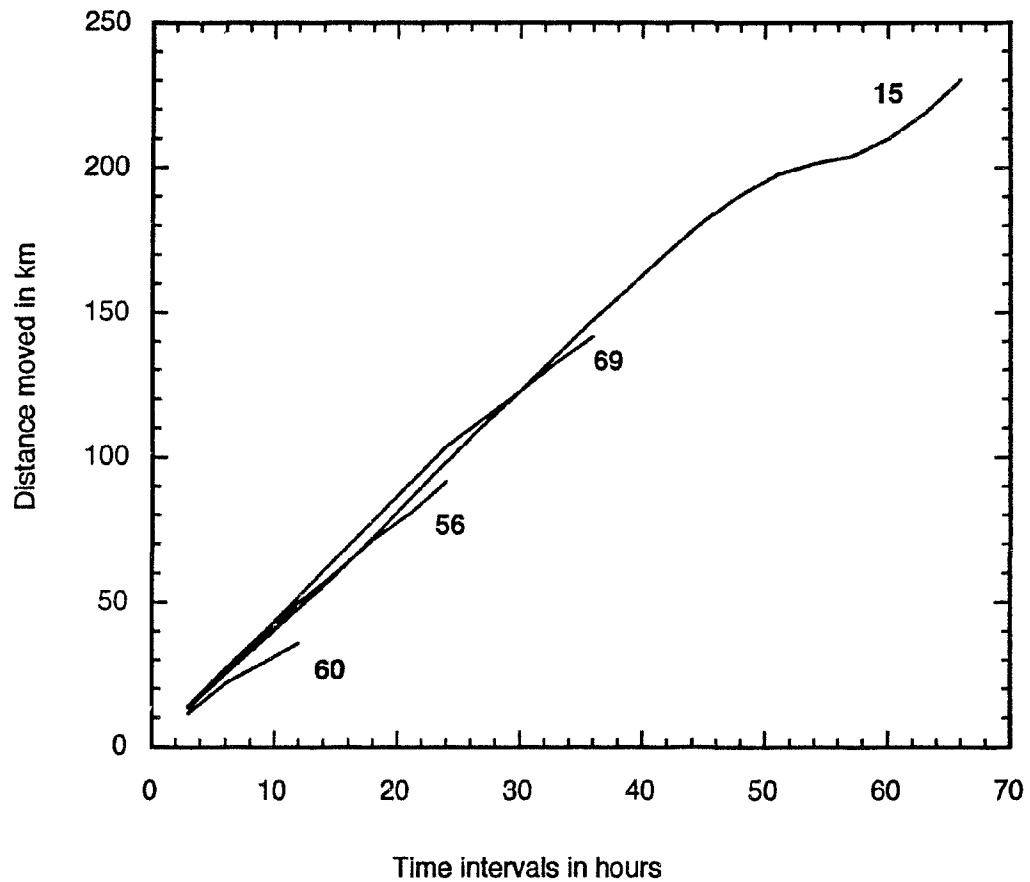


Fig. 4.4. Mean straight-line distance traveled by each sperm whale group versus time interval; for groups with low feeding success (0%-5.4%). The numbers at the end of each curve represent the identity number of the groups (as in Fig. 4.1.).

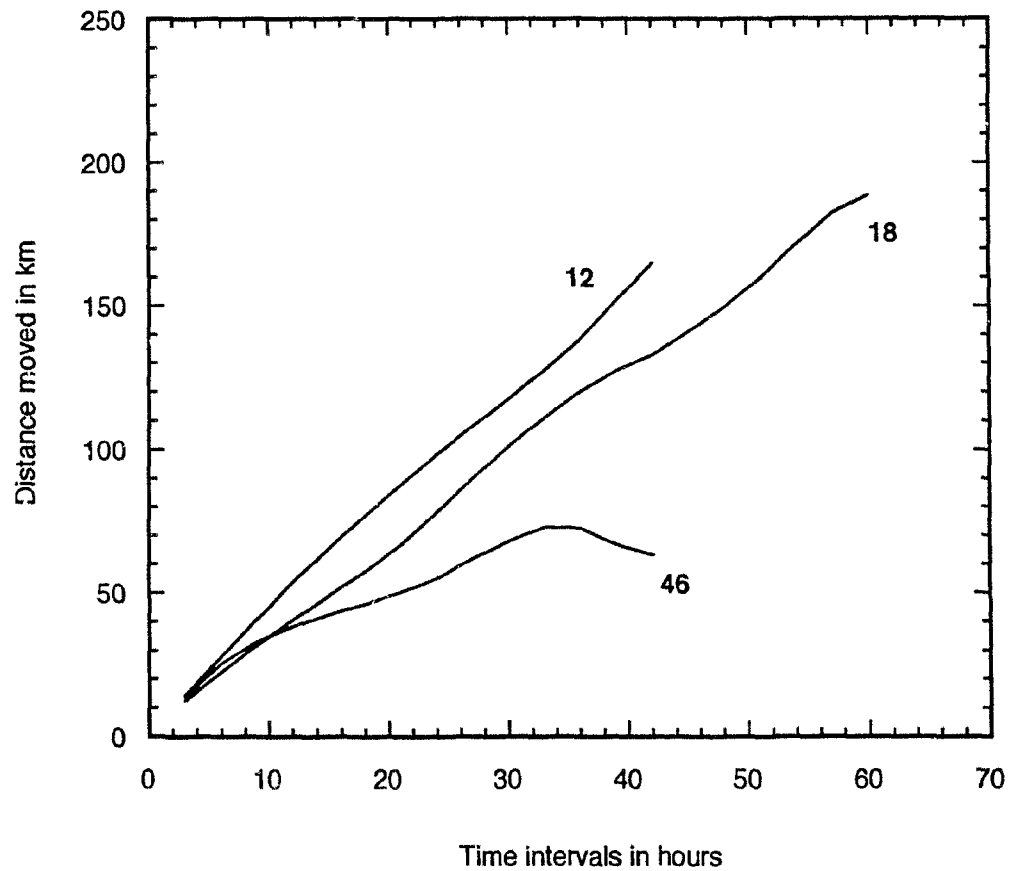


Fig. 4.5. Mean straight-line distance traveled by each sperm whale group versus time interval; for groups with moderate feeding success (6.1%-8%). The numbers at the end of each curve represent the identity number of the groups (as in Fig. 4.1.).

