INDIVIDUAL PHOTOGRAPHIC IDENTIFICATION- A KEY TO THE SOCIAL ORGANIZATION OF SPERM WHALES

TOM ARNE ARNBOM

INDIVIDUAL PHOTOGRAPHIC IDENTIFICATION - A KEY TO THE SOCIAL ORGANIZATION OF SPERM WHALES

BY

© TOM ARNE ARNBOM, B.Sc.

A Thesis Submitted to the School of Graduate Studies in
Partial Fulfilment of Requirements for the Degree of
Master of Science

Departments of Biology and Psychology
Memorial University of Newfoundland
March, 1987

St. John's Newfoundland Canada

ISBN 0-315-36966-3

ABSTRACT

Sperm whales were tracked visually and acoustically in the waters west of the Galapagos between February and April 1985. A method for photographically identifying individual sperm whales is described. Measures of the photograph quality were compared with the certainty with which individuals were identified. A total of 210 females or immatures, 7 large adult males and 6 calves were recognized with certainty and individually identified. A simple model suggested that up to 9% of the females/immatures could not be identified using this method of photographic identification, despite high quality photographs. It was shown that these individuals have a lower number of unique marks on their flukes than the 210 identified females/immatures. The assumption of random sampling when taking photographs of individual sperm whales is discussed. The time and geographical positions of the re-sightings of known individuals suggest that the sperm whales preferred a rich upwelling area.

The identified females/immatures were clustered into 23 discrete groups. Thirteen of these groups contained more than six associated members. Observations of calves and the high frequency of dorsal fins with a callus suggested that the groups of sperm whales off the Galapagos fell into the category of "mixed groups". Whales recorded as escorting a calf were most probably females. Different females/immatures were observed to escort the same calf, and identified females/immatures were observed with several different calves.

Large males were observed either as singles, pairs or a set of three. In the observations of identified individuals there was no indication that particular pairs of large males, or large males of a similar size, were preferred companions. No fresh wounds or agonistic behaviour between large males was observed. The lack of sightings of medium-sized males suggest that they do not take part in reproduction in this area. The proportion of large males to mature females suggests that all large males do not migrate to the breeding grounds and do not participate in breeding every year. Identified large males were observed with different mixed groups and, further, different large males were associated with

particular mixed groups. There was no indication that some mixed groups associated more with large males, than others. Large males seemed to follow a strategy of searching for mixed groups, instead of holding harems.

During an attack by killer whales on sperm whales a high degree of coordination of the sperm whales' behaviour was noted. Twenty-one percent of the sperm whale flukes had tooth mark scars of which a majority were probably derived from shark attacks. A difference in the number of unique marks on the flukes between different geographical areas suggests that the method of individual photographic identification relying on uniquely marked flukes may be less successful in other areas.

ACKNOWLEDGEMENTS

I thank Mel Brooks, Vassili Papastavrou, Linda Weilgart and Hal Whitehead for their parts in the research at sea, and Dr. Günter Reck, Dr. Mario Hurtado and the other staff members at the Estacion Cientifica Charles Darwin. Also, I would like to thank Captains Galo Davila and Mario Pinto of INOCAR and Miguel Cifuentes of the Galapagos National Park Services for assistance with the study in the Galapagos. I especially thank my supervisor Dr. Hal Whitehead for his helpful ideas and his faith in my ability as a graduate student. I appreciate the constructive discussions with J. Gordon (Deptartment of Zoology, University of Cambridge, U.K.) and Drs. J. Lien and D. Renouf (Department of Psychology, Memorial University of Newfoundland). Fleming Mengel 's (Department of Earth Sciences, M.U.N.) and J. Lawson's help with figures and computing were greatly appreciated. I also wish to thank my examiners, Drs. W. Montevecchi and S. Katona. World Wildlife Found-Neatherlands, David Day and Dieter Plage kindly loaned us vital equipment. The following companies donated equipment or provided minimally priced equipment used for this study; Canon Ltd, Expert Foto, Fjällräven Ltd and Helly-Hansen Ltd. The field research was funded by M. Clark, F.C.P. Whitehead, D. Plage, the O. Engkvist Foundation, the Green Island Foundation, the Connecticut Cetacean Society, and the Center for Studies of Whales and Dolphins. Analysis was supported by the O. Engkvist Foundation and Memorial University. I appreciate the generous student loans I received from the Swedish Government and the scholarship from the Swedish-American Foundation which made it possible for me to complete my studies in Newfoundland. The Swedish Ministry of Agriculture made funds available for me to attend and present parts of my study at the 1986 scientific meeting of the International Whaling Commission. I finally thank Drs. F.A. Aldrich and J. Strawbridge (School of Graduate Studies and Department of Psychology, Memorial University of Newfoundland) for their invaluable support in the form of a bursary and other financial assistance during my studies at Memorial University of Newfoundland.

THE TAIL

The compact round body of its root expands into two broad, firm, flat palms or flukes, gradually shoaling away to less than an inch in thickness. At the crotch or junction, these flukes slightly overlap then sideways recede from each other like wings, leaving a wide vacancy between. In no living thing are the lines of beauty more exquisitely defined than in the crescentic boarders of these flukes.

The more I consider this mighty tail, the more do I deplore my inability to express it. At times there are gestures in it, which, though they would well grace the hand of a man, remain wholly inexplicable. In an extensive herd, so remarkable, occasionally, are these mystic gestures, that I have heard hunters who have declared them akin to Free-Mason sign and symbols; that the whale, indeed, by these methods intelligently conversed with the world.

HERMAN MELVILLE
Moby-Dick

TABLE OF CONTENTS

List of Tables

List of Figures

Chapter 1
INTRODUCTION

During the last two centuries more than 1,300,000 sperm whales have been caught by whalers around the world. Despite this large catch, our knowledge of sperm whale biology is still incomplete (Best, Canham and Macleod, 1984). Descriptions of the social behaviour of the sperm whale are almost exclusively anecdotal (e.g. Caldwell, Caldwell and Rice, 1966). Despite recent improvements in our knowledge of sperm whale social organization, it should be stressed that nearly all the observation made so far have been based on examination of whole schools of whales (or members from them) at one moment of time (normally after death), and such synoptic observations provide very little information on inter- and intraschool relationships (Best, 1979). Sperm whale social behaviour is of special interest to the members of the Scientific Committee of the International Whaling Commission (IWC) because of its implications for management of the species (Gordon, 1986). Two issues are of special concern for management: the nature of the interactions between groups of female sperm whales and large males; and whether "medium-sized" males take part in breeding (IWC, 1983).

This thesis presents information on the social organization and behaviour of sperm whales using the method of individual photographic identification. Sperm whales were tracked from a small vessel, in the waters west of the Galapagos Islands in early 1985. The study provided a unique opportunity to compare systematic observations of live animals with anecdotal descriptions and conclusions based on whaling data. Photographs of flukes and dorsal fins made it possible to identify individual sperm whales. These individual identifications were used to investigate associations and interactions between individuals and groups of sperm whales.

1.1. USE OF NON-INTRUSIVE METHODS

During the past 20 years increasing numbers of studies of free-living whales have used the technique of individual photographic identification using natural marks and scars. This technique has widened our knowledge of the migrations, population biology and social behaviour of several cetacean populations including killer whales (Bigg, 1982); humpback whales *Megaptera novaeangliae* (Katona and Whitehead, 1981; Whitehead, 1982; Darling and Jurasz, 1983); minke whales *Balaenoptera acutorostrata* (Dorsey, 1983); right whales *Eubalaena australis* (Payne, Brazier, Dorsey, Perkins, Rowntree and Titus, 1983); and blue whales *Balaenoptera musculus* (Sears, 1984). Until recently, the emphasis for this work had been on species which spend at least some of their time close to shore. The sperm whale, which generally inhabits deep water, had attracted very little non-intrusive research, until the World Wildlife Fund Tulip Project began in 1982. This thesis develops and test the reliability of fluke photographs as a mean of individual identification of sperm whales.

1.2. ADOPTED TERMINOLOGY

The following terms have been adopted in this thesis (except where direct reference is made to the findings of other authors):

"Aggregation". A set of several groups.

"Association". Members from different groups were identified within 120 min of one another. Of the 120 min, 110 min correspond to twice the mode dive cycle (ie. dive period plus time spent at surface between dives; Whitehead, 1986c) and the remaining 10 min are allowed for the vessel to come within range for identification.

"Calf". A whale less than 6.1 m in length and one year of age (Best et al., 1984).

"Cluster". A term for either a single whale or a set of whales swimming in a coordinated manner, each less than 100 m from its nearest neighbour within the cluster.

"Encounter". A 5 min observation period.

"Escort". A whale swimming less than 1.5 m from a calf. A whale was only scored as an escort if confirmed from a photograph.

"Female". A mature female.

"Female/immature". A whale for which it is not known whether it is a mature female or a immature of either sex.

"Follower". A whale identified within the same encounter and cluster as a calf, with a maximum cluster size of 3 (excluding calves).

"Group". A set of whales which is presumed to be closed over periods of weeks.

"Immature". Either a female or male immature.

"Large male". Male more than 13.7 m long, presumed mature (Best, 1979).

"Lob-tail". Flukes lifted above the surface, and brought down flat onto the surface, often with great power (Whitehead, 1985).

"Mixed group". *Nursery* and *harem* schools are groups of females with their young and a large male present (*harem*) or not present (*nursery*). I will follow Best (1979) and refer to these as mixed groups.

"Non-intrusive". Not purposely killing, injuring or disturbing whales.

"Set". A general term for whales observed together.

"Side-fluke". The whale swims on its side and only a part of the fluke is above the surface.

1.3. THE SPERM WHALE

The sperm whale (*Physeter macrocephalus, Linnaeus 1758*) belongs to the order Cetacea. Two taxonomic names, *P. catodon* and *P. macrocephalus*, which both refer to the sperm whale, occur in the literature on the species. In general, *P. macrocephalus* was most widely used before the early 20th century, and *P. catodon* was favoured thereafter for some 60 years until about 10 years ago when *P. macrocephalus* was generally reinstated (Husson and Holthuis, 1974; Schevill, 1986).

The sperm whale (Figure 1-1), the largest odontocete, is more sexually

dimorphic than any other cetacean species (Best, 1979). Males reach a length of 18 m (Clarke, Aguayo and Paliza, 1968) and females 12.3 m (Clarke, 1956). Males may weigh up to 60 tons and females up to 15 tons (Lockyer, 1981). Sperm whales throughout the world are similar in their external characteristics (Best and Gambell, 1968; Clarke et al., 1968). The skin is more wrinkled than that of any other whale species and the colour varies from a dark bluish grey to iron grey (Matthews, 1938; Clarke, 1956). This variation may depend on the geographic location where the whales were caught by whalers, but may also arise from differences in environmental conditions within an area (Best and Gambell, 1968).

1.3.1. General life-history

In an unexploited population female sperm whales reach sexual maturity at approximately 9 years of age and a length of 8.5-9.5 m (Ohsumi, 1965; Best, 1974). The gestation period is 14-16 months, estimated from mating and calving periods (Matthews, 1938; Ohsumi, 1965; Best, 1968; Gambell, 1972), and 18.9 months when estimated from neonatal and adult brain weight (Best et al., 1984).

At birth the calves are approximately 4.0 m long (Clarke et al., 1968; Best et al., 1984) and after a year the calves have grown to 6.1 m (Best et al., 1984). There is no difference in length between the sexes at this age (Ohsumi, 1965; Best et al., 1984).

The lactation period is normally 24-25 months (Ohsumi, 1965; Best, 1974) and lactating calves will eat solid food before one year of age (Best et al., 1984). There is one record of a male having milk in its stomach at an age of 13 years (Best et al., 1984). Females older than 20 years have a more prolonged lactation period than younger females (Best et al., 1984).

The resting period between lactation and conception is usually 8-10 months long (Best, 1974) although it may be prolonged up to 5 years (Gambell, 1972). The calving interval is every 5-6 years which is one of the lowest birthrates (6%) observed in mammals (Best, 1979). Ohsumi (1965) concluded that females are commonly reproductively active for 15-20 years which agrees with Best et al. (1984) who stated that females give birth to 4 calves in their lifetime.

Figure 1-1: Photograph of breaching sperm whale, *Physeter macrocephalus*

Males reach puberty at an age of 9-10 years and a length of about 9.5 m (Nishiwaki, Ohsumi, and Maeda, 1963; Berzin, 1971; Best, 1974). Only 2.5% of males 10.7-11.6 m long and 13-16 years of age are mature, 14% of those 12.2-13.7 m long and 15-29 years of age are mature, while 75% of the males larger than 13.7 m are mature (Best, 1979).

An inflection point in the male growth curve occurs at about 19-20 years of age (Best, 1970; Gaskin and Cawthorn, 1973) which is about the time when males are maturing (Ohsumi, 1966; Gaskin and Cawthorn, 1973; Best, 1979). Around a length of 14 m heavy scars have been observed on the heads of males from fights with other males (Kato, 1984). Best (1979) divides the males into three size classes; small bachelors (10.7-11.9 m), medium-sized bachelors (12.0-13.7 m) and large bachelors (larger than 13.7 m).

1.3.2. Schooling behaviour

The sperm whale may have a more complex school structure than any other large whale (Mitchell, 1977). Ohsumi (1971) proposed a form of matriarchal organization. The eighteenth and nineteenth century open-boat whalers were aware that the different kinds of sperm whale schools segregated by sex and age (e.g. Beale, 1839). Clarke (1956) noted that males were either solitary or in schools while females were invariably gregarious. Males within a school tend to occupy a restricted size range with a difference of 1.8 m or less in length between the smallest and largest whales (Best, 1979). He also found ages (2.0-19.8 years range) to be more variable than length within the school, which suggests that male groups are actually more homogenous by size than by age (Best, 1979).

From modern whaling data and observations at sea, sperm whale schools have been divided into different discrete school types depending on size and sex: mixed (harem and nursery), juvenile, small bachelor, medium-sized and large adult bachelor schools (Gaskin, 1970; Ohsumi, 1971; Best, 1979). However, these proposals are not well documented with well studied groups of known individuals.

Mixed groups

The mixed group appears to be a discrete school when sighted (Best, 1979).

Caldwell et al. (1966) found tight schooling behaviour of individual mixed groups to be quite characteristic. The mean number of whales in the mixed group has been given as 28 (Best, 1979), 27.1 (Ohsumi, 1971) or 21.7-22.9 (Gambell, 1972). The proportion of females within the mixed group is estimated to be 0.78 (Best, 1979); the rest are male immatures and calves. The proportion of mature females to total females in the mixed groups is about 0.75. Within a mixed group at any time, females were found in all stages of reproduction: pregnant, lactating and resting (Best, 1979). There are several accounts of long-term 'relationships' between females. On four different occasions, two females were marked by Japanese researchers and later recaptured together after time spans of 5, 8, 10 and 10 years, respectively (Ohsumi, 1971).

