# An examination of the current knowledge on the stock structure of sperm whales (*Physeter macrocephalus*) worldwide[1]

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ABSTRACT

There is no clear picture of the worldwide stock structure of sperm whales in spite of a great deal of effort, especially in areas where there has been substantial modern whaling. Techniques to examine stock structure have included: the interpretation of catch and sighting distributions and catch per unit of effort; morphological examinations; biochemical and genetic analyses; comparisons of life history parameters; mark-recapture using artificial and natural marks; the occurrence of parasitic infestations; and the comparison of vocal repertoires. Methods which depended on the whaling industry were often limited by unequal distribution of effort and lack of standardised collection methods. Also, most analyses failed to consider the effect of social groupings. Recent research, independent of the whaling industry, has addressed some of these problems. However, the results are equally inconsistent. Variation between the results of different studies can be explained, at least partially, by the temporal scales of the measures used. In general, groups of female and immature sperm whales appear to be restricted to ranges of about 1,000km over periods of 10 years or so. Occasionally, they move much further. Male ranges are generally larger, especially latitudinally. Occasional movements across, and sometimes between, ocean basins seem to have resulted in remarkable global genetic uniformity. To effectively conserve and manage sperm whales in the face of substantial anthropogenic disturbance, we need new and good information on modal and exceptional movement patterns over a range of timescales.

KEYWORDS: SPERM WHALE; DISTRIBUTION; STOCK IDENTITY; MOVEMENTS; MORPHOMETRICS; MIGRATION; PHOTO-IDENTIFICATION; GENETICS; MARKING; MANAGEMENT

## INTRODUCTION

This paper reviews published information on the worldwide stock structure of sperm whales (*Physeter macrocephalus*). It examines the range of methods employed in these studies and considers their effectiveness and shortcomings. The sometimes contradictory conclusions drawn from the same data in the same ocean are summarised. Finally, an overview of general conclusions reached with respect to sperm whale stock structure on a global basis is presented. To elucidate such a review, it is useful to begin with a discussion of what is meant by a 'stock'.

In his review of stock boundaries used by the International Whaling Commission (IWC), Donovan (1991) noted the importance of defining stocks in the context of the use to which they were being put. The term has been used variously to describe management stocks, biological stocks or geographical divisions, although clearly none of these can be taken in isolation. Stocks have been regarded, from an exploitation point of view, as population units that can be managed effectively (Donovan, 1991). Successful management must necessarily include some knowledge of the biology of a stock. Distinct sets of animals may occupy a single area at different times of the year and thus be temporally and genetically, though not geographically, discrete (possibly the case for equatorial populations of sperm whales as discussed in Rice, 1977). Additionally, members of different genetically distinct stocks may congregate in the same area at the same time, for example, on a feeding ground (perhaps the situation for Asian and American stocks of male sperm whales in the North Pacific described in Ohsumi and Masaki, 1977). In both of these cases, whaling in a localised region may have unexpected consequences. Unfortunately, for most whale species, there is a shortage of sufficient information to delineate biological stocks (Donovan, 1991).

In addition, there is no consensus on the degree of overlap or interchange between two 'separate' stocks that is acceptable before they are treated as a single stock. For example, Dufault and Whitehead (1993) defined 'stocks' in the eastern equatorial Pacific to be geographically distinct if they did not undergo random mixing over a two year period; however movement of a few percent per year from one stock area to the other was observed. Kasuya and Miyashita (1988) described stocks in the western North Pacific as separate if there was not a 'significant' (which they did not define) number of marked individuals moving between the two areas. They deemed movement between each of the stock areas and the intervening latitudes as unimportant and their suggested stock boundaries overlapped considerably. Best (1969b) and Gaskin (1973) described stocks which they thought could be considered distinct for management purposes although they presumed that interchange between them would likely make them genetically indistinguishable.

The current[2] IWC sperm whale management divisions (Donovan, 1991) comprise: the entire North Atlantic (~3,500km across); western (~4,000km across) and eastern (~2,000km across) divisions in the North Pacific separated by a rather controversial line; and nine divisions along lines of longitude in the Southern Hemisphere from the equator to the pack ice (ranging from 3,330-7,770km wide at the equator, to 1,110-2,590km at 60°S). The extent of any shore-based whaling operation was usually less than the area of a single management division due to a limitation in the distance whalers could travel from coastal stations. In contrast, pelagic whalers could take sperm whales from both sides of the North Pacific or from any of the nine stock divisions in the Antarctic.

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[1] A version of this paper was submitted to the IWC Scientific Committee as SC/49/O 7.

[2] Although 'current', this is largely by default. The IWC Scientific Committee has not reviewed sperm whale stock divisions for over a decade and sperm whales have not been caught in the Southern Hemisphere or the North Atlantic since 1981, or in the North Pacific since 1988.

In most studies examined in this review, the word 'stock' was used without formal definition, although, since the majority of studies were carried out in a whaling context, the concept of management stocks was implied. In this paper, the term 'stock' will be used as presented in the papers reviewed, usually referring to those animals caught from a specific station (in the case of coastal whaling) or within a specified region (in the case of pelagic whaling).

In recent years, the IWC Scientific Committee has concentrated on developing a 'Revised Management Procedure' for baleen whales (see Donovan, 1995). The fact that it has not considered sperm whales is in recognition of the difficulty in managing a species with such complex social organisation and behaviour.