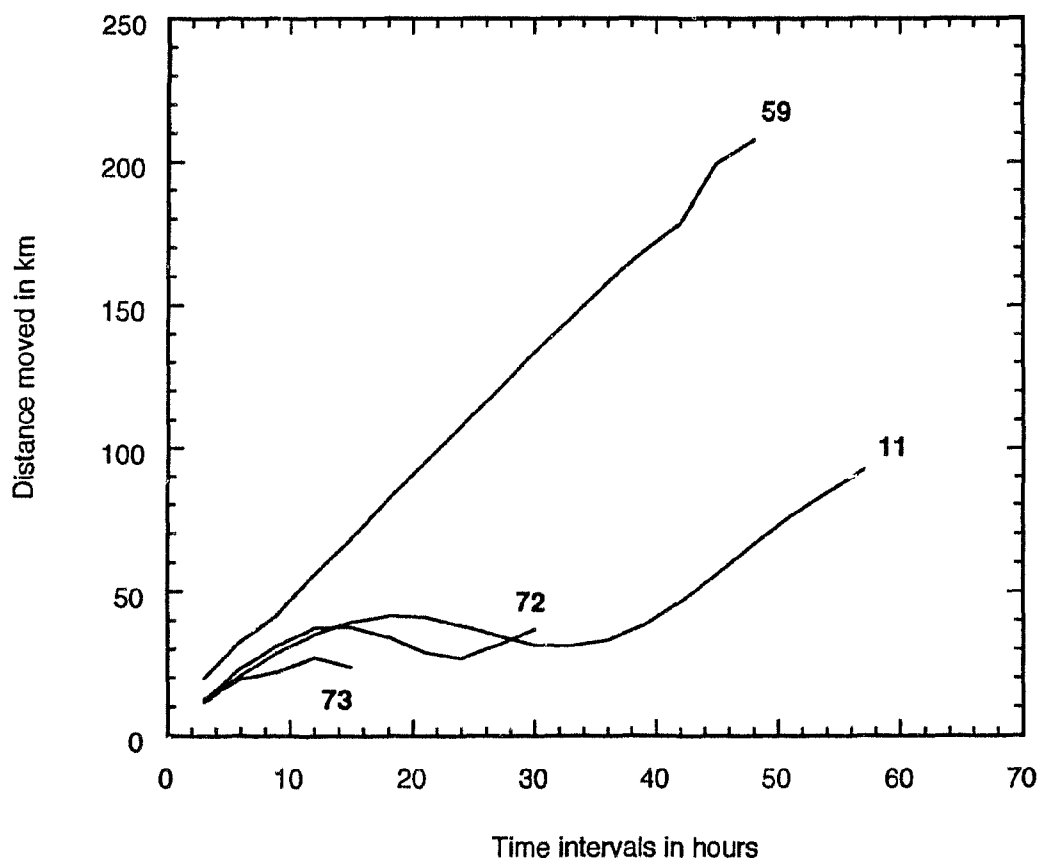


Fig. 4.6. Mean straight-line distance traveled by each sperm whale group versus time interval; for groups with high feeding success (11.4%-32.5%). The numbers at the end of each curve represent the identity number of the groups (as in Fig. 4.1.).

high feeding success (>0.11 defecations/fluke-up). For 3 of the groups (#11, #72, #73) the curves leveled after 28 to 45 km, suggesting that the groups are moving back and forth over an area with a maximum span of 45 km. As these groups have a high feeding success, it is likely that these areas correspond to patches of prey. The curve describing the movement of group #11, which was followed for a longer period of time than #72 and #73, further indicated that the whole patch of prey may have been moving at a mean speed of about 1.5 km/h. Group #59 showed the same behavior as the groups with low feeding success suggesting exceptions to the general rule of zigzagging with high feeding success and straight-line movement with low feeding success. The curves representing the groups with moderate feeding success (between 0.06 and 0.08 defecations/fluke-up) are found in between the ones representing groups with low feeding success and the ones representing groups with high feeding success (Fig. 4.5.) suggesting a continuity in foraging behavior. There were 7 encounters for which there were no data on feeding success (Fig. 4.7.). As most of these groups were only followed for a short time, they give little information on the small scale movements and sizes of patch. However, it is likely that group #4 had a high feeding success and was feeding over a small patch of prey (<20 km). On the other hand, group #38 seems to have been traveling.

There were no significant differences in foraging behavior between groups that were traveling in a straight-line and/or with a low feeding success and the groups that were zigzagging over an area roughly 30-50 km across and/or with a high feeding success. The mean speed through the water was very consistent among groups and the coefficient of correlation between *meanspeed* and both *feedsucc*

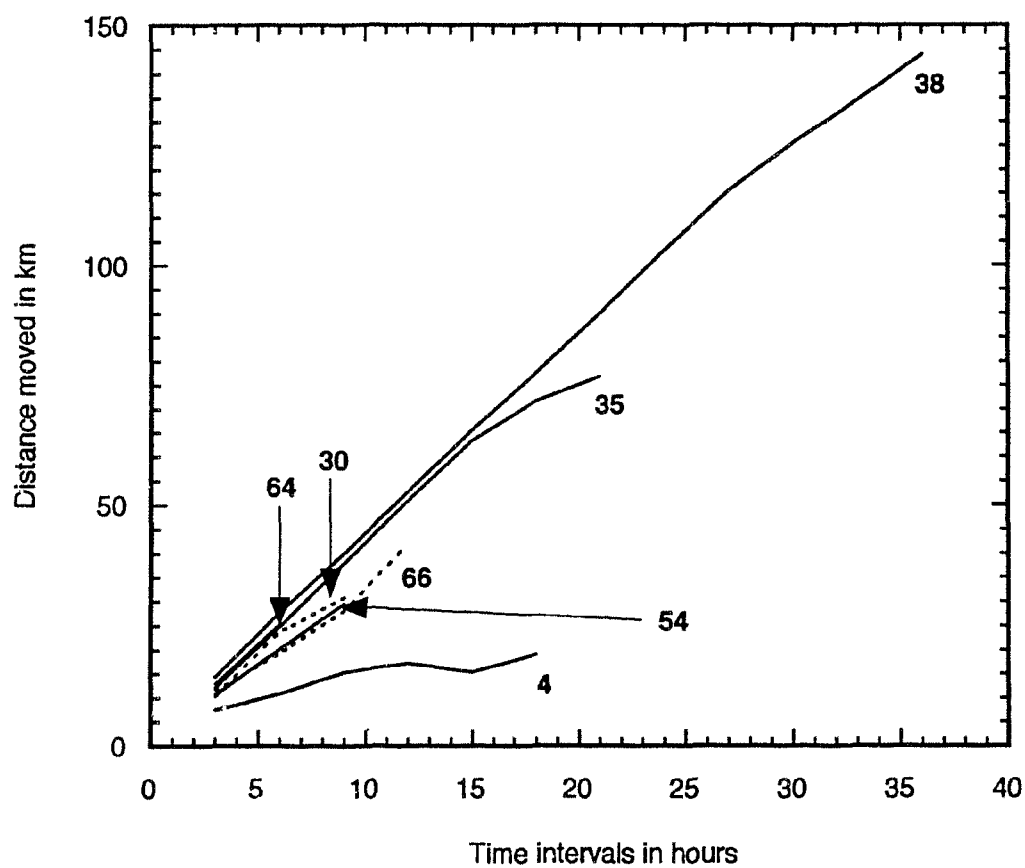


Fig. 4.7. Mean straight-line distance traveled by each sperm whale group versus time interval for groups for which no data on feeding success were available. The numbers at the end of each curve represent the identity number of the groups (as in Fig. 4.1.).

and *zigzag* was particularly low ($r_s=0.1$ and $r_s=0.0$ respectively). The coefficients of correlation between *timefeed* and both *feedsucc* and *zigzag* were not significant either, but their higher values ($r_s=0.505$; $r_s=0.482$) suggested that the whales were spending more time foraging when they had a high feeding success than when they had a low feeding success.