Juvenile groups

Best (1979) calculated the proportion of juvenile females and males observed in mixed groups and concluded that a large percentage of the juvenile females and males in the population were not present in the mixed groups, and therefore it seemed likely that both sexes may form juvenile groups. There are few catch data from these groups due to restrictions on catching whales less than 10.6 m long.

Small bachelor groups

The small bachelor groups contain 10-50 animals (Best, 1979). Males are normally 10.7-11.9 m long. Males seem to leave the mixed groups to form small bachelor groups at 10.7 m long and at an age of 15 years but they may depart as early as 4-5 years of age (Best, 1979).

Medium-sized bachelor groups

The normal number of whales in a medium-sized bachelor group is 3-15 individuals (Gaskin, 1970; Best, 1979). The medium-sized males originate from small bachelor groups. The length of the males in these groups is between 12.0-13.7 m (Best, 1979).

Large bachelor groups

Large bachelor groups contain 1-5 members (Best, 1979). These males are more than 13.7 m long and are presumed to be breeding males who join the mixed

schools during the breeding season (Best et al., 1984), although Rice (in Caldwell et al., 1966) suggested that small bachelors which are found year around in the same area as mixed groups could also breed. However, Best (1979) noted that the low spermatozoa density in the semen fluid of small bachelors indicates that it is unlikely small bachelors are active breeders.

1.3.3. Distribution and feeding

The sperm whale has the most widespread distribution of all the cetaceans (Tormosov, 1977). It is found from the tropics to the polar regions in all the oceans and is most abundant in productive waters, such as where currents meet (Bennet, 1840). According to Townsend (1935) the distribution of the sperm whale is determined by two major factors: food and reproductive needs. Sperm whales feed mainly on meso- and bathypelagic cephalopods (Best, 1979) but also on fish (Matthews, 1938). Alien objects such as stones, coconuts and glass buoys, have also been found in stomachs (Nemoto and Nasu, 1963). Clarke (1980) showed that the size of a sperm whale was correlated with size of its cephalopod prey. Stomachs from large males contained larger cephalopods than those from smaller females (Clarke, 1980). This may be attributed to different diving abilities, efficiency of catching cephalopods, spatial distribution of the whales, or a combination of these factors (Best, 1979). Early whalers were well aware of the diving ability of sperm whales (eg. Beale, 1839; Bennet, 1840). Harpooned large males sometimes hauled out 1,500 m line in a presumed vertical dive, while females and smaller whales hauled out less line (Beale, 1839). Heezen (1957) mentions ten accounts of sperm whales found entangled in deep sea cables, the deepest observation being 1,116 m.

Mixed and small bachelor groups have generally been found between 50 °N and 40 °S, especially in the tropical and subtropical waters (Figure 1-2). There are several records of female sperm whales which were marked and then recaptured in the same area within the time-span of one or several years (Best, 1979). This indicates that they may use the same migration routes in successive years (Best, 1979). Berzin (1971) speculated that females may use the same wintering grounds

but during the summer a wider area may be visited. Gordon (1986) presented data from Sri Lanka which showed that the same individually identified mixed group was re-identified within a few km from the location in which it had been observed a year earlier. Small bachelor and juvenile groups have a similar distribution to mixed groups. The medium-sized bachelors are observed in waters from the tropics to latitudes of 40-50°. The large bachelors are found in tropical and polar regions: movements into the colder waters are probably mostly seasonal.

1.3.4. Migration

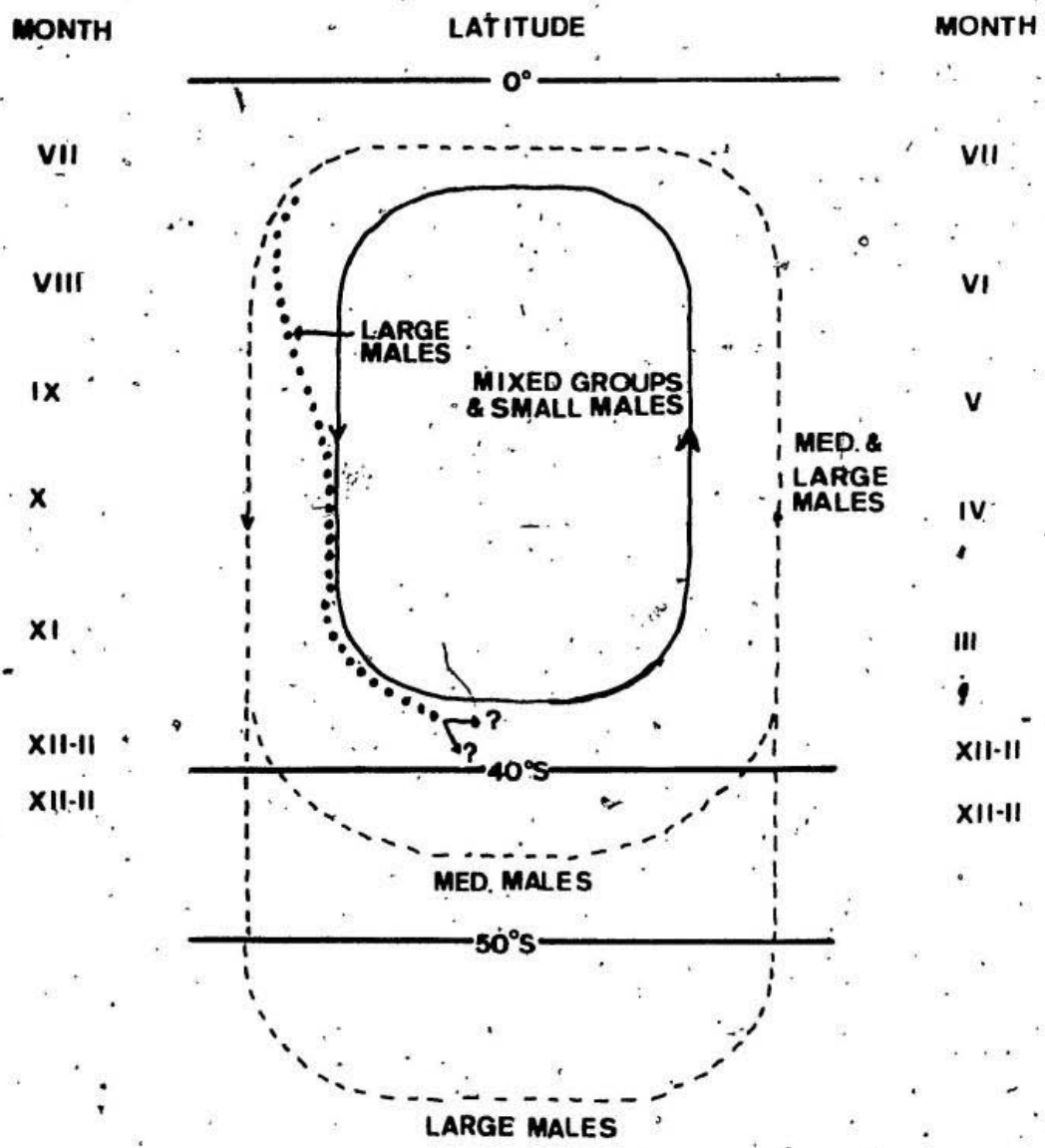
Whaling data show a general migration of mixed groups towards higher latitudes during summer (Townsend, 1935). Smaller bachelor and juvenile groups are believed to have similar migrations to the mixed groups. Medium-sized bachelors enter the polar region in small numbers during the summer. Of the large bachelors, 75-90% are found in the polar regions during the summer and 10-25% are found in lower latitudes (Ohsumi, 1966; Best, 1974). Several large males are known to have migrated from the northern to southern Atlantic (Ivashin, 1981). There may also be migration in an west - east direction. A male was marked off Newfoundland and recaptured eight years later off Spain (Mitchell, 1975). There are different migration patterns in the northern and southern hemispheres, due to the seasonal difference of six months.

1.3.5. Care giving

First year calves have poor diving ability (Best et al., 1984). The calf, at the surface, seems to follow the adults at depth (Best et al., 1984; Gordon, 1986) and calves are often rejoined by adults surfacing close to them (Gordon, 1986). Gordon (1986) found that calves associated closely with several different adults within a group and that some adults associated with more than one calf. Calves associated with adult females as well as immature males (Gordon, 1986).

Caldwell and Caldwell's (1966) review of information on the epimeletic behaviour of sperm whales show that descriptions by nineteenth century whalers and more recent observations of biologists are remarkably similar. There are

Figure 1-2: Diagram of migrations of sperm whale groupings in relation to latitude and month of the year, southern hemisphere (from Best, 1979).


MONTH
LATITUDE
MONTH
0°
VII
VIII
IX
X
XI
XII-II
XII-II
LARGE MALES
MIXED GROUPS & SMALL MALES
MED. & LARGE MALES
?
?
40°S
MED. MALES
50°S
LARGE MALES
VII
VI
V
IV
III
XII-II
XII-II

numerous accounts of females standing by other injured females and calves. No observations exist of either mature or immature males helping other sperm whales. Nishiwaki (1962) observed 20-30 sperm whales surrounding a large harpooned whale by pointing their heads towards the large whale and thrashing their flukes on the outskirts. Best et al. (1984) describe killer whales (*Orcinus orca*) attacking sperm whales when several calves were present. The calves were surrounded by larger sperm whales who appeared to protect the calf from the killer whales.

An example of the tight bond between specific members of mixed groups occurs when they strand on shore (Robson and van Bree, 1971; Stephenson, 1975; Mate, 1985). Robson and van Bree (1971) described sperm whales stranding in small subgroups one after the other in New Zealand.

1.3.6. Natural predation

Bullen (1899) describes an attack of two killer whales and a swordfish (*Xiphius gladius*) on a large male sperm whale. A review by Perkins and Whitehead (1983) of accounts of swordfish and thresher sharks attacking whales suggested that the story may often not be literally true, even though swordfish swords have been found in whales (Jonsgard, 1963). None of these whales were seriously injured by the swords. This may be due to the fact that whales which have been lethally injured are not found. Examination of killer whale stomach contents has revealed remnants of sperm whales (Yukhov, Vinogradova and Medvedev, 1975). A movie was apparently made by Russian whalers showing a killer whale attack on sperm whale females and calves (Yukhov et al., 1975). However, there is no description of the attack itself. Best et al. (1984) examined stranded and net-entangled sperm whale calves along the South African coast and found that several of the calves had severe injuries due to killer whales. Sperm whales taken by Russian whalers had tooth mark scars from killer whales, and these marks were most frequently found on pectoral and caudal fins (Shevchenko, 1975). Remains of sperm whales in killer whale stomachs were more often found in tropical and subtropical waters (Yukhov et al., 1975). During an attack observed

off South Africa, killer whales were seen swimming around a sperm whale school (Best et al., 1984). Sharks have been noted to follow schools of sperm whales (Gambell, 1968; Best et al., 1984).

1.4. WHALING OFF THE GALAPAGOS AND ADJACENT WATERS

Captain Colnett who visited the Galapagos Islands in 1793, mentioned the vast number of sperm whales and the potential for supporting future sperm whale fisheries (Colnett, 1798). Other whaling literature also cites the Galapagos as a sperm whale ground (e.g. Beale, 1839; Bennet, 1840; Melville, 1851). A study of nineteenth centuary logbooks from the open-boat whaling west off the Galapagos Islands showed a steady decline in the average weight of the whales caught and the number of whales observed, which was attributed to whaling pressure (Shuster, 1983). No reported whaling has been conducted during the last century off the Galapagos Islands. However, an intense fishery for sperm whales has been going on for several decades off the west coast of South America (Clarke, Aguayo and Paliza, 1980). It is not known if the sperm whales off Galapagos belong to the northern or southern hemisphere stock or whether it is a separate stock (Rice, 1975). There is evidence that the stock exploited off Peru has diminished since 1959-61, and it has been shown that the proportion of males of breeding status in the catch has declined from 36% in 1959-61 to about 11% in 1975-77 (Clarke et al., 1980). It was also concluded that the decline in pregnancy rate of whales killed off Peru, between 1959-61 and 1975-77, was due to insufficient large males (Clarke et al., 1980).

Chapter 2
METHODS AND MATERIALS

2.1. STUDY AREA

Using a small sloop, a total of 716 h were spent in visual or acoustic contact with aggregations of sperm whales in the waters west of the Galapagos Islands (1°00'S; 91°00'W) between February 23 - April 20 1985. This is thought to be the height of the breeding season for North Pacific sperm whales (Ohsumi, 1965; Berzin, 1971) and the time of the year that the weather should be predictably calm (Houvenaghel, 1978). The latter was a major consideration in the choice of the study area and time. Off the Galapagos, large male sperm whales and groups of females, had been observed (Colnett, 1798; Clarke, 1962; Schuster, 1983). The Galapagos Islands were also considered to be calving grounds (Colnett, 1798; Melville, 1854).

The Galapagos are volcanic islands that rise from a seafloor 2,000 - 3,500 m deep and that are situated on the Equator 965 km west of mainland Ecuador (Figure 2-1). The highest volcano rises 1,677 m above sea level. West of the islands the shelfbreak is very steep, falling from the coast to 1,500 m depth within 1 km from land. The study was conducted 1 - 175 km west and southwest of Isabela Island, 0°25'S; 91°05'W (Figure 2-2). West of Isabela, the Equatorial Undercurrent, a subsurface eastward flowing current, hits the shelfbreak. Thus a cold water upwelling is usually present west of Isabela Island (Houvenaghel, 1978).

The study was divided into four periods in 1985: 21-28 February, 5-16 March, 20 March - 3 April, and 8-23 April. Between periods the boat was re-supplied at Puerto Ayora on Santa Cruz Island (Figure 2-1).

Figure 2-1: Map of the Galapagos Islands. A dashed line indicates the 1000 m depth contour.