Sperm whales are the most sexually dimorphic of the large whales, with males reaching lengths of 18m and females 12m. Males grow more rapidly than females beyond the age of four and there is evidence that their growth rate may accelerate at the onset of puberty which occurs at 11-12m or 19-20 years. Conversely, female growth rates slow down after sexual maturity which they attain at 8-9m or about nine years of age. Females attain physical maturity around 11m (28-29 years) and males at 15-16m or 35-45 years (Best, 1970). Females from the Northern and Southern Hemispheres are believed to be six months out of phase in their breeding cycles with peaks in ovulations from April to June in the North and October to December in the South (Best *et al.*, 1984). There is no evidence of seasonal cycling in spermatogenic activity in males (Best, 1969a; Mitchell and Kozicki, 1984) although there may be seasonality in testicular androgen production (Best, 1969a). Sperm whales are widely distributed throughout all deep (>1,000m) oceans of the world (Rice, 1989). Groups of adult females and their immature offspring of both sexes reside year-round in tropical and subtropical waters limited roughly by the 15°C sea surface isotherm and rarely range beyond 45-50°N or 40°S (Rice, 1989). These groups consist of approximately 20 individuals (Best, 1979; Whitehead *et al.*, 1991) from one or more permanent matrilineal units. Individuals from different units come together for periods of days (Whitehead *et al.*, 1991) or possibly much longer (Richard *et al.*, 1996). Males leave their natal groups at very approximately 6 years of age, ranging further poleward and becoming increasingly solitary as they age (Best, 1979; Richard *et al.*, 1996). Large mature males are commonly found right up to the edges of the polar pack ice. These large males, older than about 25 years, return to warmer waters to breed (Best, 1969a) on a schedule which is unknown. Distinctive features of the biology of sperm whales, such as the different latitudinal distribution of the sexes and the permanent groupings of females, are important considerations in trying to try to understand the stock structure of sperm whales.

## TECHNIQUES USED TO STUDY STOCK STRUCTURE

Donovan (1991) considered a number of techniques and data sources that have been used in stock identity studies. These include: catch distributions; sightings distributions; mark-recapture data (using both artificial and natural marks); morphology; biochemical/genetic data; pollutant and parasite burdens; differences in life history parameters; and compatibility with models. These are discussed below with special reference to sperm whales.

### Catch distributions

The largest data sources available relevant to questions of stock structure of sperm whales are catch data. The Townsend charts (Townsend, 1935), compiled from American whale-ship logbooks, depict the locations of whaling vessels during 36,908 sperm whale catch events worldwide between 1761-1920. These charts were employed by Bannister and Mitchell (1980), Best (1969b), Gaskin (1973) and Kasuya and Miyashita (1988) in their assessments of sperm whale stock structure. Kasuya and Miyashita (1988) also included catch locations representing more than 100,000 individual whales during the period 1940-1986. Thus, their analyses were based on a great deal of information over a rather long time period. Catch positions are available for almost all sperm whale catches since 1930, although the official data submitted by the USSR are now known to be false (e.g. IWC, 1999).

The use of catch distributions to elucidate stock structure has been criticised for being misleading unless effort is also considered (Best, 1975; Donovan, 1991). Bannister and Mitchell (1980) achieved this by also examining the charts of Maury (1851 *et seq.* cited in Bannister and Mitchell, 1980) which provide a measure of effort for 18th and early 19th century American whalers. Ohsumi and Masaki (1977) and Tillman (1977) presented analyses of catch per unit effort (CPUE) in their evaluations of North Pacific stocks.

### Mark-recapture programmes

The marking of sperm whales using the 'Discovery'-type mark (a 23cm long stainless steel tube of 1.5cm diameter with a lead tip, fired from a modified 12-bore shotgun) began in 1934 (Rayner, 1940). Numbered marks were fired into whales at known geographical locations. Marks were recovered if the whale was subsequently killed and the mark found. Up to 1979, 3,558 sperm whales had been marked in the Southern Hemisphere under the USSR and international marking schemes (Brown, 1981). A total of 4,648 had been marked in the North Pacific by the Japanese and Soviet marking programmes as of 1980 (Ivashin, 1983). No large-scale marking programme was undertaken in the North Atlantic.

Any thorough examination of mark-recapture data must consider the level of effort of both marking and recovery (Donovan, 1991). A major weakness in using marking data for the examination of stock structure, was the general failure to distribute the marks widely (Best, 1975). For example, 50% of animals marked by Japan and the USSR in the North Pacific were marked in waters adjacent to the Japanese coast and the Kuril Islands and 67% of Soviet and 79% of Japanese recoveries were in this same area (Ivashin, 1983). In addition, doubt has been cast on the validity of the Soviet data (e.g. Best, 1989; IWC, 1999) requiring that caution be used in data interpretation. Discrepancies include marks reportedly fired at one species but recovered in another (e.g. Kasuya and Miyashita, 1988).

Another shortcoming was the low recovery rate of marks (e.g. the 3-7% reported by Ivashin, 1981; 1983) when expressed as the number of recoveries as a percentage of whales estimated to be successfully marked. Thus, the information gained may be considered small in comparison to the effort expended. A substantial number of mark recoveries exist for the North Pacific (Ivashin, 1983; Kasuya and Miyashita, 1988) and the Southern Ocean (Brown, 1981; Ivashin, 1981) although recovery effort also has been quite localised, especially in the North Pacific. In the North Atlantic, Aguilar (1985) used the recovery of a single Discovery-type mark plus the recoveries of two hand harpoons, lost when animals were struck but then escaped, to provide a view of the stock structure in this region where little other information exists.

Recently, the idea of using mark-recapture to reveal stock structure of sperm whales has been applied to photographically identified individuals in the South Pacific (Dufault and Whitehead, 1995). This technique has a number of advantages over Discovery-type marking programmes. The most important is that it allows for the possibility of multiple recaptures of the same individual since recapture is not dependent upon the death of the animal and the consequences of recapturing an animal shortly after marking disappear. The technique can be employed regardless of whether any whaling is taking place and can thus be used during the current hiatus in commercial whaling to provide a better understanding of stocks and, thus, better ability to manage them should whaling on sperm whales ever be resumed. At present photo-identification studies of sperm whales are rather localised, but it is of course possible to distribute effort more widely.