Feeding success was not related to either the amount of sub-surface biomass, nor to the contour index. Both coefficients of correlation were low and not significant at the 5% level (Table 4.3.).

The differences between the values of each environmental variable at time of departure from the group and at 9 km intervals up to 45 km away from a group of sperm whales are presented in Fig. 4.8. These plots show that the deviations from the reference value (at the point of departure from a group) were very low for every variable considered and greatly scattered around zero without any distinctive pattern. Moreover, the standard deviation was always very high in comparison to the mean difference. Thus, there was no consistent variation in any environmental variable while moving away from a group.

Finally, the groups were divided into 2 sets according to their feeding success, separating the groups which may have been feeding over a patch of prey from the ones which were traveling between patches. The first set contained 9 groups having a rather low feeding success (0%-6.3%), while the second set comprised 8 groups having a comparatively high feeding success (8%-32%). Similar analyses to those described above on the changes in environmental variables while leaving a group were carried out for the 2 sets. However, as there was still no pattern for the groups having a high feeding success, and as the graphs

Table 4.3. Relationships between feeding success and environmental variables.

	Spearman coefficient of correlation	p values
<i>Feedsucc</i> versus <i>biotot</i>	-0.309	$p > 0.05$
<i>Feedsucc</i> versus <i>C.I.</i>	-0.137	$p > 0.05$

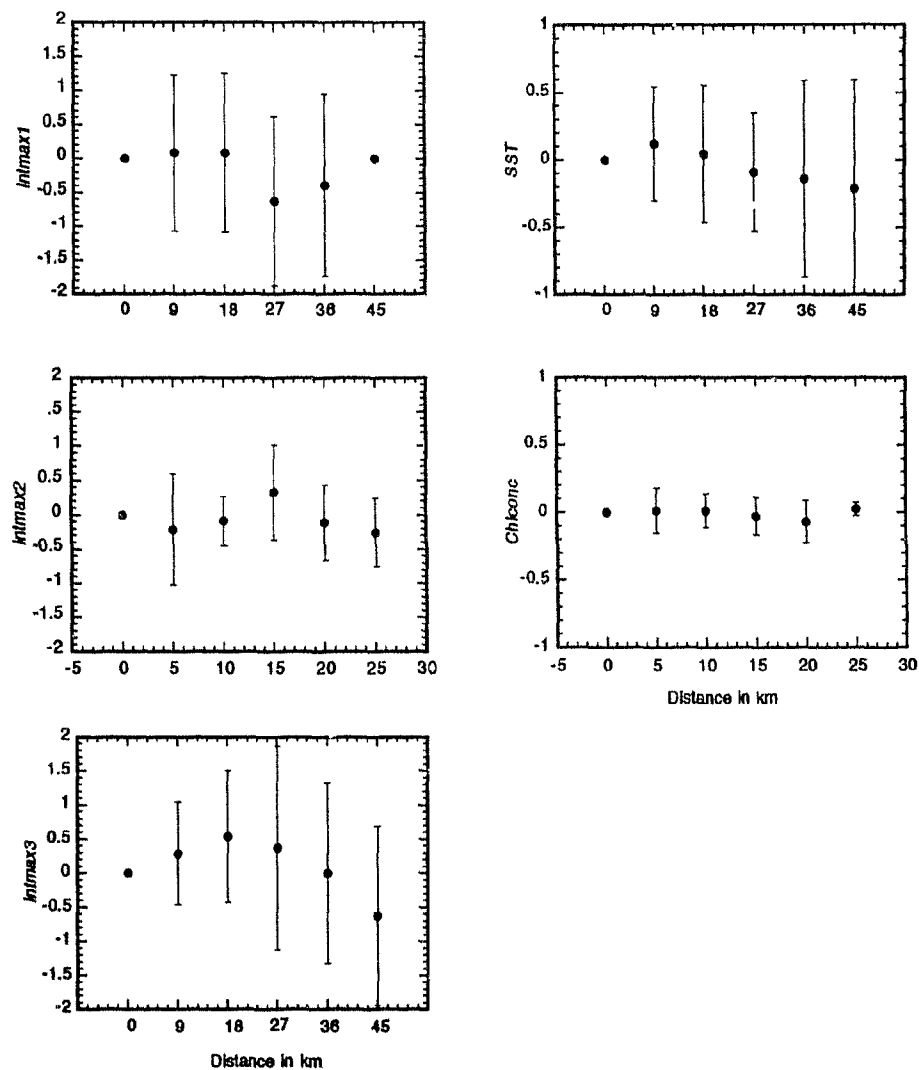


Fig. 4.8. Variation in sea surface temperature, chlorophyll concentration and intensity of scattering layers while sailing away from groups of whales. Each dot represents the mean difference between the value at this "station" and the value measured just before leaving the group; the vertical bars represent standard deviations.

representing just groups with low or with high feeding success were very similar to the ones presented on Fig. 4.8., they are not shown here.

4.4. Discussion

Despite the small sample size (18 groups), some clear patterns emerged from the analysis of the movements of groups of sperm whales over periods of a few hours to a few days. Independently of their feeding success or the amount of time that they spent foraging, the groups traveled through the water at about 4.2 km/h. This mean speed is consistent with other estimates for groups of sperm whales in different areas: 3.4 km/h (Papastavrou *et al.*, 1989, for Galápagos Islands), 4.6 km/h (Gordon, 1987, for Sri Lanka). This speed presumably represents an optimum largely determined by energetic factors.

However, over periods of a few hours, movement patterns differed greatly between groups with high and low feeding success. Groups with low feeding success moved in a rather straight line, while those with high feeding success usually zigzagged over areas about 40 km across. There were only small differences in other aspects of behavior. For example, the proportion of time a group of sperm whales spent foraging is not significantly different whether the group has a high or a low feeding success, and this is consistent with previous findings (Smith and Whitehead, 1993; Whitehead, 1996). Therefore it seems that movement patterns are determined by feeding success (i.e. the whales move away from an area where there is little food) rather than feeding success being determined by movement patterns (as could be found if foraging and migratory behavior were distinct).

This trend is consistent with the results of an analysis of the movement patterns of groups of sperm whales off the Galápagos Islands (Whitehead, 1996). Off the Galápagos, groups with defecation rates greater than 15% moved less than 12 km in a 12 hour period, whereas groups which moved 15-55 km all had defecation rates lower than 15%. Therefore, generally, the movements of the sperm whales over time scales of hours to days seem to be related quite strongly to patterns of prey abundance.

As inferred from the movements of the whales, the prey of South Pacific sperm whales may occur in patches of the order of 40-50 km across (Fig. 4.6.). The tracks of groups which traveled over 150 km in straight lines (Fig. 4.4.) suggest that some prey patches may be well dispersed and hard to find, or sufficiently small that doubling back through them would not be profitable. The track of group #11 further indicates that the patches may themselves move, probably following sub-surface currents (Zuev and Nikolsky, 1993). There is consistency in the shape and in the slope of the curves relating distances to time intervals for the groups having a low feeding success (Fig. 4.4.), suggesting that when traveling between prey patches, the behavior and movement of the whales is very similar among groups.