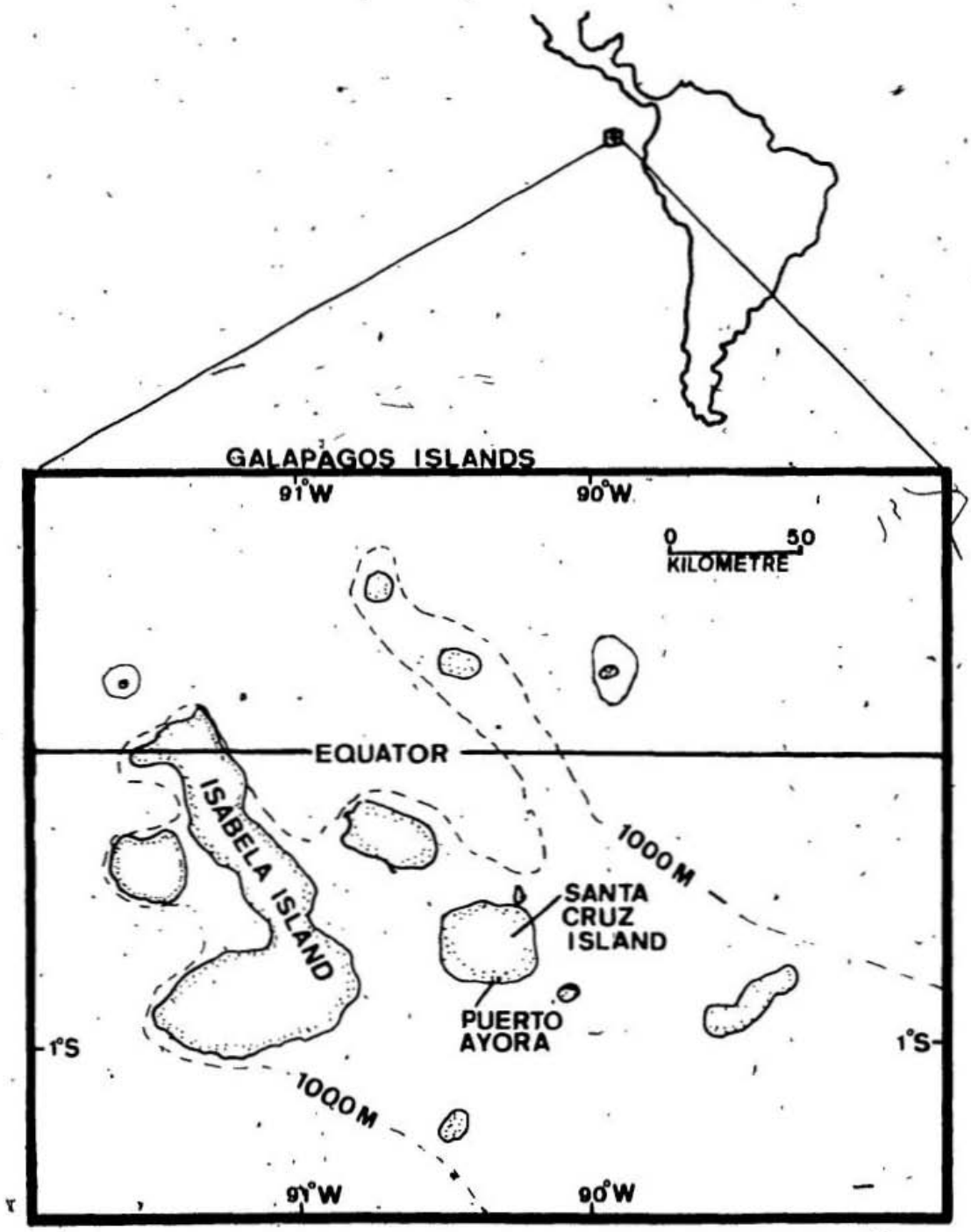
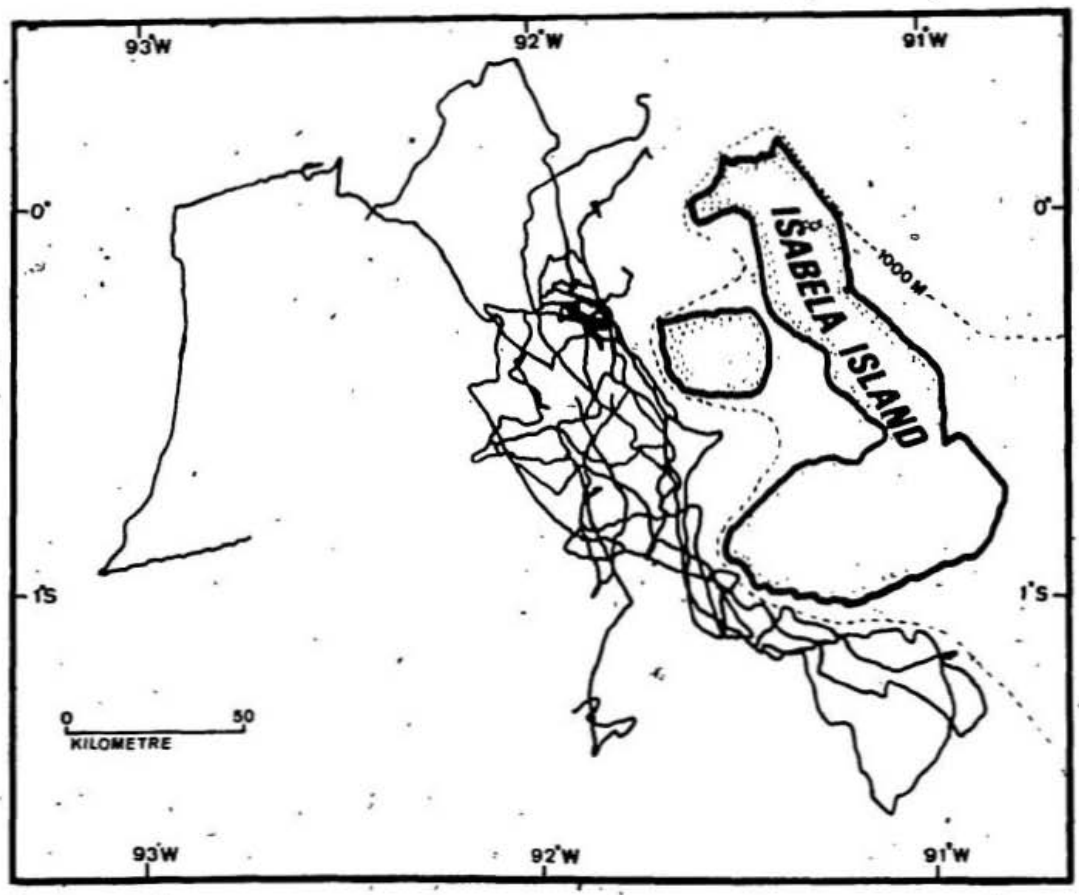

GALAPAGOS ISLANDS
91°W
90°W
0
50
KILOMETRE
EQUATOR
ISABELA ISLAND
1000 M
SANTA
CRUZ
ISLAND
PUERTO
AYORA
1°S
1°S
1000 M
91°W
90°W

Figure 2-2: Movements of the research vessel while tracking sperm whales off the Galapagos. A dashed line indicates the 1000 m depth contour.


93°W
92°W
91°W
0°
1°S
ISABELA ISLAND
1000 M
0
50
KILOMETRE

2.2. SHIP, CREW AND WATCHES

The study was carried out from the 10 m specially equipped sloop, the *Elendil*, of the Gladiateur class. The boat was manned with a crew of five who participated as scientists and sailors. *Elendil* is sufficiently small to be manoeuvrable and flexible enough to track sperm whales, yet large enough to provide a relatively stable platform from which to work. Engine noise made the sperm whales aware of the boat, but it did not seem to distress them (Arnbom, Papastavrou, Weilgart and Whitehead, in press).

Mast steps made it possible to climb up to the spreaders which were used as an observation platform with an eye height 9.2 m above sea level.

A continous record was kept of the ships' movements (Figure 2-2). Positions were given by Tracor Transtar Satellite Navigator, giving a fix, accurate to about 0.2 nautical miles (0.370 km) approximately every 2 h. In addition, compass bearings on landmarks and sun sights with a sextant were used for confirmation.

When following sperm whales during daylight the crew took 2-h shifts at four different locations, one steering, one taking notes, one observing and taking photographs while standing on the spreaders (a short range VHF walkie-talkie was used to report observations from the spreaders to the note-taker on deck), and one taking photographs from the bow. The fifth crew member either rested, cooked or helped one of the others. During the night each crew member took a 3-h watch, steering and tracking the whales. After sunset, all the data collected that day were checked.

2.3. TRACKING SPERM WHALES

Sperm whales were normally found in deeper waters (off the shelf), and the first 15 h after leaving Puerto Ayora were spent steaming towards deep water west of Isabela Island. When the boat reached the edge of the shelf, an omnidirectional hydrophone (Benthos AQ17) was lowered for 5 m every h, and monitored for the distinctive clicks of sperm whales (Backus and Schevill, 1966). The hydrophone was used in conjunction with a Barcus-Berry Standard Preamplifier. If light and visibility permitted, a "look-out" was kept from the deck and from the spreaders.

When sperm whales were heard on the hydrophone, a bearing (accurate to 15 degrees) was taken with a directional hydrophone (built by Dev-Tec Inc.), and the subjective acoustic intensity of the sperm whale clicks was noted (scale 0-5: silent to very loud). The estimated distance the hydrophone can pick up sperm whale clicks is 7.5 km. The boat was directed towards the sperm whale clicks at a speed of 7-10 km/h. Every 10-15 min a new bearing was taken according to where the sperm whale clicks were most intense. This procedure was continued until the sperm whales were seen, or at night, until sound intensity was 4-5, indicating that the whales were nearby (within approximately 500 m). Sperm whales were tracked acoustically and visually day and night until the whales were lost or left. Reasons for losing or leaving, the sperm whales included fuel shortage, engine failure and dolphin "jam" (the dolphin sounds masked out the sounds of the sperm whales).

2.4. PHOTOGRAPHS FOR INDIVIDUAL IDENTIFICATION

Whenever distance (usually less than 100 m) to whales and light conditions permitted, black and white photographs were taken of the flukes (Figure 2-3). Pictures were taken either when the flukes were raised in the air before preparing for a prolonged dive; or the whales lob-tailed or when whales side-fluked. The part of the whale which was photographed was noted together with the frame number on a film sheet. Photographs of the flukes were obtained by manoeuvring the boat as discreetly as possible behind the whales and staying there until the whales raised their flukes.

The dorsal fins were photographed when the whales were perpendicular to and less than 40 m from the boat (Figure 2-4). The photographer tried to photograph the dorsal fin of each visible whale successively, whenever possible.

The fluke and dorsal fin photographs used for individual identification were normally taken from the deck at the bow using one or more 35 mm cameras (Canon A-1, AE-1 and Ftb) and 300 mm telephoto lenses (Canon F-stop 4). During the study 154 rolls of black and white film of various lengths (20, 36 and 72 frames per roll) were used. To achieve good resolution, photographs for

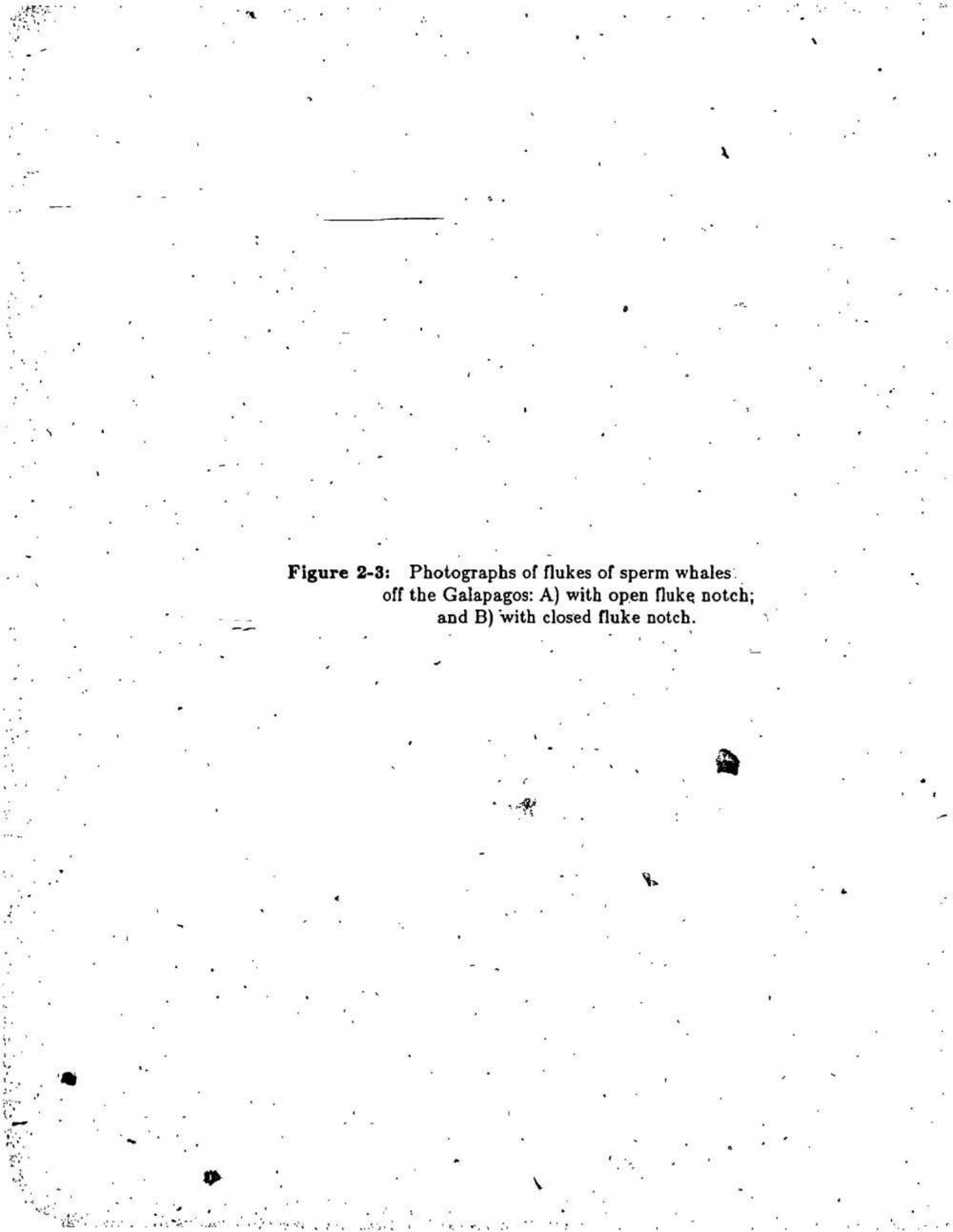
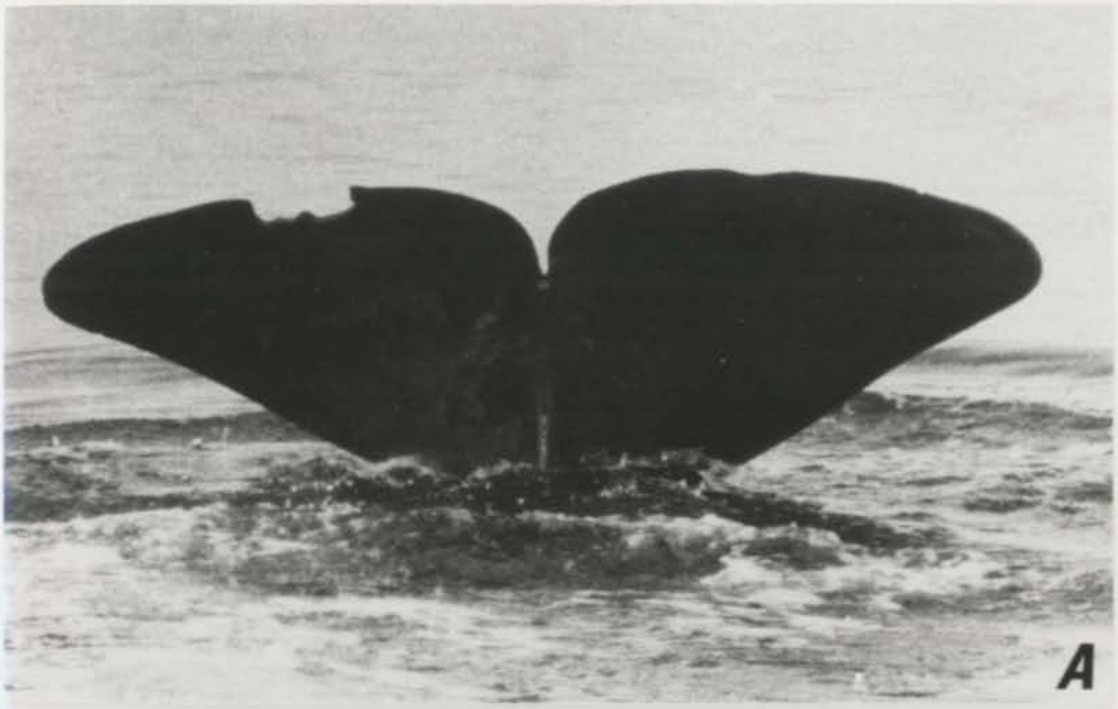
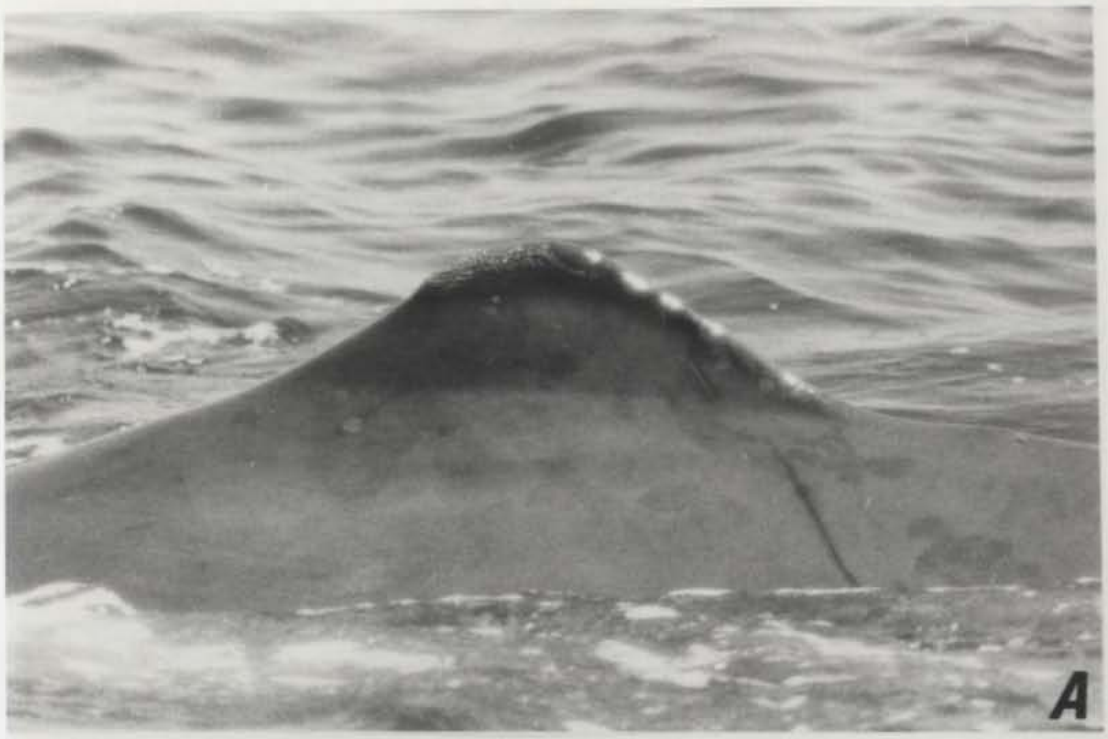