### Morphological comparisons

Morphological (and often, therefore, genetic differences) can be of value for determining stock differentiation. Past morphological studies of sperm whales were often intensive and involved substantial sample sizes and large geographic ranges. A common technique was to compare the incidence of different forms of a given external character (e.g. colour pattern, type of fluke notch or the number of erupted teeth or dorsal humps of whales from different areas—see Best and Gambell, 1968; Clarke *et al.*, 1968; Veinger, 1980; Berzin and Veinger, 1981; Dufault and Whitehead, 1998). Internal characters (e.g. the shape of the spleen and number of sternal ribs, Berzin and Veinger, 1981) have also been used, as have characteristics of the tooth structure (Klevezal' and Tormosov, 1971). Observer subjectivity in the interpretation of many of these characters is problematic and there has been a general difficulty in finding an easily identifiable and quantifiable character which gives a definitive stock distinction (Donovan, 1991). This is particularly true for sperm whales, which for the most part, are remarkably similar in the different oceanic regions of the world (Best and Gambell, 1968; Clarke *et al.*, 1968; Gambell, 1972).

Some studies used morphometrics (e.g. skull measurements and total body length) rather than presence or absence of characters. For example, Clarke and Paliza (1972) compared growth coefficients ($\alpha$) from the allometry equation, $y = bx^{\alpha}$ (where $x$ is total length and $y$ is a specific proportion), for measurements from several oceanic regions and Machin (1974) applied canonical analysis to the same set of data. The availability of sufficient data from the various regions was a limiting factor in these studies.

### Biochemical and genetic analyses

In recent years biochemical and genetic analyses have become important in stock identity studies (e.g. see Hoelzel, 1991). There are to date, however, few studies in which this has been undertaken for sperm whales. Early biochemical analyses involved comparing blood types of individuals from different regions (Cushing *et al.*, 1963; Fujino, 1963). This method provided evidence for stock distinctions but there were numerous potential difficulties such as haemolysis and contamination of samples (Best, 1975). Later, allozyme studies on Pacific sperm whales (Wada, 1980) provided similar results to those of Fujino (1963).

A potentially important feature of such studies is that analyses must consider the social organisation of sperm whales. Females and immatures travel in permanent groups within which there is substantial genetic similarity (Richard *et al.*, 1996). Thus, any dataset including more than one member from any group is not independent, and statistical tests for heterogeneity that assume independence of samples (such as ANOVA) will be invalid. This is especially the case when sample sizes are small.

The first studies of sperm whales that examined DNA directly were those of Dillon (1996) and Lyrholm *et al.* (1996) who analysed mitochondrial DNA (mtDNA) control region sequences using DNA extracted from sloughed skin, samples collected using biopsy darts or tissue archives. These have been followed by research using highly variable nuclear microsatellite markers (Lyrholm *et al.*, 1999). Sequencing studies have found significant heterogeneity among social groups and rather little geographical structure (Dillon, 1996; Lyrholm and Gyllensten, 1998; Lyrholm *et al.*, 1999). Lyrholm *et al.* (1999) discuss the important finding that, in their studies, populations of sperm whales in different oceans are discriminated using mtDNA control region sequences which are maternally inherited, but not using nuclear markers which are inherited from both parents. Given the more extensive migrations of males than females, this finding is not unexpected. However, as mtDNA in sperm whales has particularly low diversity (Lyrholm *et al.*, 1996), a consequence is that these markers give rather little information on stock structure. This is in contrast to other cetacean species such as white whales, *Delphinapterus leucas*, (O'Corry-Crowe *et al.*, 1997) or humpbacks, *Megaptera novaeangliae*, (Baker *et al.*, 1993) where significant geographic structure has been found using mtDNA and similar sample sizes.

### Other techniques

#### *Parasitology*

There do not appear to be any regional differences in the external parasites of sperm whales which can be used for stock delineation aside from latitudinal differences in cyamid species infestation and the presence of a diatom film which are merely indicative of the segregation of males to Antarctic waters (Best, 1979). Species of cyamids, copepods, barnacles and diatoms show no predilection for a particular ocean (Best, 1975). There is, however, some evidence that internal parasite fauna varies on a broad geographic basis (Berzin, 1972). Dailey and Vogelbein (1991) used helminth species of the genus *Corynosoma* to suggest the possibility of stock discrimination in the Antarctic although their sample size was too small to make firm conclusions.

#### *Pollutants*

Aguilar (1987) reviewed the use of pollutant burdens in the context of stock identity but this approach has not yet been applied to sperm whales.

#### *Life history parameters*

Comparisons of life history parameters such as pregnancy (Ohsumi and Masaki, 1977) and mortality (Holt, 1980) rates are another method that has been used in stock structure analysis. Potential problems of these studies include calculating parameters with suitable confidence limits to detect differences and, as with many other techniques, obtaining representative samples (Donovan, 1991).

*Occurrence of markings*
Marks caused by environmental agents such as predators, which may vary between regions depending on the levels of these agents, have been used to investigate stock separation. For example, the incidence of fluke damage has been compared between sperm whales from different locations (Berzin and Veinger, 1981; Dufault and Whitehead, 1998). Although the former study provided some evidence of differences between regions of the North Pacific, observed differences in the latter study could be accounted for almost entirely by variation between social groups and had little geographic foundation. Thus, the validity of results in the earlier study are called into question since the investigators in this study did not consider social grouping.

*Vocal repertoires*
Sperm whales produce patterned series of clicks, known as codas, which are used in communication (Watkins and Schevill, 1977). Coda repertoires may be different in different regions depending on their degree of isolation from one another and, thus, may indicate stock separation. Weilgart and Whitehead (1997) investigated differences in coda repertoires between sperm whales of the South Pacific and Caribbean on various spatial scales. These analyses confirmed increasing levels of dissimilarity with increasing distances which may be useful for the examination of stock separation.