Sperm whales have a wide diet consisting of many species of meso and bathypelagic cephalopods (Kawakami, 1980), which will differ in the size and density of patches (see Clarke, 1980; Clarke *et al.*, 1993). Therefore sperm whales probably feed on many different types of prey aggregation, perhaps ranging all the way from solitary squid well-separated from any other suitable prey, to dense, long-lasting aggregations tens of kilometers across. The lack of any obvious change in foraging behavior with feeding success (apart from the

directness of the whales' movements) supports the existence of such a continuum in feeding conditions.

With prey patches of the order of 40-50 km across, the lack of consistent variation in environmental measures at distances from 9 to 45 km from groups of whales was not unexpected. Results presented in chapter 3 show that some of the same environmental measures, especially those from acoustic scattering layers and bottom topography, were strongly correlated with sperm whale distribution over spatial scales of 590 and 1120 km. Over these scales the correlation increased with increasing spatial scale, so the present results might have been predicted.

More surprising was the lack of relationships between the feeding success of the groups and any of our environmental measurements, but this could be due to the small sample size ($n=11$), as only a strong and consistent relationship would have been detected with this sized study. However, the result could also suggest that, over a spatial scale of 10 to 100 km, the patches of squid that sperm whales principally feed on are found in rather unproductive waters. Several species of squid are known to spawn in warm, but nutritionally poor, waters (Mann and Lazier, 1991; O'Dor, 1992), and Clarke (1980) has suggested that sperm whales feed on spawning grounds, thus taking advantage of a high biomass of dying squid. On the other hand, a spatial lag of more than 10-100 km, and/or a time lag of more than 2 days between a peak in chlorophyll or zooplankton concentration and a peak in squid density, might also mask any relationship.

CHAPTER 5

SPATIAL ORGANIZATION OF GROUPS OF FEMALE AND IMMATURE SPERM WHALES IN THE SOUTH PACIFIC

5.1. Introduction

The spatial organization of individuals and populations plays a central role in ecology, mainly because of its importance in ecological theory (e.g. predator-prey interactions) and its practical role in population sampling (Legendre and Fortin, 1989). Intraspecific competition, life history, habitat structure, predation and spatial organization of food resources are factors which are likely to influence the spatial organization of a species. However, identifying the processes important in determining patterns is further complicated by variations apparent on different spatial scales (Thrush, 1991). Food supply is often thought to influence large scale distribution patterns while life history and interactions between individuals are thought to operate over small spatial scales (Thrush, 1991). Therefore, the spatial organization of individuals could be, for example, clumped at a small spatial scale, random at medium and regular at large spatial scales.

Spatial organization has extensively been studied in several species of plants (Steele, 1978; Ripley, 1981; Urban et al. 1987) and in some invertebrate benthic species (Thrush, 1991). However, due to the inherent problems of studying moving, widely dispersed species, the understanding of spatial organization of cetaceans over a wide range of spatial scales is still in its infancy (cf. chapter 1). As sperm whales are widely distributed pelagic deep-divers, and as very little is known about their main prey item (cf. chapter 1), it is difficult to relate sperm whale distribution and spatial organization to the distribution and spatial organization of their food resources.

Nineteenth century whalers noted that female and immature sperm whales were not randomly distributed within the oceans but were more abundant, at large spatial and temporal scales (oceans, decades), in areas that they called "grounds". These grounds are mainly coincident with areas of coastal or equatorial upwelling (Townsend, 1935; Gulland, 1974; see also chapter 2). Over small spatial scales (hundreds of meters to a few km) the distribution of individual sperm whales is also clumped: female and immature sperm whales form groups of about 20 individuals, with each group consisting of one or more permanent familial units (Whitehead *et al.*, 1991; Richard *et al.*, 1996). Within these groups, individuals may be either spaced out in a rank while foraging, or found very close together while socializing (Whitehead, 1989). Two or more of these groups may associate together for periods of hours to form what is called an aggregation (Whitehead and Weilgart, 1991). However, very little is known about sperm whale spatial organization over scales of 20 to 1000 km and about the processes which are likely to influence such distribution patterns.

Individual sperm whales have very large food requirements, between 400 kg and 1 ton of squid a day (Clarke *et al.*, 1993), and therefore, it seems likely that the spatial organization of sperm whales would be strongly influenced by the spatial organization of food resources. Their large food requirements may also enhance intraspecific competition, and it is possible that groups of whales may be spaced out to reduce interactions. Sperm whales have very few natural predators: killer whales, their most dangerous enemies, are rarely successful in their attacks on healthy adults, although they may very occasionally take calves (Jefferson *et al.*, 1991). However, as sperm whales have a very low calving rate, about 0.2 calves per mature female per year (Best *et al.*, 1984), occasional predation of a calf may

be important for both the fitness of individual females and population dynamics. Thus, predation may also influence patterns in spatial organization of individuals, especially over small spatial scales.

In this chapter, I investigate sperm whale spatial organization over spatial scales ranging from 10 to 5000 km. I also relate the results to what is known of spatial organization of sperm whale food resources.

5.2. Methods

5.2.1. Field work

Data were collected from a 12.5-meter, ocean-going cutter during two surveys: the first, between January and May 1991, around the Galápagos archipelago and off the coast of Ecuador, and the second, between June 1992 and June 1993, around the South Pacific (Fig. 3.1.). Since the survey track was designed to go through all major 19th century sperm whaling grounds of the South Pacific (Townsend, 1935), the sampling distribution of searching effort was not random. A total of 263 days were spent at sea.

Sperm whales spend about 70% to 75% of their time underwater, limiting the effectiveness of visual detection. However, while underwater, they produce characteristic broadband transient clicks with a mean duration of 10-20 ms and a repetition rate between 0.5 and 3 clicks s⁻¹ (Backus and Schevill, 1966; Goold and Jones, 1995), called "usual" clicks by Weilgart and Whitehead (1988). These clicks can be heard through a hydrophone in a radius of about 7 km depending on oceanographic conditions (Leaper *et al.*, 1992). While at the surface, sperm whales may also vocalize, producing codas, characterized by short irregularly

spaced sequence of clicks which are repeated several times within the space of a few tens of seconds (Watkins and Schevill, 1977). Therefore, in the present study, sperm whales were located by listening every half hour through an omnidirectional hydrophone for their characteristic clicks.

Each time whales were heard, the exact position of the research vessel was recorded using a Tracor Transpak GPS. Groups of sperm whales usually traveled at a mean speed of 3.3 to 5.5 km/h (Gordon, 1987; Papastavrou *et al*, 1989; see also chapter 4), and, during the surveys, the research vessel was sailing at about 11 km/h on average. Therefore, a new encounter was defined when clicks were heard at a listening station and no sperm whales had been heard during at least the 2 past hours. Encounters with solitary mature males, often characterized by slow clicks with a repetition rate of about 0.15 clicks s⁻¹ (Weilgart and Whitehead, 1988), were disregarded. As most whales were only encountered acoustically, it was not always possible to differentiate between a group of whales or an aggregation of two or more groups. Therefore, I use the term "aggregation" whenever there was doubt about whether the social structure present was a single group or an aggregation of groups.