Figure 2-3: Photographs of flukes of sperm whales off the Galapagos: A) with open fluke notch; and B) with closed fluke notch.


A


B

Figure 2-4: Photographs of dorsal fins of sperm whales off the Galapagos: A) female/immature with a callus; B) large male without a callus.


A


B

individual identification were taken with a shutter speed of 1000/sec when light permitted.

Each film was individually marked with a number which was also recorded on a film sheet. For each photograph the following data were noted on the film sheet: frame number, time, part of whale photographed, number of whales within the photographed group, photographer, and for each film, ASA rating and brand of film (Ilford FP4 and HP5, Kodak Plus-X Pan, or Tri-X). To separate series of photographs, one or several "blanks" were taken as reference points on the film. A "blank" was normally a photograph of an identifiable object.

2.5. ANALYSIS OF THE PHOTOGRAPHS

2.5.1. Measures of fluke photographs

Measures of the photograph quality were taken to investigate how they affect individual identification of sperm whales. The exposed black and white films were developed and contact sheets were printed and marked with the film number. The negatives showing flukes were analysed under a dissecting microscope (WILD M7, Heerbrugg) with a magnification of 6-30 times. For each fluke negative, the following measures of photograph quality were noted: percentage of negative covered by flukes, focus, exposure, orientation and tilt of the fluke, and percentage of the fluke visible above the water surface. Full descriptions of the measures can be found in Table 2-1. Means of the photograph quality measures were plotted against the certainty value of an individual's identification (see section 2.6.1. for certainty value).

2.5.2. Shape of the fluke notch

Veinger (1980) stated that the shape of the fluke notch can be used to distinguish different populations of sperm whales. He divided the shape of the fluke notch into three types but he did not explain the different types. I divided the fluke notch into two types - open and closed (Figure 2-3). This was noted for each identified whale with a certainty value of 4 or 5 (section 2.6.1).

Table 2-1.

Description of photo quality measures (X1-X6).

X1	Focus;	the sharpness of the photograph. Each photograph was given a focus grade between one and five: 1. Very blurry; 2. Blurry but general outlines visible; 3. Reasonable but small nicks not visible; 4. Reasonable and small nicks visible; 5. Excellent, everything in focus, a very good picture.
X2	% of negative;	an estimate of the percentage area the individual fluke occupied relative to the total area of the negative. A semi-transparent measuring paper was used with different enclosed area-sizes (0.75, 1.56, 3.13, 6.25, 12.5, 25.0, 50.0 and 100%) drawn to scale which gave the percentage of the negative the fluke covered. Flukes covering less than 1% were estimated to the nearest 0.1%, more than 1% and less than 5% to 0.2%, and more than 5 % to the nearest 0.5%.
X3	Tilt;	the angle between the axis of the fluke and the water surface. When the fluke was perpendicular to the water surface, the tilt was 0 degrees. When the fluke was aligned with the water surface the tilt was 90 degrees.
X4	Exposure;	the relative darkness or lightness of the photograph. Exposure was divided into seven light conditions, with the very light photograph at +3, the normal at 0 and the very dark at -3. (Absolute value used in regression).
X5	Orientation;	the angle between the surface of the fluke and a plane perpendicular to the axis of the camera lens. When the ventral side of a fluke was perpendicular to the axis of the camera lens, the deviation was 0 degrees. When the fluke was aligned with the axis of the camera lens, the deviation was 90 degrees.
X6	% visible;	percentage of area of fluke photographed i.e. 100% when the whole fluke is visible.

2.5.3. Dorsal fins and calluses

Kasuya and Ohsumi (1966) have shown that 63% of the females and 30% of the immature males have a callus present and no large males have a callus. The callus is a deformity of the epidermis and thought to be regulated by hormones (Kasuya and Ohsumi, 1966). Negatives of dorsal fins were examined visually and it was noted whether a callus was either present, not present, or if its presence was uncertain (Figure 2-4).

2.6. CATALOGUING, MATCHING, AND INDIVIDUAL IDENTIFICATION

2.6.1. Unique marks and certainty value of flukes

Individual flukes varied from having smooth to rough edges. In extreme cases, large portions were missing. Marks used for individual identification of flukes were small and distinct nicks, waves, scallops, tooth mark scars, missing portions, holes, the general shape of flukes and the fluke notch and, in one case, growth of barnacles (Figure 2-5 and Table 2-2). Each photograph was given a certainty value (Q) of 0-5 with 0 representing non-identifiable, and 5 indicating absolute certainty of identification. An identified whale has the potential to be re-identified on a later occasion, while a whale which was not identifiable from the photograph has no potential to be re-identified. The certainty value graded the certainty of an individual's identification, and not the quality of the photograph. Certainty values of 4 and 5 indicate a photograph with certain individual identification (see reliability test, section 2.8).

2.6.2. Matching of flukes and dorsal fins and development of a catalogue

Each negative was first observed under a dissecting microscope and compared with prints in a fluke catalogue. If the fluke on the negative did not match with any print, or if there was any uncertainty, a print was made of the negative. A fluke on a negative which did not match with any print was given a new

Figure 2-5: Photographs showing different unique marks on flukes of sperm whales off the Galapagos.

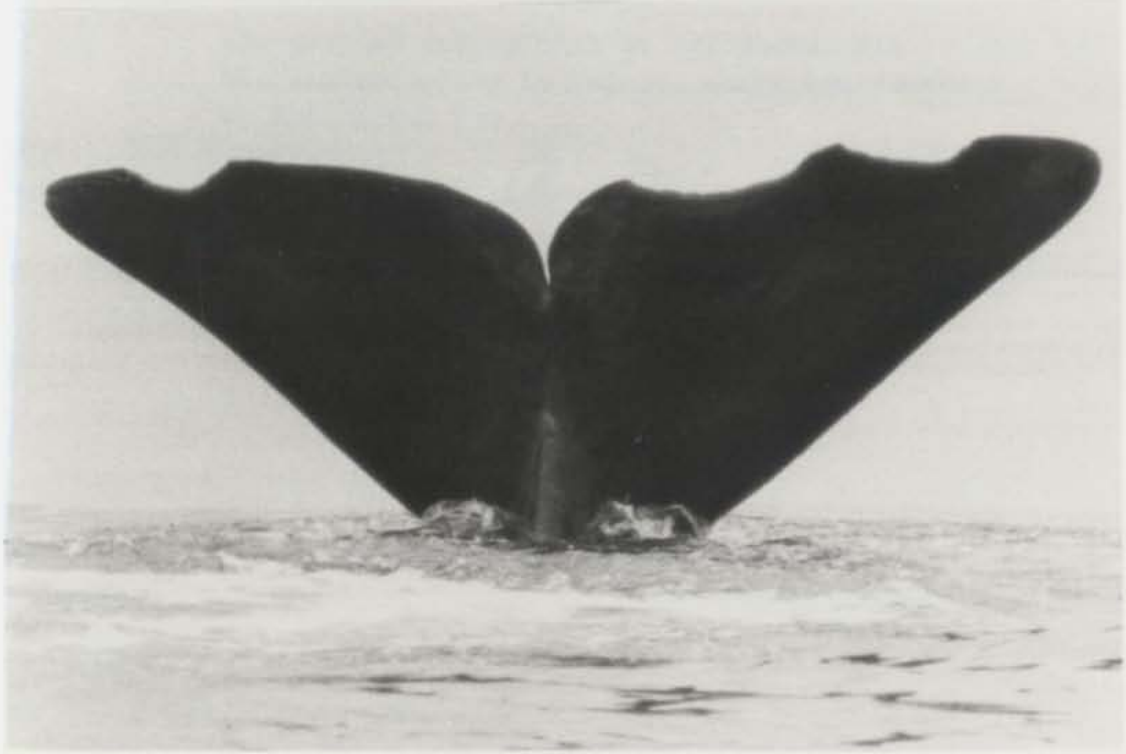


Table 2-2.

Description of unique marks on flukes and dorsal fins which are useful for individual identification of sperm whales.

Small nicks;	are only distinguished when the fluke was relatively close when photographed.
Distinct nicks;	are distinguished at relatively long distances.
Waves;	are shallow depressions along the trailing edge of the fluke.
Scallops;	were only recorded for flukes. Looks as though a semi-circle has been carved out of the trailing edge.
Missing portions;	are large parts of the fluke-tips missing. These marks are distinguishable at distance.
Holes;	are only recorded when the fluke is perpendicular to the axis of the camera.
Tooth mark scars;	are often seen as several parallel white lines.
Calluses;	are greyish deformities on the dorsal fin. The callus varies in colour, shape and position on the dorsal fin.
Skin sheddings;	are observed as lighter areas or lines on the backs of the whales.

identification number. When a match (Figure 2-6) was found the identification number of the matching catalogue print was given to the fluke on the negative. A print was made if the negative was of better photographic quality than the print already catalogued. The best print of each identified individual was used to estimate the number of unique marks on the flukes. The order of the prints in the catalogue was based on the smoothness of the trailing edges of the flukes, with the most rugged edges at the beginning, and no marks at all on flukes at the end of the catalogue.

Each analysed dorsal fin negative was given a classification which represented either the possibility or impossibility of identifying individuals. Those negatives which were classified as "possible to identify individuals", were printed and a catalogue was made. Matched dorsal fins (Figure 2-7) were given the same identification number. The matching was repeated twice to ensure that all identifiable dorsal fins were included in the catalogue. Catalogued dorsal fins were separated into those with certain and not certain individual identification. This was done to screen out those whales which were possibly but not certainly individually identified. The catalogue was divided into left and right dorsal fins depending on which side of the dorsal fin was photographed.

Dorsal fin and flukes of the same identified individual were matched when possible. Although it was not always possible to identify the individual with certainty from the dorsal fin, it was sometimes possible to determine whether a callus was present or not. These dorsal fins were matched, whenever possible, with flukes from identified individuals, and the presence of a callus was recorded (Section 2.5.3).

2.7. GROUPS

To achieve an objective description of the social organization of the females/immatures off the Galapagos, identifications of particular individuals were used. A coefficient of association, R(x,y), was calculated between each pair of identified female/immature whales x and y:

$$R(x,y) = \sum_{i} 5/(5+t(i)) \cdot (1/N(x)+1/N(y))/2$$

Figure 2-6: Photographs of matching flukes of an individually identified sperm whale: A) identified on 24 February, B) on 23 March, and C) on 11 April, 1985.