*Model fitting*
In an attempt to settle the controversy over the dividing line between North Pacific stocks, Cooke and de la Mare (1983) used length distributions of whales caught in potential stock regions to find which proposed division best fit their model. One major problem with this technique is the assumption that the model and the data it uses are accurate (Donovan, 1991); for example, with respect to data, there are indications of misreporting of catch lengths (e.g. Best, 1989).

## RESULTS OF STOCK STRUCTURE STUDIES

Despite the importance of stock identity to sperm whale management, relatively few studies were designed with the objective of addressing stock identity. Most of the data used were standard data collected during whaling operations (e.g. catch, sightings and CPUE distributions). Genetic studies were poorly developed during the peak of sperm whaling.

### Within-ocean comparisons

*North Pacific*
As a result of the need to manage whaling operations, (e.g. both Japan and the former Soviet Union took large numbers of sperm whales), a considerable amount of time has been spent trying to elucidate the stock structure of sperm whales in the North Pacific; despite this, there is no clear picture to date. While it is likely that some stock segregation exists, it is unlikely that any stocks are completely discrete; the degree of any mixing is unknown. The exact number of stocks in the North Pacific is also controversial and the location of a boundary dividing management stocks has been the subject of much debate (see Donovan, 1991).

Catch and sightings data have shown discontinuities in distributions between western and eastern regions (Ohsumi and Masaki, 1977; Bannister and Mitchell, 1980; Kasuya and Miyashita, 1988) and latitudinally between different areas within the west (Bannister and Mitchell, 1980; Kasuya and Miyashita, 1988). CPUE data were found to show differing trends in western, central and eastern regions of this ocean (Tillman, 1977), although the interpretation of falsified Soviet data is no longer applicable. Mark-recapture studies have provided an abundance of markings and recoveries from the same area along the coast of Japan suggesting the possibility of some site fidelity (Ohsumi and Masaki, 1977; Ivashin, 1983; Kasuya and Miyashita, 1988) but the concentration of effort in this region is a confounding factor. Despite the level of effort in other areas of the North Pacific, instances of long-distance latitudinal and longitudinal movements have been found. Some morphological differences have been suggested between western and eastern regions (Veinger, 1980; Berzin and Veinger, 1981) and between areas within the west (Machin, 1974). Finally, biochemical studies suggest heterogeneity in western (Fujino, 1963) and lower central (Wada, 1980) portions.

Most authors have considered stock separation in the North Pacific to be longitudinal with an unquantified degree of intermingling near stock boundaries and in the Bering Sea. Ohsumi and Masaki (1977) analysed catch distributions reported by IWC member nations during the 1954-75 period (over 200,000 animals) as well as almost 180 mark recoveries from Japanese whaling during the 1949-75 period. Based on a discontinuity in female distribution, they proposed two female stocks divided at 160°W. They presumed the same division for males and suggested that the central and northern regions are areas of intermingling of 'surplus' (i.e. not part of the breeding population) males from the two stocks. Of their 71 female mark recoveries, 67 were marked and recovered near the coast of Japan, while two of the remaining four show movement across the proposed boundary. Male mark recoveries demonstrate much longitudinal movement including that between western and eastern regions.

Using 305 marks recovered by Japanese and Soviet whalers between 1949-1980, Ivashin (1983) concluded that there were western and eastern migration routes for both sexes in the North Pacific, but believed that it was not possible to define a border between them. He did not consider there to be mixing of males from the American and Asiatic regions in the Bering Sea but rather that this was a feeding area for the western males. The single mark recovery between the American region and the Bering Sea was from a female, although it is thought that they rarely enter this area.

Other authors proposed a third, central stock based on a number of differences among the three regions. Tillman (1977) defined Asian and American stocks near their respective coasts with the bulk of the North Pacific animals belonging to a central stock. His comparison of CPUE trends over the 1949-75 period is problematic as he found that on occasions the Japanese and Soviet data revealed differing trends (this may be explained by the falsification of the Soviet data); interpretation of such data can be confounded by possible shifts in whaling interest unrelated to sperm whale abundance. His analysis suggested that central male and Asian female stocks thus defined showed some decline (the others did not). He also recognised the importance of stock identity assumptions to such analyses and recommended further effort towards better stock delineation.

Based on an essentially qualitative review of the incidence of certain morphological characters, Berzin and Veinger (1981) suggested three (western, central and eastern) 'populations'. The most notable differences were between eastern and western regions with the central region being sometimes more like the west and sometimes more like the east. The lack of: (1) statistical analyses; (2) separation of the data by sex; and (3) consideration of sperm whale social groupings, renders their findings questionable. In an analysis of fluke notch morphology between the three proposed regions, Veinger (1980) had in fact suggested that unequal harvesting of sperm whale groupings could account for within region between-year differences but had failed to consider this for between-region comparisons.

In addition to these much-debated longitudinal divisions, there is also evidence for latitudinal separation, at least within the western portion of the North Pacific. Kasuya and Miyashita (1988) found a gap in female distribution between 30° and 40°N in this region and proposed two latitudinally segregating female stocks in the west and a single stock in the east. Support for a similar division for males came from 20 adult male mark recoveries that had suggested Bering Sea, Kuril Islands/coastal Japan and eastern North Pacific segregation. Their stock boundaries varied with season and oceanographic conditions. Despite considerable overlap, especially between male and female stock boundaries, they believed that interbreeding between stocks was rare. Further evidence for latitudinal stock separation in the west comes from discontinuities in distribution and CPUE from historical whaling records (Bannister and Mitchell, 1980), differences in morphologies (Machin, 1974) between Japan and the Bonin Islands and the possibility of blood type differences between coastal Japan and the Aleutian Islands (Fujino, 1963).