When a group was encountered, it was sometimes followed for a few hours to 2 1/2 days to collect data relevant to other issues. Upon leaving one of these groups, we usually sailed on a course roughly perpendicular to the general heading of the group, and listened for the whales every 1.8 km in order to examine the spatial organization of the individuals within the aggregation containing the group.

5.2.2. Data analyses

The distances between encounters were calculated and grouped into intervals: 0-9; 9-18; 18-37; 37-74; 74-148; 148-295; 295-595; 595-1185; 1185-2370; 2370-4740; 4740-9480 km. For each i - j interval the rate of encountering a new group and the 95% confidence interval were calculated using the following formulae:

$$R_{i-j} = \frac{N_{i-j}}{\left[(Nd_{0-j} * D_{i-j}) + \sum_{k=1}^{k=j} d_k \right]} \pm \frac{1.96 * R_{i-j}}{\sqrt{N_{i-j}}}$$

where: $-R_{i-j}$ is the rate of encountering a new group at a range within the interval i - j

$-N_{i-j}$ is the number of encounters at ranges of i - j

$-Nd_{0-j}$ is the number of times we surveyed the i - j interval without any sperm whale encounters

$-D_{i-j}$ is the width of the interval i - j

$-d_k$ is the distance sailed within the interval i - j before the k^{th} sperm whale encounter

The frequency distribution of the numbers of encounters in the different intervals was tested against that expected if the rate of encounter did not vary with range using a χ^2 test (Sokal and Rohlf, 1981).

The percentage of times individual sperm whales were heard at ranges of 1 to 46 km after leaving a group was plotted against range to investigate spatial organization within an aggregation.

5.3. Results

During the first survey (Galápagos-Ecuador) we encountered 19 groups of sperm whales and one solitary mature male. During the second survey (around the South Pacific), we encountered sperm whales 70 times. Of these, 47 encounters were with groups or aggregations of groups, 8 were with single mature males, and in 15 encounters we heard only a single whale making usual clicks in the distance (Fig. 3.1.). In these last cases, it was not possible to determine if the clicks were produced by a female or immature within a group or by a solitary male making usual clicks. However, as of the identified encounters, only 17.4% were with solitary males, and as it has been found that mature males form about 2% of sperm whale population around the Galápagos Islands and the west coast of South America (Whitehead 1993), and often make characteristic slow clicks (Weilgart and Whitehead, 1988), it is unlikely that more than about 2 to 3 of the unidentified encounters were with males. Moreover, I also analyzed the data set omitting the 15 unidentified encounters and obtained similar results. Therefore, I assumed that these 15 encounters in which single usual clicks were heard were with females and immatures.

During the 1991 survey, in 83% of the cases, there was less than 300 km between consecutive encounters, and in 17% there was between 300 and 1200 km between consecutive encounters. During the 1992-93 survey, in 68% of the cases, there was less than 300 km between consecutive encounters, and in 32% there was between 300 and 9500 km between consecutive encounters. Fig. 5.1. shows that, for the second survey, the greatest probability of finding a new group of whales occurred when the vessel was 9-72 km away from the last group, then

the probability decreased, but there seems to be a second plateau of fairly constant probability in the interval of 150-300 km. The probability of finding a new group decreased substantially at intervals greater than 300 km. The results of the first survey, although based on a small sample size and so with wide confidence intervals, seem to confirm this pattern: a high rate of encountering new groups between 9 and 36 km, a sharp decrease in rate before a second plateau, and again a sharp decrease when 300 km or more from the last group (Fig 5.2.).

For the second survey, the frequency distribution of distances between encounters was also tested against an expected distribution assuming a similar rate at all distances using a χ^2 test. The results show that there was a statistically significant difference between the 2 distributions ($p < 0.0001$).

Therefore, it seems that most aggregations are found less than about 300 km from each other; and so the span of the areas occupied by these aggregations separated by less than 300 km was calculated. On average, such areas were about 550 km across. These areas, characterized by a high density of sperm whale groups, were then called "concentrations". The high rate of encountering a new aggregation when 9-72 km away from the last one (the first plateau) further suggests that the distribution may also be clumped at a smaller scale, these clumps were called "super-aggregations" (Fig. 5.3.).

Ranges at which it was still possible to hear one or several individuals of an aggregation were investigated in 17 cases after leaving a group during the second survey. Fig. 5.4. shows that in 30% of the cases, sperm whales could not be heard through the hydrophone after 7 km (maximum distance to which it is usually possible to hear a click), and in 60% of the cases, they could not be

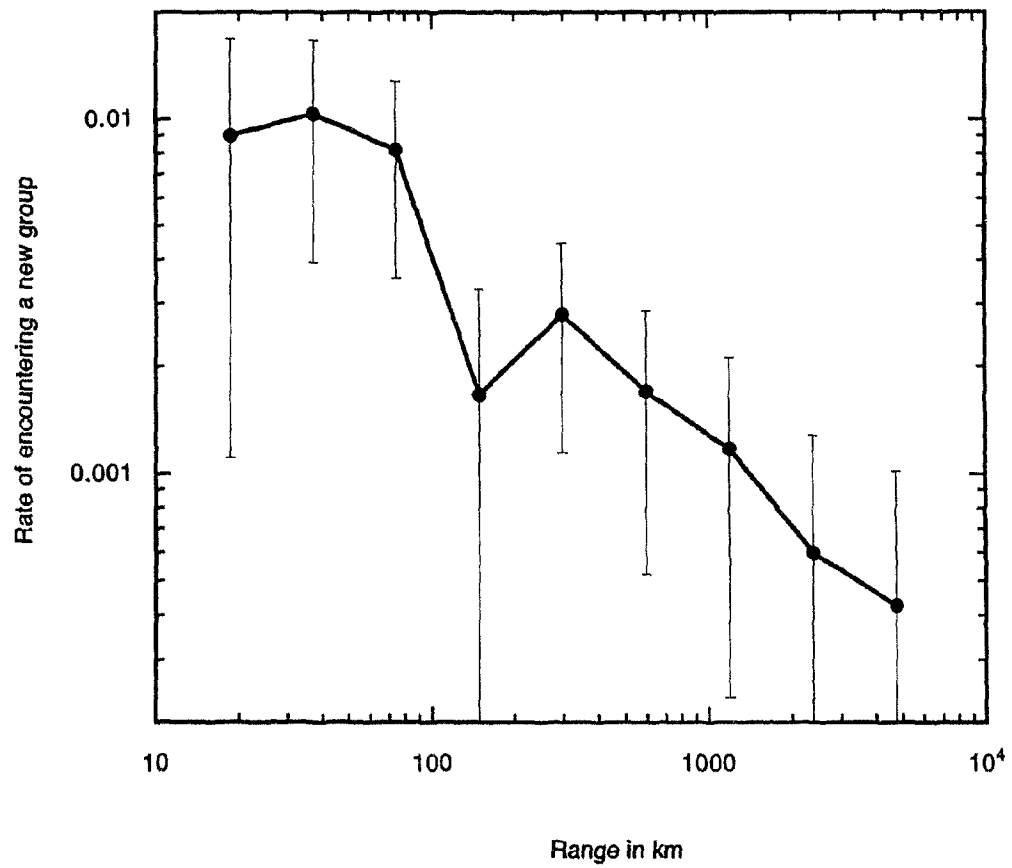


Fig. 5.1. Rate of encountering a new group of sperm whales (number of encounters/km) versus range from the last group during the 1992-1993 survey. Error bars are approximately 95% confidence intervals.