A


B

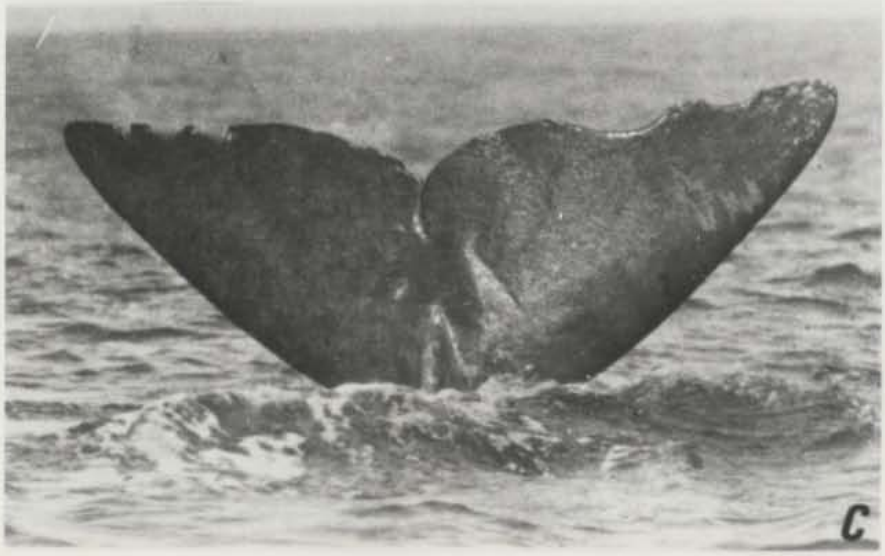

C

Figure 2-7: Photographs of matching dorsal fins of an individually identified sperm whale: A) identified on 21 March, and B) on 31 March, 1985


A


B

where the summation is made over i, those occasions on which x and y were identified <240 min apart (240 min was chosen as the cut-off, as there appeared to be occasional changes in the primary set of whales being followed over intervals of this duration); and t(i) is the time interval in min between the identification of x and y on occasion i (times recorded to nearest 5 min). N(x) and N(y) are the total number of identifications of x and y. Thus if 2 whales were each identified on 3 occasions, always within 5 min of one another, then:

$$t(i) = 0 \quad \text{(observed within the same encounter)}$$
$$1/N(x)+1/N(y)=1/3+1/3 = 2/3, \text{ then}$$
$$R(3,3)=\sum_{i=1}^{i=3} 5/5+0 \quad (2/3)/2 = 1.0$$

The association matrix, [R(x,y)], was used as input in a Group Average Hierarchical Cluster Analysis (Everitt, 1974). Groups were merged using this clustering technique until a likelihood ratio test showed a significant (at $P<0.05$) decrease in the fit of the data (of the days on which individuals were identified) for the resultant group to a model of closure compared with its two constituent groups.

2.8. RELIABILITY TEST

A reliability test was conducted to see if the analyser (Arnbom) was consistent in his estimate of matching and grading the negatives (Table 2-3). Two rolls of film were randomly selected with 10 and 22 fluke photographs respectively. The matching and grading method was explained by a written statement and was presented to an experienced cataloguer (H. Whitehead). Whitehead was not permitted to see the negatives before the test. The flukes graded at certainty values 4 or 5 (N=22) were matched identically by Arnbom and Whitehead, except for three flukes, which Whitehead scored 4 while Arnbom scored 3. Although the two analysts had significantly different means for the measures X1-X6, all, but one, were correlated (Table 2-3). The only measure in which Arnbom's and Whitehead's estimates were not correlated significantly was exposure ($r=0.24$, $P<0.20$).

Table 2-3

The two analysers' means, the absolute value of the difference between the analysers' means, correlation between the analysers' scores and the significance level for 2-tailed t-test of the means, used for the evaluation of the method of individual photographic identification. The analysers, Arnbom (A) and Whitehead (W), examined the same 32 photographs.

Measure	Mean (W)	Mean (A)	Absolute value diff. mean	2-Tailed t-test r	2-Tailed t-test P <
Focus	3.59	3.25	0.34	0.662	0.001
% cover	4.23	3.91	0.32	0.935	0.001
Exposure	0.53	-0.37	0.90	0.235	0.196
Orientation	23.06	13.59	9.47	0.845	0.001
Tilt	13.44	18.09	4.65	0.908	0.001
% visible	76.00	82.66	6.66	0.979	0.001
Quality	2.59	2.19	0.40	0.911	0.001

2.9. IDENTIFIABILITY

When using the method of individual photographic identification for mark-recapture population estimates, it is usually assumed that all members of the population are equally identifiable (Hammond, 1986). To test this assumption multiple regression techniques (Edwards, 1979) were used to make a preliminary investigation of the identifiability of individual sperm whales in the Galapagos population. The certainty value (Q) was regressed on the 6 measures of photograph quality (Table 2-2). The regression model was used to derive predicted certainty values given the photograph quality measures for identified individuals. These predicted certainty values were compared with actual certainty values.

2.10. SPEED OF THE WHALES

The speed of the whales was estimated by measuring the distance between the positions of the first identification of a particular individual on 2 consecutive days, divided by the time between the identifications. It was expected that the whales' speed over bottom was effected by the westward flowing South Equatorial Current. Speed was therefore entered into one of 4 categories: moving NW, NE, SW and SE. Because of the small sample size, the categories were combined to calculate the mean speed of animals moving generally E (SE + NE categories), W (SW + NW), S (SW + SE) and N (NW + NE). When several whales from the same group were identified, on the same consecutive days, the mean speed was used.

Chapter 3
RESULTS

3.1. EVALUATION OF THE METHOD

3.1.1. The importance of different measurements for identifying whales from flukes

The 6 measurements used for the assessment of the method of individual photographic identification were focus, percentage of negative covered, tilt, exposure, orientation and percentage visible (Table 2-1). The measurements were entered in a stepwise linear regression on fluke certainty Q (section 2.6). The regression accounted for 79% of the variance in Q. The final regression was:

$$Q = 0.30 + 0.78X_1 + 0.57X_2 - 0.013X_3 + 0.24X_4 - 0.0065X_5 + 0.017X_6$$

Measurements were entered in this equation in the order of their contribution to explaining the variance in Q. Focus or resolution of the photograph was the most important mechanical measurement, followed by the percentage of the negative covered by the fluke. The percentage of the fluke visible was the least important measurement; only a small proportion of the fluke needs to be visible to show the trailing edge, where marks for identification are found.

Each measurement's (X1-X6) mean and standard deviation for each of the certainty values of 3, 4 and 5 are given in Table 3-1. The mean for each of the 6 measurements was plotted against the different certainty values (Figure 3-1 to 3-4).

From a knowledge of the mean dimensions of sperm whale flukes and the focal length of the lens, measurement X2, the percentage of the negative covered by the fluke, could be converted into the distance between the photographer and the fluke (Appendix 1). It was found that the median distance from the photographer

Table 3-1 a-c.

Measurements of photograph quality related to the certainty of identification. Their mean, median, minimum and maximum values, and the number of photographs for the different quality values.

a) Certainty value 3: Likely, but not certain of identification

Measure	Mean	(Standard deviation)	Median	Minimum	Maximum	Number of photographs
Visible	78.17	(26.94)	90.00	10.00	100.00	169
Tilt	26.42	(17.58)	20.00	0.00	135.00	165
Orientation	24.64	(20.33)	20.00	0.00	145.00	165
Negative	2.29	(2.17)	1.70	0.20	19.00	169
Focus	3.04	(0.56)	3.00	2.00	4.00	169
Exposure	-0.14	(0.72)	0.00	-3.00	3.00	169

b) Certainty value 4: Certain identification

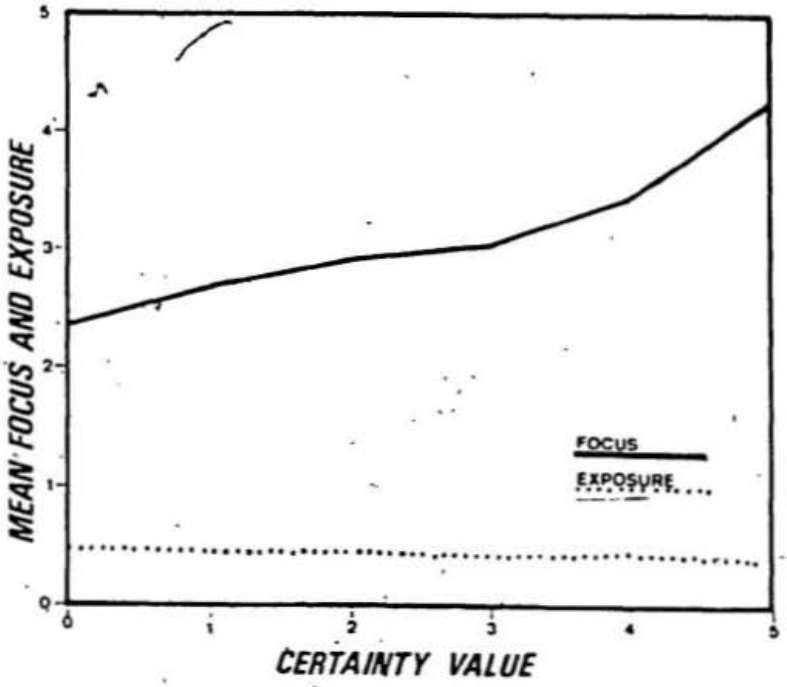
Visible	76.66	(21.51)	80.00	10.00	100.00	523
Tilt	22.60	(16.80)	17.00	0.00	170.00	521
Orientation	20.35	(11.29)	20.00	0.00	150.00	523
Negative	3.14	(2.42)	2.50	0.10	16.00	523
Focus	3.44	(0.63)	3.00	1.00	5.00	523
Exposure	-0.15	(0.75)	0.00	-3.00	3.00	523

c) Certainty value 5: Certain identification, small details visible

Visible	82.50	(16.90)	90.00	50.00	100.00	8
Tilt	15.88	(6.79)	15.00	5.00	30.00	8
Orientation	17.13	(6.79)	15.00	10.00	30.00	8
Negative	6.06	(2.63)	6.00	2.50	10.00	8
Focus	4.25	(0.71)	4.00	3.00	5.00	8
Exposure	0.13	(0.64)	0.00	-1.00	1.00	8

Figure 3-1: Mean focus and exposure, measured from photographs of sperm whale flukes, plotted against certainty values.

Figure 3-2: Mean percentage of the negative covered by the fluke plotted against certainty values.


MEAN FOCUS AND EXPOSURE
FOCUS
EXPOSURE
0
1
2
3
4
5
CERTAINTY VALUE

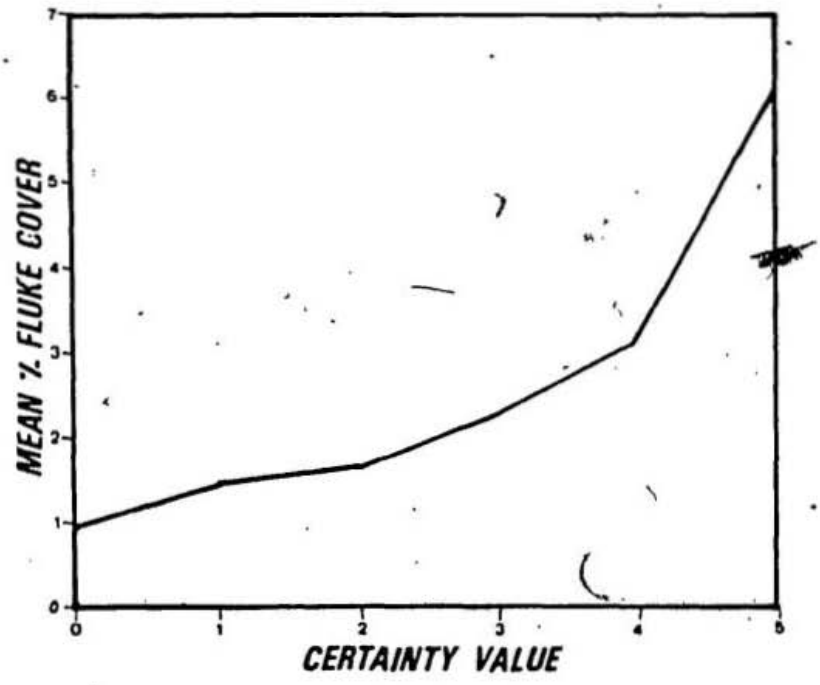
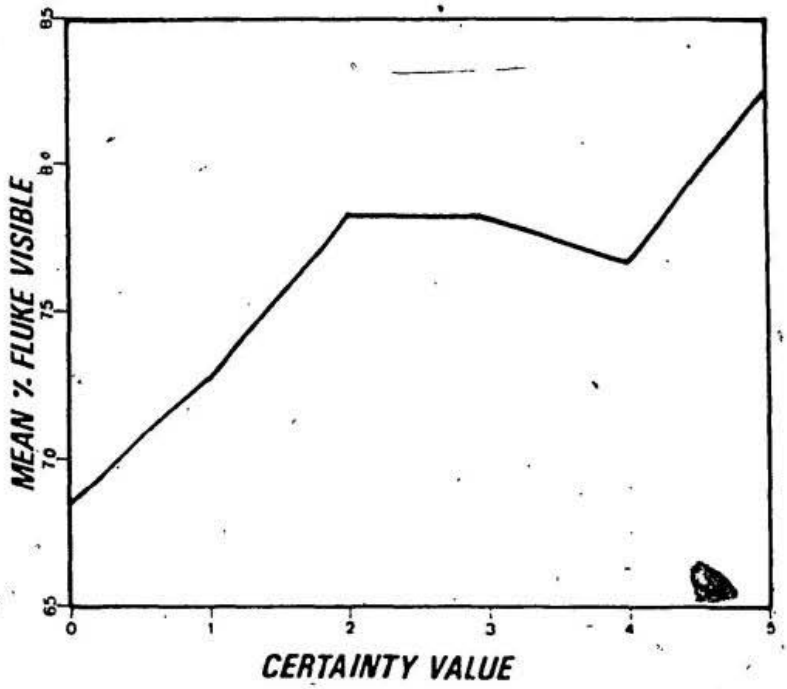
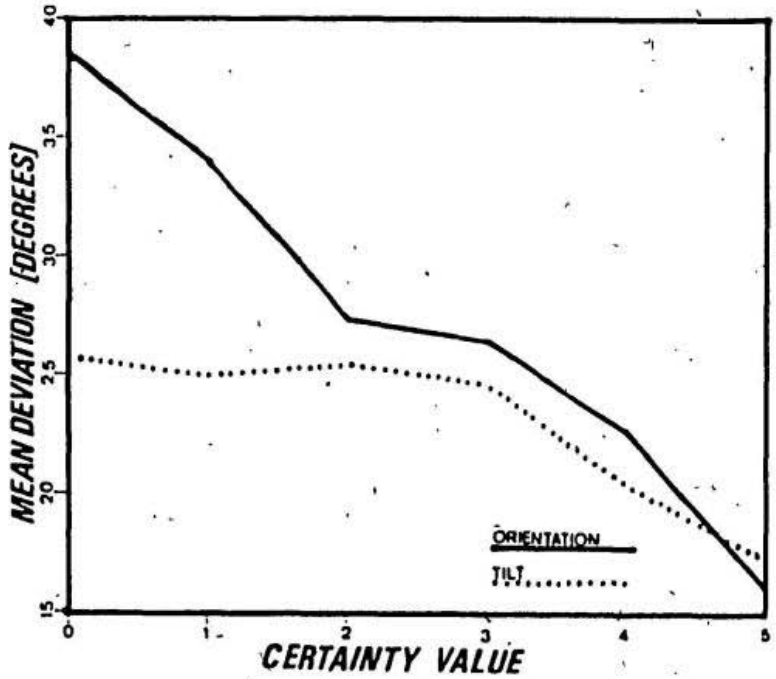

MEAN % FLUKE COVER
0
1
2
3
4
5
6
7
CERTAINTY VALUE

Figure 3-3: Mean deviation of orientation and tilt of the flukes from being perpendicular to the camera axis, plotted against certainty values.