The most recent genetic analyses found no significant differences between areas of the North Pacific in the mtDNA control region or microsatellites of sperm whales once social structure had been accounted for (Lyrholm and Gyllensten, 1998; Lyrholm *et al.*, 1999). Failure to consider this important feature of sperm whale biology casts doubt on many of the results of earlier studies.

### *South Pacific*

Much less information exists for the southern portion of the Pacific. There is some evidence for stock separation from catch and sightings data (Gaskin, 1973; Berzin, 1978), mark-recaptures (Brown, 1981; Ivashin, 1981; Dufault and Whitehead, 1995) and vocal repertoire comparisons (Weilgart and Whitehead, 1997). However the available morphological (Clarke *et al.*, 1968; Clarke and Paliza, 1972; Machin, 1974) and genetic (Dillon, 1996) information does not suggest stock separation.

Gaskin (1973), examined sighting and catch distributions of almost 10,000 individuals from the western South Pacific. From this he believed that it was possible to define two separate management stocks off New Zealand, one to the west and north from the Tasman Sea to the Fiji-Tonga region, varying with the season, and a second to the east off the Chatham Islands, with an eastern limit to both stocks of 170-150°W. However, he also believed that interchange of males and some intermingling of breeding schools north of New Zealand would maintain genetic homogeneity between the two stocks. The limited number of mark recoveries from this area do not contradict his ideas (Brown, 1981; Ivashin, 1981).

In the eastern South Pacific, mark-recapture of photo-identified individuals suggests geographic distinctiveness between stocks of female and immature sperm whales north and south of about 10°S and between equatorial stocks off the Galápagos Islands and mainland Ecuador, although a limited amount of movement has been observed between these latter two areas (Dufault and Whitehead, 1995). This supports the work of Berzin (1978) who proposed a separate Galápagos population between 10°N and 10°S based on sightings distributions. In contrast, intensive and extensive morphological investigations, some involving the examination of over 2,000 individuals, found no differences between sperm whales caught off Peru (at Paita and Pisco) and those caught off Chile (at Iquique and Talcahuano) along the western coast of South America from the equator to about 40°S (Clarke *et al.*, 1968; Clarke and Paliza, 1972; Machin, 1974).

On a broad basis within this ocean, mark-recapture suggests little or no movement of female and immature stocks between western and eastern regions (Dufault and Whitehead, 1995). Stock distinction within the South Pacific is supported by significant differences in the vocal repertoires of groups of females and immatures from western, eastern equatorial (north of 10°S), and southeastern (south of 10°S) areas of this ocean (Weilgart and Whitehead, 1997). No broad regional distinctions were detected from either genetic or morphological analyses. In a comparison of mtDNA haplotype distribution of female and immature sperm whales from these same three areas, all of the variation could be accounted for by differences within and between social groups (Dillon, 1996). No geographic differences in fluke notch morphology throughout the South Pacific were found except those which could be explained by differences between social groups (Dufault and Whitehead, 1998). In a synthesis of data collected on vocalisations, genetics and fluke markings from a survey of sperm whales of the South Pacific (Whitehead *et al.*, 1998), social grouping was found to be the strongest determinant of variation in all these attributes. Except for some between-area differences in vocal repertoires, no geographic structure was apparent.

### *North Atlantic*

In the absence of any large-scale harvesting of sperm whales in this ocean, there have been few attempts to examine their stock structure. Best (1975) reviewed the published sighting information from merchant and whale-marking vessels in this region. He concluded that there are concentrations on either side of the North Atlantic with a connecting band between 30° and 60°N. From this limited information he suggested that the sperm whales in this ocean should be considered as a single stock for management purposes.

Aguilar (1985) examined data on movements in this Ocean. He included published reports on the recovery of an Azorean hand harpoon in a male sperm whale caught off Iceland (Martin, 1982) and the recovery of one Discovery-type mark from Nova Scotia in a male caught by a Spanish shore station (Mitchell, 1975). He presented a further incident of the recovery of an Azorean hand harpoon, this time off Spain, and concluded that all of the available evidence suggested a single North Atlantic stock. Aguilar and Sanpera (1982) found a decreasing trend in the average lengths of males caught by both Spain and Iceland though they caution that this does not mean that the catches came from the same stock since they have all followed the same history of exploitation. Holt (1980; unpub.) had examined the lengths of sperm whales caught in the Iceland, Azores and Madeira, Norway and Faroes fisheries to calculate mortality rates. Despite the limitations of such an approach, and particularly the lack of statistical power, the fact that the estimated rates were all similar does not contradict the hypothesis of a single North Atlantic stock.

The scale and scope of genetic analyses in this ocean are, as yet, insufficient to reach any conclusions on stock identity. Dillon's (1996) comparisons of mtDNA haplotype distributions included samples from the Caribbean, the southwestern North Atlantic, the Azores, the Canary Islands and off Nova Scotia but these five geographic areas were represented by only six social groups. Therefore, although there were different haplotypes in different areas, it is impossible to distinguish between group differences and area differences.

### *South Atlantic*

Best (1969b) examined sperm whale catch and sightings distributions in the South Atlantic. An apparent discontinuity in the central region led him to suggest that for management purposes separate stocks should be considered on the east coast of South America and the west coast of South Africa. However, he noted that mixing of males in the Antarctic and breeding schools in the central regions may make the two stocks genetically indistinguishable. There are little other data available for this region. The scant mark-recovery data mostly demonstrate long-distance latitudinal movement of both males and females up the western coast of South Africa (Brown, 1981; Ivashin, 1981) which does not contradict the idea of separate stocks. Interestingly though, Brown's (1981) data also show a movement from the Indian Ocean past the southern tip of South Africa to about 200km from the eastern coast of South America providing not only evidence of inter-ocean movement but of longitudinal movement across almost the entire width of the South Atlantic.