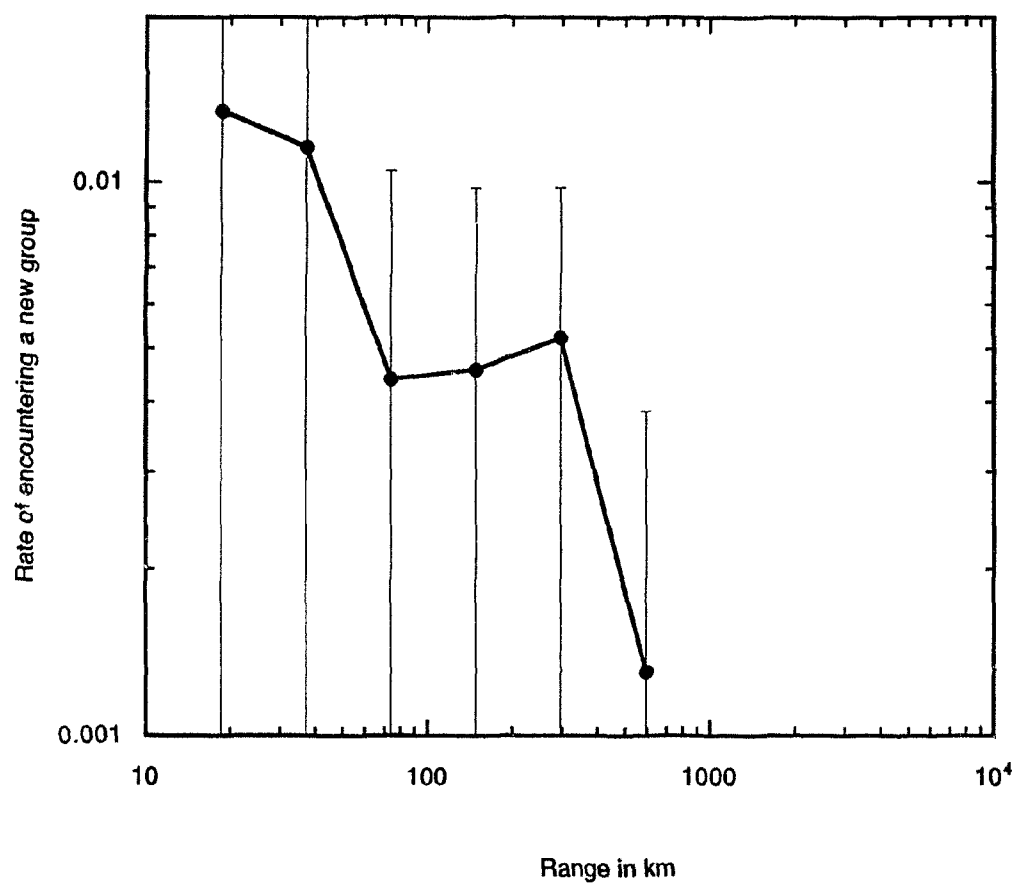


Fig. 5.2. Rate of encountering a new group of sperm whales (number of encounters/km) versus range from the last group during the 1991 survey. Error bars are approximatively 95% confidence intervals.

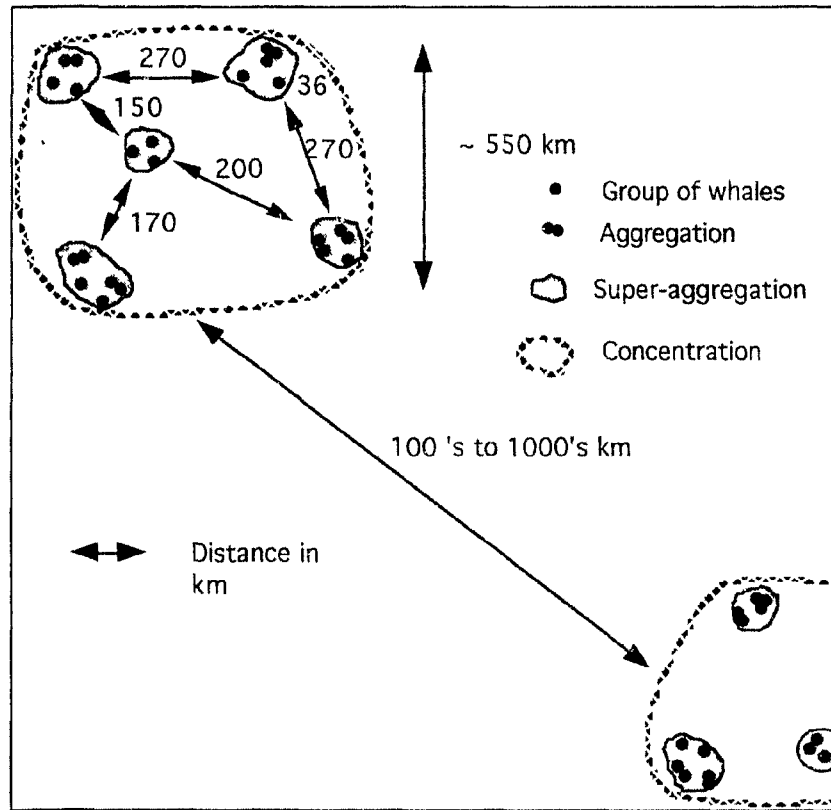


Fig. 5.3. Diagram of sperm whale spatial organization.