Figure 3-4: Mean percentage of flukes visible above water surface against certainty values.


MEAN % FLUKE VISIBLE
85
80
75
70
65
0
1
2
3
4
5
CERTAINTY VALUE


MEAN DEVIATION (DEGREES)
40
35
30
25
20
15
0
1
2
3
4
5
CERTAINTY VALUE
ORIENTATION
TILT

to the whale flukes decreased when the certainty value increased: 90.2 m (Q=3), 71.4 m (Q=4) and 60.2 m (Q=5). The maximum distances between the photographer and the whale fluke, for which certainty values of 3, 4 and 5 were obtained were also calculated: 265 m (Q=3), 301 m (Q=4) and 77.2 m (Q=5). The maximum distance for a photograph of certainty value 4, was from a photograph of a female/immature which had a very distinct fluke.

3.1.2. Marks useful for individual identification

The marks most useful for individual identification were nicks, scallops, missing portions and tooth mark scars. At greater distances, missing portions and scallops were the most helpful features for identification: as they were the most visible marks.

Marks useful for identifying whales from dorsal fins were tooth mark scars, the shape of the fin, patterns of skin shedding, and the presence and form of the callus. During underwater observations much dead skin was observed behind the whales. Therefore it was believed that patterns of skin shedding could only be helpful for identification over short periods.

3.2. INDIVIDUAL IDENTIFICATION

3.2.1. Identified flukes

From the 1,268 photographs of flukes 41.8% (531/1,268) were given a certainty value of 4 or 5 (Table 3-2). These represented certain individual identification of 210 females/immatures, 6 males and 1 calf. Additionally there was one large male and one calf whose best photograph had certainty values of 3, but which were definitely different individuals from the other identified males and calf. Thus 210 females/immatures, 7 large whales and 2 calves were individually identified with certainty from photographs of flukes (Table 3-3).

Table 3-2.

Number of fluke photographs and their certainty values.

Certainty value	0	1	2	3	4	5	TOTAL
# of photographs	337	81	150	169	523	8	1268
% of total number of photographs	26.6	6.4	11.8	13.3	41.2	0.6	100

Table 3-3.

Number of whales with certain identification (certainty value 4 or 5) and number of occasions these individuals were identified using photographs of flukes.

Number of days identified	1	2	3	4	5	6	TOTAL
# of females + immatures	147	41	16	5	0	1	210
# of adult males[1]	4	2	1	0	0	0	7[1]
# of calves[2]	2	0	0	0	0	0	2[2]
Total # of whales identified	153	43	17	5	0	1	219

1 one of the 7 adult males has a certainty value of 3 (likely but not certain of identification), but the adult male is certainly a different individual from the other 6 large males.

2 one of the calves (less than 1 y) has a certainty value of 3, but the calf is certainly a different individual than the other calf.

3.2.2. Identifiability of flukes

Using the regression of certainty value (Q) on the measurements of photograph quality (X1-X6), the best photographs of 20 females/immatures were predicted, but not given, an actual individual identification certainty value of 4 or 5. These are animals photographed with "good" photographs, but not identifiable by a method that considers only identification of certainty 4 and 5. These constituted 8.7% (20/(210+20)) of the estimated females/immatures with good photographs. The mean number of unique marks on the flukes of these whales was 5.1 (s.d. 2.4) while the whales with an actual certainty value of 4 or 5 had a mean of 8.4 (s.d. 3.6) unique marks. A one-tailed t-test gave a significant difference in the number of marks on the flukes between these two categories ($t=4.58$, $P < 0.01$). None of the individuals with a predicted certainty value of 4 or more, and an actual certainty value of less than 4, had a predicted certainty value of 5. This may imply that it is not possible to identify 8.7% of the photographed sperm whales off Galapagos, using the method of individual photographic identification. But it may also imply, which is more likely, that if a better photograph of predicted certainty value of 5 was taken of the individual, it might have been possible to identify that particular individual. Therefore 8.7% is an estimated upper limit for the number of females/immatures not identifiable by the method described above.

3.2.3. Identified dorsal fins

From 1,568 negatives showing 2,164 dorsal fins, 38 females/immature males, 6 large males and 6 calves were individually identified with certainty. For 3 females/immatures, 5 large males and 2 calves identification was based on photographs from both left and right side of the dorsal fin. Twenty-four of the females/immatures were identified from photographs of the left side of the dorsal fin and the remaining 11 from the right side. Of these 35 one-sided identifications, 24 (19 left and 5 right) were definitely from different individuals. The remaining 11 (5 left and 6 right) which may represent as few as 6 different individuals: if an individual was first identified from the left side and then later from from the right side it may erroneously have been individuals might have

been identified from the different sides catalogued as 2 different individuals. Because of the low probability of positively identifying animals from their dorsal fins, this technique was not subjected to the same detailed analysis as the fluke identifications.

3.3. RE-IDENTIFICATIONS

3.3.1. Flukes

There were 107 females/immatures and 1 male which were only identified once. Forty females/immatures and 3 large males were re-identified on the same day and 63 females/immatures and 3 large males were identified on 2 or more days (Table 3-3). The greatest time span between the first and last identification, of a particular female/immature was 46 days, and of a large male 4 days.

3.3.2. Dorsal fins

Using dorsal fins for identification, 8 females/immature males were re-identified on the same day, and 5 on 2 or more days. Five large males were re-identified, 1 on the same day, and 4 on 2 or more days. Two calves were re-identified on the same day and 3 on 2 or more days. The largest time span between 2 identifications for large males and females/immatures was 36 days and for calves 10 days.

3.3.3. Matching flukes and dorsal fins

It was possible to match dorsal fins and flukes for 8 females/immatures and 6 large males. The dorsal fins were identified on 2 or more days for 3 females/immatures and 4 large males. By combining dorsal fin and fluke re-identifications an additional 55 re-identifications from dorsal fins could be added to the more extensive re-identification data from flukes. The total number of re-identifications of flukes and dorsal fins for 103 females/immatures (individuals re-identified on the same day + individuals identified on 2 or more days) was 327 and for 6 large males 49.

3.4. CHANGES OF MARKS

There were 338 re-identifications of flukes from 109 individually identified whales (females/immatures + large males), including the first sighting of the whale. The time span of the re-identifications ranged from 5 min to 46 days, and no changes of the marks along the trailing edges of the flukes were recorded during the study period. Three of the females/immatures and 4 large males which were identified from both dorsal fin and flukes were seen on 2 or more days, and none of these whales showed any changes on the flukes or the dorsal fin. One female/immature was identified from both dorsal fin and flukes over a period of 36 days.

3.5. PRESENCE OF CALLUSES

There were 576 whales (not individually identified: the same whale may have been photographed during several encounters but no animal was counted twice within the same encounter) from which it was possible to say, whether or not there was a callus present on the dorsal fin. Of the females/immatures, 84% (484/576) were recorded with a callus and 16% (92/576) without a callus. None of the 6 large males had a callus.

Following Gordon (1986), these results were tested, to see if they were different from the expected values from all sperm whales on the tropical grounds and from mixed groups alone. Gordon (1986) assumed that a callus indicates mature females, and that various life history parameters from Best (1979) applied. According to Best (1979) tropical populations should include both mixed groups and groups consisting entirely of immature individuals. A mixed group contains 58.5% mature females, and on the tropical grounds 33% of the total population are mature females (Best, 1979).

Assuming that 58.5% in the mixed groups are mature females and all have a callus, a chi-square test showed a significant difference between observed (484) and expected (337) number of calluses in mixed groups ($X^2 = 154.62$, d.f. $= 1$, $P < 0.001$). Assuming that 33% of the total whale population on tropical grounds are mature females that all have a callus, a chi-square test showed a significant

difference between observed (484) and expected (190) number of calluses ($\chi^2 = 524.56$, d.f. = 1, $P < 0.001$). Hence, there were more calluses than expected for both of these tests.

Thirty-four individuals positively identified from fluke photographs were analysed for callus presence. Thirty had a callus; 4 did not. Four of these individuals were noticed with a callus on 2 different encounters, and no discrepancy was detected.

3.6. GROUPS

3.6.1. Number of groups and individuals

There were 13 groups (as produced by the methods described in section 2.7) with more than 6 identified whales each (Table 3-4), and 9 other groups with from 1-3 identified members; these latter groups may have been unidentified members of the larger groups. The number of days on which the different groups were identified varied between 1-8.

3.6.2. Differences in marks and notches between groups

The mean number of marks (section 3.1.2) on the flukes, of animals from different groups varied from 5.9-10.8 with a mean of 8.2 (Table 3-5). The overall ratio of animals with open rather than closed fluke notches (section 2.5.2) was 105:79. There was an overall significant difference in the proportion of open and closed fluke notch between the groups ($\chi^2 = 27.03$ d.f. = 12, $0.001 < P < 0.01$). Two groups (G3 and G11) were significantly different from the overall ratio ($\chi^2 = 5.33$ and 6.00, d.f. = 1, $0.02 < p < 0.05$). Group G3 had more closed and G11 had more open fluke notches.

Table 3-4.

Derived groupings of whales, with the number of animals identified, a population estimate and its estimated standard error (from Whitehead and Arnbom, in press), the number of days on which the grouping was identified, the time span between its first and last sighting in days, and associations (members of both groups identified within 120 min of one another) with other groups. The number of days pairs of groups were associated is given in parentheses if greater than one.

Group identification	# of whales identified	Population estimate (S.E)	Days identified	Span of identifications	Associations with:
G1	14	14.1 (1.0)	8	48	G2,G8,G9,G10(5 days)
G2	20	29.8 (6.9)	4	13	G1,G3,G9
G3	18	18.3 (1.0)	6	43	G2,G5(2),G8(2)
G4	18	20.9 (2.8)	5	36	G1,G5,G8,G10
G5	20	22.5 (2.8)	7	40	G3(2),G4,G6(3),G8(2),G9
G6	16	28.2 (6.9)	5	41	G5(3)
G7	17	20.7 (4.0)	2	14	-
G8	14	17.8 (3.5)	5	36	G1,G3(2),G4(2),G5(2),G10
G9	9	10.6 (2.4)	4	48	G1,G2,G4,G5,G10
G10	12	13.7 (2.6)	6	23	G1(5),G4,G5,(2)G8,G9
G11	10		1	1	-
G12	8		1	1	-
G13	7		1	1	-

3.6.3. Calves, escorts and followers

Both records of visual observations and inspection of photographs suggested the 13 groups possessed between 0-2 calves per group (Table 3-5). Six calves were individually identified from dorsal fins and 2 from flukes. The identities of the escorts and followers of the calves were examined. Four of the individually identified females/immatures were observed with calves on 3 different occasions and 1 female/immature on 11 occasions. However, the ratio (number of observations with a calf/total number of observations) shows that none of females/immatures mentioned above were identified exclusively with calves. The identification ratio for these females/immatures varied between 0.48-0.75.

On 3 separate occasions a particular calf was recorded as escorted, and each time by a different individually identified female/immature. Two particular females/immatures were identified together with different calves on different occasions. Thus, it seems that different females/immatures accompany more than 1 calf at different times.

Assuming that the proportion of mature females in mixed groups is 0.59 and the calving interval is 6 y (Best, 1979; Best et al., 1984), the expected number of first y calves for the mixed groups in Table 3-4 can be estimated as follows: estimated number of individuals in mixed groups x proportion of mature females in mixed groups (0.59)/calving interval (6 y). The observed number of calves for the mixed groups was lower than expected (Table 3-5).

All 7 females/immatures which escorted calves, and for which the presence/absence of a callus could be determined, had a callus on the dorsal fin. The only sperm whale observed with remoras, presumably *Remora australis* (Rice and Caldwell, 1961) was a calf, which had 7 remoras attached to its back.

Table 3-5.

Summary of attributes of groups: mean number of marks/individual, percentage of individuals per group with tooth mark scars, identified individuals with and without callus, number of calves observed and expected per group (see section 3.6.2), individuals with open or closed notch in the fluke and number of identified individuals per group.

ID of group	Marks/ ind.	% with tthmk.	Callus	No callus	Calves obs.	Calves expect.	Notch open	Notch closed	Total number
G1	8.63	11.8	2	-	2	1.4	12	3	14
G2	7.57	38.1	2	1	1	2.9	11	5	20
G3	10.83	23.5	4	-	1	1.8	5	12	18
G4	7.07	11.1	4	-	2	2.0	7	8	18
G5	7.95	16.7	-	-	1	2.2	14	4	20
G6	7.56	13.3	-	2	-	2.8	7	7	19
G7	7.47	6.7	3	1	1	2.0	5	8	17
G8	8.47	41.7	4	-	1	1.7	4	8	14
G9	9.25	16.7	3	-	-	1.0	3	3	9
G10	7.71	28.6	4	-	1	1.3	4	1	12
G11	10.00	37.5	2	-	-	-	6	-	10
G12	5.88	12.5	-	-	1	-	5	3	8
G13	8.67	0.0	1	-	1	-	5	1	7

3.7. INTERACTIONS

3.7.1. Between groups

On 19 occasions 2 or more groups associated (see section 1.2 for definition). with each other (Table 3-4). For 15 of these 19 associations (79%) there were 2 groups observed together; the remaining 4 occasions involved 3 groups (21%). There were very short time intervals between the identification of groups G1 and G10 on the 5 days they were seen together (on 4 days within the same encounter and once within 20 min of one another).

3.7.2. Between groups and males

All 7 identified males were seen in association with mixed groups. Four of the mixed groups were observed with different identified males at different times (Table 3-6 and Figure 3-5).

Three of the males were seen repeatedly with the same mixed group, but 2 of these associations were on consecutive days. Two or more large males were observed together with a mixed group within the same encounter on 5 occasions. For 4 of these occasions, there were 2 large males present and once 3 large males were observed together with a mixed group. However, these large males were not always individually identified. Particular males associated with other individual males at different times (Table 3-6). There seemed to be no individual preferences in the associations of the large males, or tendency for large males of the approximate same length, to associate (Table 3-6). No agonistic behaviour was seen between the large males.