### *Indian*

Bannister (1974) examined aerial sightings survey data and two mark recoveries for the eastern Indian Ocean and concluded that sperm whales off the western and southern coasts of Australia were part of the same stock. Subsequent mark-recovery data concur with this conclusion (Brown, 1981).

In the western region, Gambell (1972) used the CPUE of pelagic factory ships and two mark recoveries to propose that the stock of sperm whales fished off Durban, South Africa is of a local nature extending out to about 70°E. Best (1974) concurred with these two assessments but suggested an eastern limit to the east African stock of 60°E and proposed further that there is a central Indian Ocean stock between 60° and 90°E. Mark-recovery data agree reasonably well with these delineations although there exist instances of sperm whales crossing all of these proposed boundaries (Brown, 1981).

### *Antarctic*

Females and their young rarely travel south of 40°S and so only large males are found in Antarctic waters. It is thought that large males may intermingle on summer Antarctic 'feeding grounds'. The degree of mixing and the possibility of site fidelity are as yet unknown. Most mark recoveries in the Southern Ocean showed principally latitudinal movements, but twelve of 93 marks recovered up to 1979 showed movement across the boundaries of the nine IWC divisions, including one movement from the Indian to Atlantic Ocean (Brown, 1981). Thus, the potential exists for intermingling in the Antarctic of individuals from the three oceanic regions.

Cushing *et al.* (1963) suggested the possibility that individuals in Divisions III and IV of the Indian Ocean region of the Antarctic may be of different stocks, based on their respective frequencies of each of four blood sub-types. Their assessment, however, was based on only 17 samples (12 of which were from Division III) making it impossible to draw any firm conclusions.

Dailey and Vogelbein (1991) found some evidence that helminth species of the genus *Corynosoma* may be unique to the Atlantic, Pacific and Indian Ocean regions of the Antarctic. In this study, two ($n = 35$) individuals from the Pacific area were infected with *C. bullosum*, 18 ($n$ = unspecified) from the Indian Ocean were infected with *C. mirabilis* and a single individual ($n$ = unspecified) from the Atlantic region was infected with *C. singularis*. There was no co-occurrence of more than one of these species in the same ocean area. Although such data are inconclusive, they at least suggest the possibility of inter-ocean distinctiveness of these parasites. Of these three species, Berzin (1972) referred only to *C. mirabilis*, noting it occurred primarily in the Indian Ocean and describing its distribution as Divisions III, IV and V of the Antarctic (i.e. from 0° east to 170°W) which includes portions of the eastern South Atlantic and western South Pacific. Although sample sizes are small, making any conclusions tenuous, the results are interesting, particularly given the absence of any geographic specificity of external parasites.

## Between-ocean comparisons

It has been generally assumed that sperm whale stocks in different oceans (and in different Hemispheres within the Atlantic and Pacific Oceans) are discrete and mixing between oceans has been presumed to be extremely rare, if it occurs at all. However, in practice this is based on rather limited and inconclusive data (Table 1). The major evidence for distinctiveness between the three major oceans comes from the almost complete lack of inter-ocean mark recoveries (Best, 1969b; Brown, 1981; Ivashin, 1981). Other supporting evidence includes the internal parasite information discussed above (Dailey and Vogelbein, 1991); and the analysis of coda vocalisations (for the Atlantic and the Pacific) in which groups of female and immature sperm whales from the South Pacific and Caribbean were found to have significantly different vocal repertoires (Weilgart and Whitehead, 1997). Best and Gambell (1968) cite some morphological evidence that sperm whales from the Atlantic coast of South Africa differ from those from the Indian Ocean coast (the former generally have a higher incidence of light markings) but the authors noted that observer differences could explain the apparent dissimilarities.

Evidence to support the view that limited intermingling can occur between oceans is also provided from marking data. Movement between the North and South Atlantic has been shown by two males travelling distances of approximately 4,000 and 7,400km (Ivashin, 1981). The same author reported that a single female was found to have moved between the North and South Pacific (2°52'N,

Table 1

Summary of types of evidence that have been considered to either support or contradict the hypothesis that mixing between sperm whales from different oceans does not occur. Note that none of this evidence can be regarded as unequivocal.

| For | Against |
|---|---|
| (1) almost all marking data | (1) 4 mark returns |
| (2) internal parasites | (2) external parasites |
| (3) morphology | (3) morphology |
| (4) growth coefficients | (4) growth coefficients |
| (5) vocalisations | (5) nuclear genetics |
| (6) mtDNA genetics | (6) mtDNA genetics |

94°55'W to 4°40'S, 82°50'W), a distance of about 1,580km. A sperm whale of unidentified sex (the mark was recovered during the processing rather than the flensing procedure) was found to have moved from the South Indian to the South Atlantic Ocean around the southernmost point of Africa (Brown, 1981).

External parasite fauna seems not to differ worldwide. Cyamids of the species *Neocyamus physeteris* have been found infesting sperm whales of the North (Buzeta, 1963) and South Atlantic (Best, 1969a) as well as the North and South Pacific (Buzeta, 1963). *Cyamus catodonti* have been found on sperm whales from the North Atlantic and North Pacific (Buzeta, 1963) and also from the Pacific, Atlantic and Indian Ocean sectors of the Antarctic (Best, 1979). The other two species of cyamid described for sperm whales come from single whales in the Indian (*C. boopis*) and South Pacific (*C. bahamondei*) Oceans. The former was thought to be specific to humpback whales on which they have been found on many occasions and in many different regions and this occurrence on a sperm whale is thought to be exceptional (Buzeta, 1963). Data on other external parasites are scarce, but there do not appear to be any clear distinctions between oceans in either copepod, barnacle or diatom infestations (see Berzin, 1972).