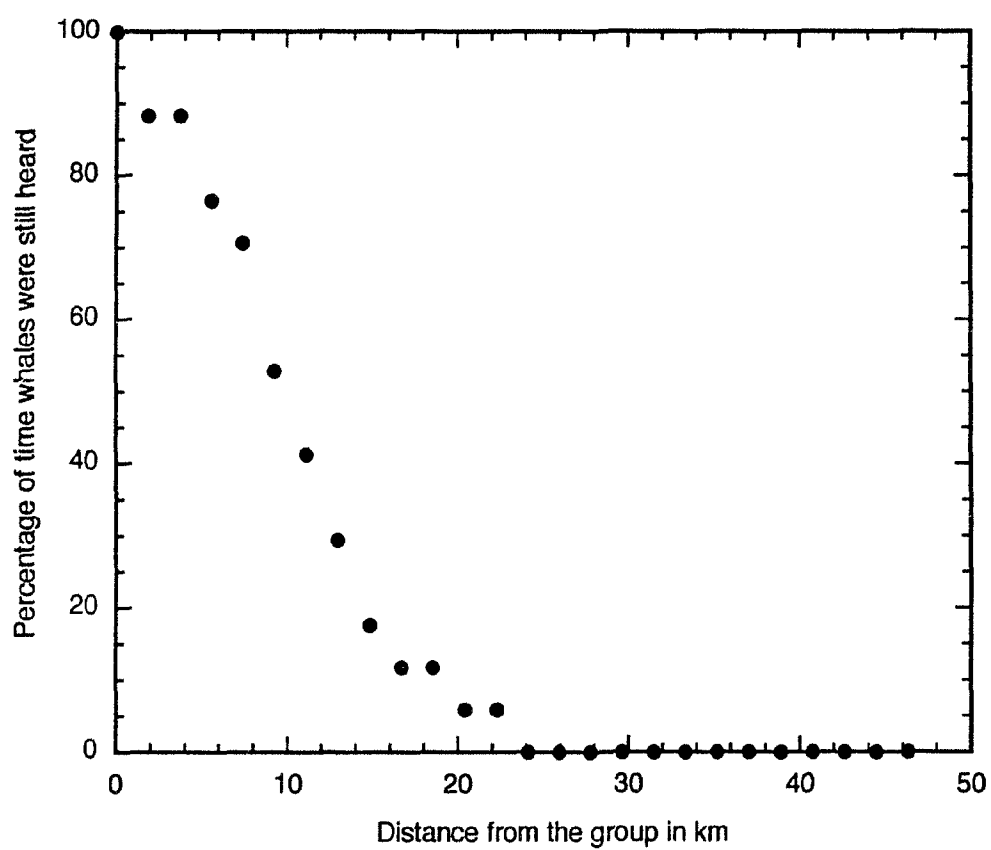


Fig. 5.4. Percentage of time that one or several sperm whales were heard through the hydrophone while sailing away from a group versus distances to the group.

heard after 11 km. However, there was a small percentage of occasions where sperm whales were heard continuously until 18 to 22 km.

5.4. Discussion

It is very difficult to study the distribution of moving organisms over scales of a whole ocean, and thus my study has limitations. The major limitation in using a boat to study spatial organization of whales over such a large scale (South Pacific Ocean, ~38900 km of survey), is that the vessel is sampling the ocean in only one horizontal dimension, a strip of about 14 km wide. Therefore, any sperm whale groups which are more than 7 km from the boat in a lateral direction will be missed by the survey. However, during the first survey (Galápagos-Ecuador), as a much smaller portion of the ocean was investigated, the boat was sailing in different directions effectively sampling over the same patch of ocean. The consistency between the results of the surveys suggests that, even if the method used has limitations, it gives reasonably valid results on sperm whale spatial organization in the South Pacific.

This study suggests that groups of sperm whales were clumped over two different spatial scales. Several groups were often found close together (9-72 km apart) and formed what was called super-aggregations. These super-aggregations, distant from each other by 150-300 km, were usually found in areas about 550 km across called concentrations. There were sometimes thousands of km between concentrations.

The spatial scale of both super-aggregations and concentrations is strikingly coherent with the inferred spatial scale of patches of sperm whale prey and with

the spatial scale of areas of high sub-surface biomass and high underwater relief. Investigations of movement patterns of groups indicate that the extent of sperm whale prey patches is about 25-55 km across (cf. chapters 3 and 4). Therefore, several groups of sperm whales seem to be often foraging over the same patch of prey. It is likely that sperm whales can hear each other underwater in a radius of up to 36 to 55 km (G. Goodson, comm. pers.), and so groups foraging over the same patch of prey could change their behavior and/or movements in response to what they hear from other groups. However, not enough data were available in the present study to investigate the distribution of whale groups within a super-aggregation and further work is needed to determine whether these groups tend to forage cooperatively or tend to avoid each other to limit intraspecific competition. Using movement patterns of groups, I have suggested that the distance between "good quality" prey patches in the South Pacific is in the order of at least 110-240 km (chapter 4). Therefore, the distances between super-aggregations (150-300 km) seems to reflect the distances between prey patches. I also have shown that groups of sperm whales are usually found in areas about 600-1200 km across, characterized by intense scattering layers at depths of 0-600 m and uneven bottom topography (chapter 3). The spatial scale of these areas is again coherent with the spatial scale of sperm whale concentrations. These results suggest that the spatial organization of sperm whales matches the spatial organization of their prey (Table 5.1.).

Table 5.1. Spatial organization of sperm whales and relationship with spatial organization of food resources.

Agglomeration of whales	Approximate spatial scale	Type of spatial organization within the agglomeration	Remarks
Groups	3 X 3 km	- clumped - spaced (rank)	→ social → coordinated foraging
Aggregations	9 X 9 km	clump	→ ?
Super-aggregations	55 X 55 km	random?	Same spatial scale as a patch of prey → exploitation of food resources
Concentrations	550 X 550 km	random?	deep water biomass and underwater relief higher than in adjacent areas → exploitation of food resources

It is difficult to draw many conclusions regarding the spatial organization of individual sperm whales within an aggregation because so few data are available and because the distances to which clicks propagate are highly dependent on oceanographic conditions. However, the present results suggest that most aggregations do not spread out over more than 2-6 km. In 3 cases, whales were heard until respectively 15, 18 and 22 km. Two of these aggregations were very large, and it is therefore possible to find groups or, more likely, aggregations of groups which spread out over at least 15 km.

CHAPTER 6

GENERAL CONCLUSIONS

The work described in this thesis represents the first study of the factors influencing sperm whale distribution and spatial organization over spatial scales of a few km to an entire ocean, and using data averaged over temporal scales of a few hours to 130 years. Therefore, it represents an important contribution to knowledge of sperm whale ecology. Despite the difficulty of studying such a species, and thus the small sample size and the large confidence intervals involved, consistency among the results makes it possible to sketch a "big picture" of the distribution and spatial organization of groups of female and immature sperm whales in the Pacific Ocean.

6.1. Distribution

Indirect evidence indicates that distribution of groups of sperm whales seems to be related to the distribution of food resources over most spatial scales investigated (from tens of km to thousands of km).

Over small spatial scales (10 to 300 km), there was no relationship between chlorophyll concentration, the amount of sub-surface biomass or an index of underwater relief and sperm whale distribution. However, my study of movement patterns (cf. chapter 4) indicates that, over these scales, sperm whale distribution may be directly associated with the distribution of prey patches. It is therefore likely that the absence of relationship between sperm whale distribution and biological and environmental variables is partly due to the existence of a spatial lag between a peak in primary and/or secondary productivity and a peak in cephalopod (or other prey) density. It may also partly be explained by sperm

whales feeding on spawning squid in unproductive waters (Clarke, 1980) or to the inability to measure prey biomass directly.

At spatial scales of hundreds to thousands of km, sperm whales are found in areas roughly 500 to 1200 km across, characterized by a high bottom relief and high sub-surface biomass. The high underwater relief likely contributes to the concentration of squid, while a high subsurface biomass suggests high secondary productivity.

When the data are averaged over a large temporal scale (8-130 years), this study shows that sperm whale grounds are usually found in upwelling and high primary productivity zones about 200 km to 2000 km across. However, when survey data were used, there was no correlation between sperm whale distribution and chlorophyll concentration over any of the spatial scales considered, even the largest. This result suggests the existence of spatial and temporal lags between peaks in chlorophyll concentration and peaks in squid density.

6.2. Spatial organization

Spatial organization of groups of sperm whales seems also to be directly influenced by the spatial organization of their food resources. Several groups and/or aggregations may form "super-aggregations" in areas about 55 km across, and the size of these "super-aggregations" seems to match the size of patches of prey. Super-aggregations are clumped together, forming "concentrations" over areas roughly 500 to 1200 km across. The waters within

these areas are characterized by higher sub-surface biomass and higher underwater relief than adjacent waters.