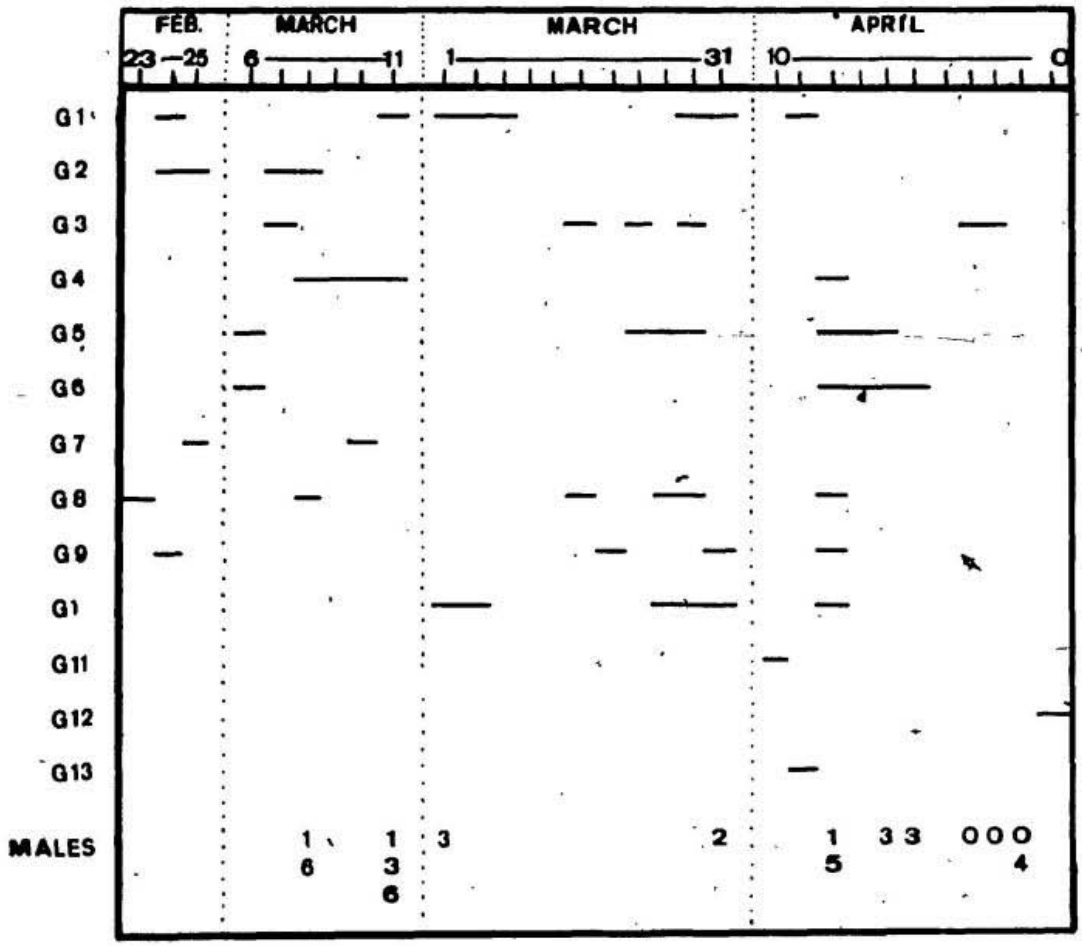
The following describes the occasion when 3 large males and 2 mixed groups were sighted together. On 11 March at 14:00, 2 unidentified mixed groups were approaching one another. One group consisted of approximately 20 females/immatures accompanied by 2 large males, and the other group had approximately 15 females/immatures accompanied by 1 single large male. The 2 groups and the males were swimming at a normal speed of 2-4 km/h. When the groups and the males were 100-150 m apart, the single male in the smaller group

Table 3-6.

Identified mature males (identity numbers:500-506), with estimated length (mean of 1-6 photographic measurements per individual, from Whitehead and Arnbom, in press), estimated age using Ohsumi's (1977) age-length key, number of days identified, span of days over which identified, and associations (identified within 120 min of 1 another) with other males and groups of females. The number of days a male was associated with other males or groups is given in parentheses if greater than one.

Identify number	Length (m)	Age (y)	Days identified	Span of days	Associated with: Males	Groups
500	15.05	37	3	3	-	G3(2)
501	16.38	>39	3	36	503, 506(2)	G4(2), G5, G8, G9
502	14.03	27	1	1	-	G1, G9, G10
503	13.74	25	4	36	501, 506	G1, G6(2)
504	-	-	1	1	-	not identified
505	-	-	1	1	-	G4, G5
506	14.39	30	2	4	501(2), 503	G4

Figure 3-5: Days on which mixed groups (G1-13) and large males were identified. Each identification of the males is represented by the last digit of the identification code (e.g. 503 = "3").


FEB.
23 25
MARCH
6 11
MARCH
1 31
APRIL
10
G1
G2
G3
G4
G5
G6
G7
G8
G9
G1
G11
G12
G13
MALES
1 1
6 3
6
3
2
1 3 3 0 0 0
5 4

accelerated to a speed of 8-10 km/h and swam towards the larger group containing the pair of large males. When the distance between the single and the pair was 50-75 m, the 3 large males dove, more or less simultaneously, and disappeared out of sight. The boat was less than 75 m from the nearest large male when they dove. No sound except sporadic clicks from the females/immatures was heard on the hydrophone when the large males submerged. Normally we would hear series of clicks (Backus and Schevill, 1966) from the females/immatures. After approximately 30 s (the large males were still out of sight) the characteristic "slow click" (Weilgart and Whitehead, in prep.) from 1 large male was heard. However, it was not possible to determine from which male the sound came from. The 2 mixed groups converged into 1 aggregation when the males were out of sight. Four to 5 min after the submergance, the 3 large males resurfaced in a loose cluster. At that time, the large males and the aggregation were swimming with a speed of 1-4 km/h.

3.8. PREDATION

The analysis of flukes showed that 21% (39/190) of the identified individuals had tooth mark scars. It was only possible to record the presence or absence of tooth mark scars on 190 of the 210 individually identified females/immatures because, for the others, the photograph quality was not sufficient to distinguish tooth marks on the fluke. There was no significant differences in the proportion of individuals with tooth mark scars from the different groups given in Table 3-5 ($X^2 = 12.07$ d.f. $= 12$, $P > 0.30$).

Apart from the tooth mark scars there were small round holes, missing pieces and scallops which could have been made by sharks or other animals. The total number of each different kind of mark was divided by the number of individuals from which it was possible to record the presence of the mark. Holes and missing pieces were found on 8% and 19%, respectively and 1.7 scallops were recorded per individual whale (Table 3-7). Tests of observed number of marks and scallops between mixed groups showed no significant overall differences ($X^2 = 5.70$, d.f. $= 12$, $P > 0.99$ for marks; $X^2 = 1.46$, d.f. $= 12$, $P > 0.95$ for scallops).

Table 3-7.

Types and number of marks/individual, standard deviation, maximum number of marks/individual, and the number of identified whales for which presence of marks could be determined.

Type of mark	mean/ ind	s.d.	max/ ind	number of whales
Small nicks	3.1	(2.6)	15	201
Distinct nicks	1.4	(1.3)	6	214
Wayes	1.1	(1.3)	7	214
Scallops	1.7	(1.4)	7	216
Missing portions	0.19	(0.48)	2	213
Holes	0.082	(0.31)	2	208
Toothmarks	0.21	(0.41)	-	190

3.8.1. A killer whale attack

The following description is a summary from Arnbom et al. (in press). A mixed group was followed for 2 consecutive days on 17-18 April. The group was attended by 1 large male from 10:20 17 April to 17:20 18 April. The mean size of the observed clusters was 1.9 on 17 April and 1.5 early on 18 April. At 09:45 on 18 April the sperm whales suddenly clumped together and killer whales were observed heading for the mixed group. The boat was maneuvered into the vicinity of the whales. During the next 3 h (09:45-12:30) we watched and recorded the killer whales attacking. The maximum number of sperm whales observed was 31, including 1 large male and 1 calf (Group G3 is estimated to contain 18.3 (s.d. 1.0) members, thus during the attack another mixed group was probably present). The estimated number of killer whales was 20-25, including 2 large males and 2 calves. During the attack the mean cluster size for the sperm whales increased dramatically to 16.2 (from 1.9 and 1.5 earlier, see above). The sperm whale calf was positioned in the middle of the cluster and the male was normally seen on the flank or behind. The killer whales attacked the sperm whales from either the flank or from behind, while the sperm whales tried to orient their heads towards the killer whales. The only injuries observed were gashes on the sperm whales.

At 12:30 the killer whales left and swam away in a southwestern direction. The sperm whales swam around in several 360 degrees turns, and then moved off in a northeastern direction. No sounds were heard during the 5 h the sperm whales were followed, except for the large male whose distinctive "slow clicks" were heard at 17:00. During the flight the mean cluster size was 18.2 with a maximum of 34 sperm whales observed. The whales swam in a coordinated manner, all fluking up within a few min of each other. They stayed under the surface for about 20 min and at the surface for about 10 min. At sunset the decision was made that we should keep the same course and speed during the night. No sounds were emitted and we could not use the directional hydrophone to follow the whales.

The following day (19 April) at 07:00 several female/immature sperm whales,

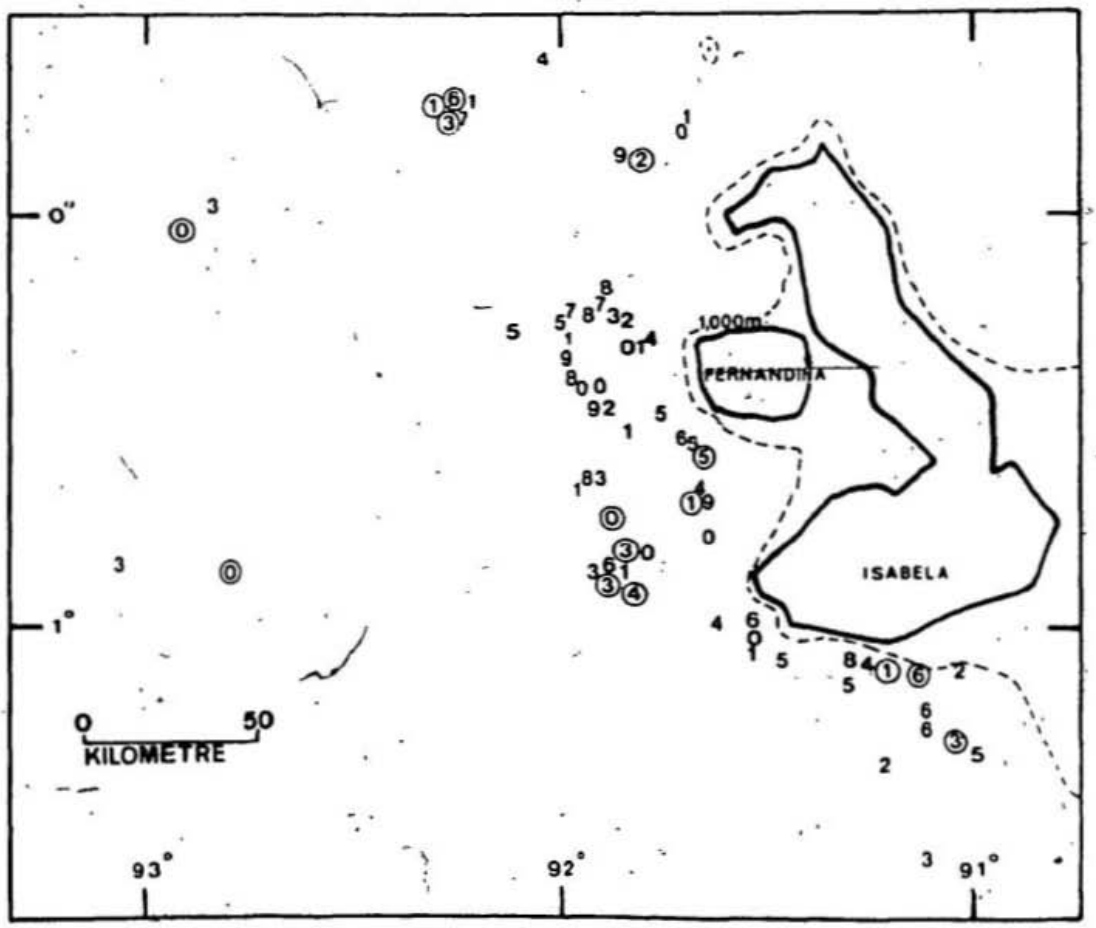
and a large male sperm whale, were observed and photographs of the flukes were taken. The large male was identified; it was the same male as the day before but the mixed group was new. The group may either have been the unidentified group from the day before or a totally new mixed group.

3.9. MOVEMENTS AND SPEED

The positions of the first identification of mixed groups and large males on different days are shown in Figure 3-6. There seemed to be no tendency for a particular group or a large male to be identified in a specific area. The whales were generally observed within a distance of 55 km from the shelf break in waters deeper than 3,500 m. There seemed to be 2 latitudes where the whales turned, 0°25'N and 1°20'S (Figure 2-2).

The sperm whales' mean speed over the bottom was 2.53 km/h (s.d. 0.94). However, the mean speed varied with the compass heading. The mean speed of the whales swimming towards north (N=7) was 2.54 km/h (s.d. 0.37), south (N=4) 2.52 km/h (s.d. 0.77), west (N=5) 3.28 km/h (s.d. 0.37) and east (N=6) 1.91 km/h (s.d. 0.33). There was a significant difference ($H=5.63$, d.f.=1, $P < 0.02$) in speed (1.37 km/h), using a Kruskall-Wallis test, between times when the whales were heading west or east.

Figure 3-6: Positions in which mixed groups, represented by uncircled numbers, and large males, represented by circled numbers, were first identified on each day. Each first identification is represented by the last digit of the identification code (e.g. G3="3", G10="10" for groups; 506="6" and 503="3" for the males). A dashed line indicates the 1,000 m depth contour. (Modified from Whitehead and Arnbom, in press)


1000m
FERNANDINA
ISABELA
0
50
KILOMETRE
0°
1°
93°
92°
91°

Chapter 4
DISCUSSION

4.1. EVALUATION OF THE METHOD USING INDIVIDUAL PHOTOGRAPHIC IDENTIFICATION

A key to successful individual photographic identification, is good quality photographs. Focus (resolution) of the negative and the distance to the whales were the most important determinants of photograph "quality". More than 50% of the fluke photographs with certainty values of 4 or 5 were taken when the whales was within 70 m of the photographer. The significance of the focus of the negative emphasized the importance of using a fast shutter speed. By selecting a film with 400 ASA or even exposing the film at 1200 ASA it is possible to maintain a higher shutter speed than with slower films and also to use a narrow aperture which will increase the depth of field. The latter is important for flukes photographed at an angle. Bigg, Ellis and Balcomb (1986) stressed the importance of focus and distance when taking photographs for individual identification.

A fluke photographed perpendicular to the axis of camera, is most desirable. However this occurs rarely. It was found that flukes with a deviation of less than 30-35° from "flat on" were useful. Small variations in exposure did not change the identifiability of flukes. However, negatives which were very dark or light made some identifications impossible. As long as the trailing edge of the fluke was visible, it was usually possible to identify individuals.