Morphological comparisons have revealed little differences between sperm whales worldwide. Best and Gambell's (1968) examination of colour patterns, tooth eruption, number of mandibular teeth, number of dorsal humps, incidence of deformed mandibles and incidence of double teeth, led them to conclude that 'sperm whales throughout the world are remarkably similar in their external characters'. In a similar study of external characters, Clarke *et al.* (1968), found no evidence indicating that sperm whales from different oceans are in general different in the traits, but noted that more data were needed.

Analysis of growth coefficients (i.e. rates of growth of certain parts of the body relative to growth in body length) has proved equivocal. Clarke and Paliza (1972) compared growth coefficients (for a number of measurements for five regions of the body: head, trunk, flippers, flukes and dorsal fin). With respect to adult males, the authors found that animals from South Georgia and in the pelagic Antarctic were similar to each other and different from those in the other areas considered (Japan and the Bonin Islands in the North Pacific; Durban, South Africa in the Indian Ocean; and Paita, Pisco and Iquique in the eastern South Pacific). They found no differences between these other regions for males or females. From this they hypothesised that sperm whales from the Atlantic (the only ocean not included in their analysis) may be so different from other oceans that the Atlantic component in the animals from South Georgia and the Antarctic made them look similar to one another and different from all the rest. Critical to their analyses were assumptions made concerning the maximum proportion of physically mature individuals in their samples and of constancy in the growth coefficient of each character through the entire growth phase of an individual beyond eight or nine metres. These assumptions are based mostly (for the former) or entirely (for the latter) on samples from lower latitudes. However, the length distributions of the South Georgia and Antarctic pelagic samples when compared to the other regions (fig. 1 of Clarke and Paliza, 1972), show, perhaps unsurprisingly, that samples from these high latitudes represent the biggest males in the population; extrapolation from these regions may not be appropriate; their result may simply reflect a distinction between the largest, mature males and younger, smaller ones. Clearly, further samples from the Atlantic would be needed to confirm or refute this hypothesis.

Machin (1974) applied canonical analysis to Clarke and Paliza's (1972) data. Prior to a between-region comparison, Machin performed a principal components analysis on the measurements for individuals from each region to isolate those which were most informative. In his between-region analysis, however, insufficient data from some regions forced him to use only seven of the 27 possible measurements – and these seldom corresponded to those considered most informative. Unlike Clarke and Paliza (1972) he found three distinct female groups: Paita/Pisco/Iquique; South Africa; and Japan/Bonin Islands. However, sample sizes were small ( $<$ 10 for four out of six areas) so these conclusions should be treated with caution. In addition, as in many of the studies, no consideration was given to social groupings. Observed differences may reflect uneven sampling of groups if the growth coefficients were genetically determined. Machin's results were less clear for males, perhaps because the most-informative characters were better represented for females than males. A distinction was found between: South Georgia, South Africa, the Antarctic and the rest; Japan and the Bonin Islands; and between South Georgia/Antarctic and South Africa for the first three canonical variates respectively.

Neither Clarke and Paliza (1972) nor Machin (1974) provided features for practical distinction between individuals from different stocks. The former study found that males from South Georgia generally grew faster in the head region and slower between the dorsal fin and flukes than those at lower latitudes, whilst the latter found only overall differences in body proportions.

Three sequencing studies have examined oceanic differences in sperm whale DNA. Dillon (1996) and Lyrholm and Gyllensten (1998) both used control region sequences of mtDNA. These studies were similar in techniques used, sample sizes (182 *vs* 231 individuals) and geographic coverage (3 oceans each), and both considered social structure in their analyses, although Dillon sequenced more of the control region (600 *vs* 330 base pairs). However, whereas Dillon (1996) found no significant difference between oceans ($P = 0.56$ using nested analysis of molecular variance), the population differentiation found by Lyrholm and Gyllensten (1998) was highly significant ($P = 0.0007$ from an exact test). In contrast to their results with maternally-inherited mtDNA, Lyrholm *et al.* (1999) report negligible, and statistically insignificant, differences between sperm whales in different oceans using nuclear microsatellites, which are inherited from both parents. They conclude that movements between oceans have been more common among males than females.

## DISCUSSION

### General overview of distribution

Commercial whaling data have provided a great deal of information on sperm whale distribution (e.g. Townsend, 1935) but not stock identity. They show that sperm whales concentrated in certain areas (termed 'grounds' by whalers) of approximately 1,000km across that are often associated with oceanic islands or other areas where the depth drops quickly from the coast (Clarke, 1956). More recent studies have suggested that sperm whale concentrations are correlated with oceanographic features including high secondary productivity and steep underwater topography (Jaquet and Whitehead, 1996). Sperm whale stocks are commonly viewed as being of a local nature with most individuals remaining in or returning to the same grounds (Berzin, 1972; Gambell, 1972; Ivashin, 1983). However, some interchange is considered likely even between stocks which can be considered discrete for management purposes (Best, 1969b; Gaskin, 1973; Dufault and Whitehead, 1995).

It is generally thought that northern stocks of sperm whales do not interbreed to any large degree with southern ones, since female breeding cycles are six months out of phase (Best, 1974) and the socially mature males are only present with females during the respective breeding seasons. However, Clarke (1956) suggested that females moving between hemispheres could alter their breeding rhythm and Best *et al.* (1984) noted that spontaneous ovulations can occur outside a female's usual breeding cycle. In addition, the absence of evidence of seasonal cycles in spermatogenesis suggests that males travelling between hemispheres could breed with either northern or southern females. In summary, physiological data do not preclude genetic exchange between hemispheres.