6.3. Movements

The behavior and movements of groups of sperm whales seems to be largely determined by the necessity of finding food at minimal cost. Their mean traveling speed is quite constant, and this speed may represent an optimum which minimizes energy expenditure. In addition, independently of squid abundance, sperm whales spend most of their time feeding or looking for food (showing foraging behavior). However, the directionality of the movements of the group vary in relation to food availability and abundance. When feeding success is high, groups tend to zigzag over areas roughly 30 to 45 km across (which seem to correspond with the extent of squid patches). On the other hand, when feeding success is low, the groups travel in a nearly straight-line for at least up to 250 km (which may correspond to the distances between "good" quality prey patches). As sperm whales form matrilineal groups (Richard *et al.*, 1996), and live for at least several decades, it is possible that older females have knowledge of the locality of potential prey patches, which can assist other members of the group.

Breeding requirements do not seem to affect the distribution and movements of groups of female and immature sperm whales. Unlike baleen whales which undertake extensive annual migrations to satisfy breeding requirements, groups of sperm whales do not change their distribution during the breeding season. Therefore, the extensive seasonal migrations, suggested by several authors after

studying the Townsend's (1935) charts, seem to be largely an artifact due to wind conditions and uneven whaling effort between seasons.

As it has been shown that female sperm whales seldom travel more than 1100 km over a time scale of a few years (Best, 1969; Ivashin, 1981; Dufault and Whitehead, 1995), it is likely that the concentration represents the "home range" of a group of sperm whales. Many groups may be foraging within these large areas. In high food availability patches, several groups form super-aggregations and move in zigzags over these patches. When the patches have been depleted, the groups travel in nearly straight-lines to other parts of the concentration. Nineteenth century whaling grounds seem often larger than the size of a concentration as year to year variability in productivity is likely to induce year to year changes in the localization of sperm whale concentrations.

6.4. Conclusions

In conclusion, figure 6.1. indicates the temporal and spatial scales of the social and spatial organization of sperm whales. All the structures which are socially related are found over small spatial scales (<10's of km), but extend over decades or possibly centuries. It is likely that about a few 10's of km represents the extent to which individual sperm whales can effectively communicate with other individuals. The large temporal scale involved suggests that these social bonds can be maintained over at least several years. On the other hand, there is a strong relationship between temporal and spatial scales for the structures which are food related. Structures found over small spatial scales are also found over small temporal scales and vice-versa. This last result indicates once more

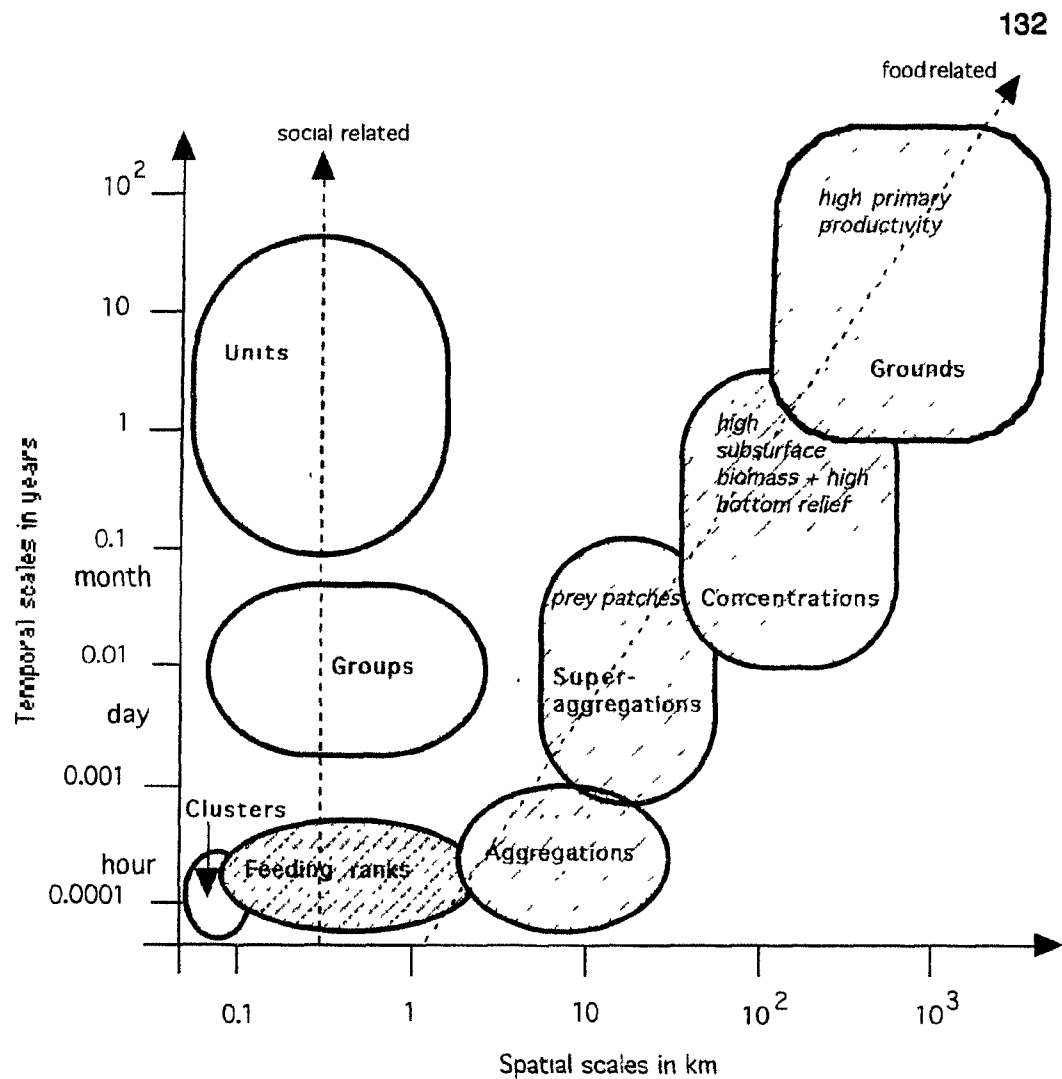


Fig. 6.1. Temporal and spatial scales of the spatial and social organization of sperm whales. The shaded areas represent primarily social structures, while the striped areas represent structures mainly driven by extrinsic factors (distribution of food resources). The bold captions are the names given to the different type of structure and the italic captions the characteristics of the environment.

Sources: Grounds (chapter 2); concentrations and super-aggregations (chapters 4 and 5); aggregations (chapter 5); groups and units (Whitehead *et al.*, 1991); feeding ranks and clusters (Whitehead, 1989).

the existence of a spatial and temporal lag between sperm whale distribution and the distribution of high productivity patches: the larger the time lag, the larger the space lag.

This study shows therefore that the distribution, movements and spatial organization of sperm whales are closely related to the distribution of food resources, and that underwater relief, amount of subsurface biomass and primary productivity are good indicators of sperm whale distribution only if the existence of temporal and spatial lags are taken into account. These factors cannot therefore be used to describe the small scale distribution of sperm whales.

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