Within the Northern Hemisphere, the Atlantic is largely separated from the Pacific by land rendering interchange between these two areas to be doubtful. In the Southern Hemisphere, it is unlikely that any but the largest males range far enough south to round the tip of South America (Rice, 1989) and thus the Atlantic and Pacific can be for the most part considered geographically isolated. Movement has been observed between the Indian and Atlantic Oceans around the southern point of Africa (Brown, 1981) and interchange may also be feasible between the Indian and Pacific Oceans (Clarke and Paliza, 1972; Rice, 1989) although there is, as yet, no proof that this occurs.

Marking data have revealed lengthy latitudinal movements by large males (Best, 1969b) as well as some extensive longitudinal movements within (Ohsumi and Masaki, 1975; Aguilar, 1985) and between (Brown, 1981) ocean basins. Thus, the potential exists for some genetic exchange over large geographic scales. However, the fact that the vast majority of mark-recaptures have been within the same ocean basin and usually within the same whaling ground suggests that such large-scale movements are rare.

### Temporal scales of stock structure measures

The different methods of examining sperm whale stock structure provide insights on different timescales. Catch and sightings survey data, for example, provide a single data point within the lifetime of an individual. Particularly where effort covers a wide area and a long time period, such data are useful for demonstrating general patterns of where and when sperm whales are likely to be found and may be related to the suitability of the habitat. However, discontinuities in distribution do not necessitate complete segregation and such studies are unable to provide information on movements between concentrations of animals. For example, photo-identification data have shown that groups of females and immature sperm whales can travel distances of 40-55km within a 12 hour period during times of presumed low feeding success (Whitehead, 1996); they could thus travel between areas of preferred habitat separated by 1,000km or so in roughly 10-20 days. Male movements are likely in the same order of magnitude; three males in the Southern Hemisphere travelled 55-250km during three days between marking and recapture (Ivashin, 1981).

Discovery-type marking programmes can provide direct evidence of movements in that they provide information on the location of individual animals on two separate occasions. Recoveries have generally been made within 10 years of marking and, thus, give a medium timescale view of movements on the order of a single generation or less. Studies using mark-recapture of photo-identified individuals clearly have the advantage that they can generate multiple sightings of a single individual. To date, these studies are also based on medium timescales of 10 years or so. When sperm whale stock structure is examined over temporal scales of this magnitude, it is clear that stock delineation may not be a simple matter of drawing lines between concentrations of animals. Many exceptions to the general pattern of distribution begin to emerge, including not only short-distance (1,000km) movements between concentrations of animals, but also long-distance movements across and between ocean basins.

Studies of genetics, or of traits which are presumed to be genetically determined, present a perspective over the timescale of generations. When sperm whale stock structure is examined over this scale, few distinctions are evident. This implies that, on the timescale of generations, there may be enough mixing to make individual stocks indistinguishable. A single individual moving between populations per generation would be sufficient to prevent complete genetic differentiation between these populations (Slatkin, 1987). However, movement would necessarily have to be greater than this in order to prevent any detectable differences. That few obvious differences have so far been found in the genetics and morphologies of sperm whales worldwide implies that inter-oceanic movements may occur more frequently than has thus been detected, perhaps on the order of a few individuals every generation or so. Discrepancies between studies using maternally inherited mtDNA and those using nuclear DNA (contributed by both parents) suggest these movements are more common for males.

## CONCLUSIONS

In summary, it seems that groups of female and immature sperm whales are usually restricted to ranges of about 1,000km over periods of a decade or so. Sometimes, they will move much further. Male ranges are, in general, larger, especially latitudinally. Long-distance movements across and, occasionally, between ocean basins have resulted in remarkable genetic and morphological uniformity in sperm whales worldwide, especially in biparentally-inherited genes.

To effectively manage and conserve sperm whale populations, information is needed on the likely geographical extent of the effects of local perturbations, be they caused by direct exploitation, anthropogenic environmental change or extreme natural events, such as El Niño. This requires knowledge of movement patterns over a variety of timescales, including not only the modal behaviour (normal geographical ranges over years, decades and lifetimes), but also the relatively uncommon long-distance movements which are vital in determining genetic structure and rates of recolonisation of depleted areas.

Such data could come from several sources. Satellite tags can give detailed movement patterns of individuals over periods of months (e.g. Mate, 1989; Dietz and Heide-Jørgensen, 1995), which could be particularly useful in tracing the breeding migrations of mature males, if sample sizes are sufficient. Photo-identification becomes especially valuable when a substantial portion of individuals from a given region is identified, as is now the case for the sperm whales off the Galápagos Islands (Whitehead *et al.*, 1997), and can be continued over long periods. For sperm whales, the logistics of wide-scale photo-identification are difficult due to their deep-water, cosmopolitan distribution, but a great deal of progress has been made and we may soon have useful information on movement patterns over periods of 10 years and more. Over longer timescales, the most useful information could potentially come from additional studies of highly variable genetic markers, such as microsatellites.

Once we have a reasonable picture of the modal and exceptional movement patterns of sperm whales over a range of timescales, we can begin to construct reasonably realistic population models. Such models could be based on traditional, or newly defined, stock boundaries, and include rates of interchange between stocks. Alternatively, basin-wide, geographically specific models incorporating the movement patterns of sperm whales could be constructed. As sperm whale movement patterns are related to feeding success (Jaquet, 1996; Whitehead, 1996), models incorporating density-dependent habitat selection (e.g. MacCall, 1990) may be particularly appropriate (Whitehead *et al.*, 1997).

In the absence of sufficient data to construct such models, knowledge of stock structure in sperm whales is constrained to be little better than anecdotal. This calls into question our ability either to manage any resumption of substantial sperm whaling, or to predict the population effects of a disturbance such as that caused by a large pollution event or epizootic. Alternative strategies that incorporate uncertainty in stock boundaries into a management procedure have yet to be explored in the case of sperm whales.

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