The number of animals identified from flukes was nearly a magnitude larger than from dorsal fins, partially because more emphasis was placed on photographing and analysing flukes. Also marks were more visible and thus easier

to recognize on flukes than on dorsal fins. The trailing edge of a fluke is much longer than a dorsal fin ridge and therefore more marks can be recognized than on a dorsal fin. When photographing a fluke, the boat was stationed behind the whale, while for a dorsal fin the boat was perpendicular and relatively closer to the animal which may have disturbed and altered the behaviour of the whales, and thus made them more difficult to approach.

Gordon (1986) had better success using dorsal fins for identification of sperm whales than I had. Gordon used colour-slides which show more detailed patterns of colour differences than black and white film (Bigg et al., 1986). The colouration of the callus on the dorsal fin was useful for the individual identification (J. Gordon, pers. comm.).

I was able to identify 14 animals based on both their dorsal fins and flukes. This increased the number of certain identification/re-identifications by 73% for these individuals. I recommened that future studies should use colour film for dorsal fins and place more emphasis on photographing and matching dorsal fin and fluke of single animals.

Trailing edges of sperm whale flukes may change with time. However, no changes in marks were noticed during the 2 month study period. Studies are needed to investigate the rate of change of natural marks and the long-term usefulness of individual photographic identification. Gordon (1986) matched 7 individual sperm whales between 2 consecutive y and Bigg et al. (1986) reported that natural marks on 1 killer whale remained unchanged for at least 20 y. The pigmentation patterns on flukes of young humpback whales change over time while the fringe of the fluke seems to be more stable (C. Carlson, pers. comm.).

When using individual identification for population estimates, based on mark-recapture techniques, it is desirable to photograph whales at random. However, Hammond (1986) suggests that there exist in most populations of animals inherent differences in the characteristics and behaviour of individuals such that capture and recapture probabilities are heterogeneous, regardless of the method of sampling.

A number of sampling biasses are possible in my study. Fluking behaviour

seemed similar for individual female/immature sperm whales. However calves rarely raise their flukes in the air. Thus fewer photographs of calf flukes were obtained. One of the mature males did not raise its flukes more than 45° from the water surface and no good photograph, with the fluke perpendicular to the water surface, could be taken. Fortunately, this particular male had an unusual curled fluke which allowed identification by this means.

During the study off Galapagos most emphasis was placed on photographing whales which had just returned to the surface after a dive. The sperm whales spent about 10 min at the surface between 45 min dives. This may have led to a biassed effort towards smaller, sick, injured animals or mothers accompanying calves which may have surfaced at more frequent intervals. When different groups surfaced at the same time and distance from the boat, we steered towards the larger group, and thus, perhaps, biassed our sample towards social animals. Similarly when a mature male was present more effort was directed towards the male and the whales near him. Within the same day individuals were probably not photographed at random, as whales were spread over several km and the boat tended to remain with 1 subset of the whales, but between days (after at least 1 night) individuals were photographed more randomly. On a few occasions, for unknown reasons, the whales were harder to approach. Despite these problems, statistical tests on the Galapagos data, using days as sampling units, did not reject the assumption of equal catchability (Whitehead, 1986b).

It was not possible to identify with certainty up to 8.7% of the photographed female/immature sperm whales off Galapagos, using the method of individual photographic identification. These whales had fewer unique marks on their flukes than the ones which were individually identified with certainty.

The only other method used for recognizing individual sperm whales has been shooting stainless-steel "Discovery tags" into the whale and later recovering the marks during whaling operations. There are some disadvantages to using Discovery tags: the distance to the whale has to be within 10-35 m to implant a mark (Kato, 1981); there is only one possibility of re-identification; whales have to be killed to read the number on the Discovery tags; and tags are frequently

"shed" (IWC, in press). Off the Galapagos 1 female/immature sperm whale was identified on 23 different occasions.

4.2. MOVEMENTS, DIVING, SITE-FIDELITY AND SPEED

4.2.1. Movements

The sperm whales off the Galapagos Islands stayed off the shelf but generally within 55 km of it. Their distribution seemed to be centred on a 200 km long area where the Equatorial Underwater Current hits the shelf west of Isabela Island and creates upwelling (Houvenaghel, 1978).

Gaskin (1976) showed that sperm whales off New Zealand were often observed in newly upwelled waters. However, Volkov and Moroz (1977) were not able to relate the distribution of sperm whales in the eastern part of the tropical Pacific to oceanographic surface water conditions. They pointed out that this might be attributed to the distribution of the prey species of the sperm whales, meso- and bathypelagic cephalopods, being affected by water masses far below the water surface.

4.2.2. Diving

The study off the Galapagos was carried out in waters deeper than 3,500 m. Papastavrou's (1986) preliminary results of identified squid beaks, collected from faeces left by diving sperm whales, suggested that they consisted mainly of the family Histioteuthidae. Analyses of dive traces of the sperm whales of the Galapagos showed that the whales usually levelled out at 410 m (Papastavrou, 1986). The dive time for the individually identified females/immatures was about 45 min (Whitehead, 1986b) which is longer than the 20 min which has been recorded for females. The only original source, to my knowledge, which mentions dive times for females under non-stressed conditions, is Beale (1839). He was cautious because he could only distinguish groups of females, not individuals. Several other authors mention dive times for females but all seem to either quote Beale directly or indirectly, or use observations on hunted whales. The only time,

during the study off Galapagos, when the sperm whales were regularly diving for about 20 min and staying at the surface for 10 min, was during the flight after the killer whale attack (Section 3.11). The sperm whales were obviously stressed and the dive time is similar to the 20 min which has been recorded for females during whaling operations (Best, 1974).

4.2.3. Site-fidelity

Particular individuals were identified off the Galapagos Islands for approximately 7 weeks which was close to the total study period. During the study the mixed groups were followed and identified in an area along the shelf-break (section 4.2.1) where they presumably were foraging for squid (section 4.2.2). The results show that the sperm whales preferred an area west of Galapagos and they stayed there for the study period. This area may be described as some sort of foraging and perhaps reproductive home-range. Future studies are needed to survey adjacent waters off the Galapagos to achieve more conclusive evidence of home-ranges for sperm whales. From re-identification of a particular mixed group within a few km between 2 consecutive y, Gordon (1986) proposed that there may be site-fidelity for mixed groups. Similar results are available from whaling data (Best, 1979). Animals were tagged and later re-captured in the same area off South Africa, suggesting that mixed groups use the same migration route in consecutive y (Best, 1979). However more field studies are needed at different times of y to find out whether the mixed groups off the Galapagos are resident year around.

A female marked in May 1975 with a stainless-steel Discovery tag 400 km northwest of the Galapagos was killed 10 months later off the Peruvian coast approximately 1,500 km southeast of the islands (Ivashin, 1977). This finding shows that females migrate through the general area of the Galapagos but it does not imply that the whales from just west of Galapagos migrate to the South American coast. There is apparently a general southward migration of sperm whales along the South American coast from February to May (Christensen, 1926; Clarke, 1962), although sperm whales are found y round in the eastern tropical

Pacific (Townsend, 1935; Bannister and Mitchell, 1980). It is not known whether the sperm whales off the Galapagos are resident y around or belong to northern or southern hemisphere stocks or both (Rice, 1975). Berzin (1974 in Berzin and Veinger, 1981) suggested that the sperm whales off the Galapagos form a separate population. Future studies using the method of individual photographic identification may be useful for identifying stocks.

4.2.4. Speed

The mean speed of identified whales over the bottom between consecutive days of 2.5 km/h was less than the 3.9 km/h Whitehead (1986c) estimated over shorter periods. The differences can be explained by the whales not always moving in straight lines over periods of 1 day. Undisturbed animals have been recorded to swim at a speed of 4.5-5.5 km/h (Beale, 1835). Beale did not say whether any calves were present. Lack of data hindered a comparison of speed between mixed groups with and without calves. Groups with calves might swim at a slower speed.

The mean speeds over the bottom for whales moving in a northern and southern direction were similar (2.5 and 2.5 km/h, respectively). However, there was a difference in mean speeds over the bottom for whales moving in a westerly or easterly direction. This can be attributed to the westward flowing South Equatorial Current (SEC). A crude calculation of the speed of the current gave:

$$v_{west} - v_{current} = v_{east} + v_{current}$$

$$3.28 - X = 1.91 + X$$

v_{west} = mean speed (km/h) of whales heading west
$v_{current}$ = speed (km/h) of the current
v_{east} = mean speed (km/h) of whales heading east

$$X = 0.69$$

The actual speed over bottom of the whales from west and east heading whales, was 2.6 km/h. This was calculated by correcting for the speed of the current (3.3-0.7). The estimated speed of the current was 23 cm/sec west flow which is within the range of earlier recorded speeds of 20-100 cm/sec west flow for the SEC for this time of the year (Firing, Lukas, Sadler and Wyrtki, 1983). The

estimated current speed of 23 cm/sec of the SEC is not the actual speed because the eastward moving Equatorial Undercurrent's influence of the diving whales could not be estimated.

4.3. SOCIAL ORGANIZATION

4.3.1. Females and immature males

The predominance of whales 7-11 m in length (Whitehead and Arnbom, in press), observations of calves and the high frequency of calluses on the dorsal fins, strongly suggest that most of the whales encountered during February to April 1985, off the Galapagos, were mature females and immatures. The 210 females/immatures with certain individual identification were always observed in the vicinity (less than 500 m) of other females/immatures. Individual whales were observed alone, but only for short time periods (approximately 10 min). This confirms Clarke's (1956) observations that females are invariably gregarious.

The 210 females/immatures were clustered into 23 groups, and 13 of which contained more than 6 identified individuals. These 13 groups were assumed to be mixed groups. Ten of the mixed groups were identified on 2 or more days. The estimated median size of these groups was 19.5 animals (Whitehead and Arnbom, in press). This is similar to the median figure of 25 for mixed groups, which Best (1979) derived from a literature review. The largest time span between first and last identifications of a particular mixed group (G8) was 49 days, which is close to the total study time of 57 days. The largest time span between 2 identifications of a particular individual was 46 days. The mixed groups were observed to associate on several occasions, and 2 groups (G1 and G10) were observed to associate more than other groups. The data suggest that identified individuals did not switch groups during the study, although it may have occured.

Only once did the observed number of whales exceed the estimated number of individuals in the identified group. This was on the 18 April when killer whales attacked group G3 (section 3.11). Group G3 is estimated to have 18.3 (s.e. 1.0)

members (Whitehead and Arnbom, in press), but on that particulate date 34 whales were observed. This suggests that another group was present but not identified. An alternative explanation could be that the estimated number of members in G3 was to low. Statistical tests to the estimated grouping of G3 showed no significant departure from the multinominal model (Whitehead, 1986c). Therefore the grouping of G3 was retained.

There was an overall difference between the groups when comparing the shape of the fluke notch, which suggests that there are morphological differences between groups and may imply that these groups are genetically discrete.

Studies of killer whales off British Columbia (Bigg, 1982; Ford and Fisher, 1983) show that discrete pods associate regularly but when they disassociate each pod contains the same individuals as before the association. During 15 y of study no killer whales have been recorded to switch pods.

It has also been shown (Ford and Fisher, 1983) that the more commonly associated different pairs of killer whale pods had more similarity in their sound repertoire. Ford and Fisher (1983) suggested that those pods which associate more than others are more genetically related to one another, but no concrete evidence of genetic similarities has been put forward.

The largest terrestrial mammal, which is relatively well studied, is the African elephant (*Loxodonta africana*). The African elephant is in several ways similar to the sperm whale: it has a long gestation, a calving interval approximately 6 y, is long lived and shows group segregation by sex and age (Douglas-Hamilton and Douglas-Hamilton, 1975; Laws, Parker and Johnstone, 1975). Groups of female elephants and their offspring have a mean group size of 22.5 animals in high density areas (Laws et al., 1975) which is similar to the estimated mean group size of 19.7 animals for sperm whales off Galapagos. Douglas-Hamilton and Douglas-Hamilton (1975) suggested that for these female elephant groups the ties between individuals may be strongest between calves of similar age and their different mothers. When a female elephant group reaches a certain size, which may depend on a balance between competition for food and clumping for mutual protection, a mother and her offspring may leave the group to start their own

female group (Douglas-Hamilton and Douglas-Hamilton, 1975). In Douglas-Hamiltons' study several elephant groups showed splitting tendencies, with well developed sub-units, but never actually separated by more than 1 km, which is probably the limit at which female groups could remain in vocal contact (Douglas-Hamilton and Douglas-Hamilton, 1975). It is not known at what distance sperm whales can detect each other acoustically, although we could hear the sperm whales with the hydrophone at approximately 7.5 km. During an attack by killer whales on sperm whales, 2 mixed groups were observed to merge and behave as 1 cohesive unit against the attackers (Section 3.11 and 4.5). These groups may have originated from a common kin group. Strong family ties between these groups may have led to the frequent associations. Alternatively, these groups may have associated frequently, and therefore developed group coordination against predators.

4.3.2. Calves and escorts

The number of calves observed within each mixed group varied from 0-2 individuals and was lower from the expected number (section 3.6.2). The observation of fewer calves than expected may be explained by the high mortality for calves during their first y (Best, 1979), if the calves had been born several months before the start of my study. No births of sperm whales were observed during the Galapagos study. Future studies are needed to investigate the calving season or seasons off the Galapagos.

Different individual females/immatures were observed to escort the same calf on different occasions. Further, identified females/immatures were observed with several different calves on different occasions. These observations suggest that females/immatures may accompany 1 or several calves, and also that different females/immatures accompany particular calves. The sex of the escorts could not be confirmed. However, all the 7 individuals that scored as escorts and from which it was possible to decide if a callus was present or not, had a callus on the dorsal fin, indicating that these were females.

These findings are very similar to Gordon's (1986) results from Sri Lanka.

Gordon showed that calves associated closely with several different adult females, and some females associated with a number of different calves. These studies off Galapagos and Sri Lanka confirm Ash's (1962) speculation that calves are attended by different individuals at different times.

The observations of remoras on a calf's back and the very few times calf flukes were raised in the air suggest limited diving ability of calves. These observations concur with Best et al. (1984). As sperm whales feed at considerable depth and the calf probably cannot follow the mother for several consecutive deep dives, there would be an advantage in being able to share the caring of calves with other escorting individuals especially since predation by sharks seems to be an important threat to the calves (section 4.5).

In African elephants, siblings and adult females (which are not the mother or a sibling) have been observed to take care of calves (Douglas-Hamilton and Douglas-Hamilton, 1975). Communal suckling has been recorded in several large mammals with complex social organization such as lions (*Panthera leo*) and African elephants (Schaller, 1972; Douglas-Hamilton and Douglas-Hamilton, 1975). It has not been observed in the Cetacea although it might occur in sperm whales (Best et al., 1984). There is circumstantial evidence which supports communal suckling in sperm whales such as the finding that there is always a surplus of lactating females to number of calves in mixed groups and that milk traces have been found in stomachs of juveniles up to 13 y of age (Best et al., 1984). There is one account from the Indian Ocean of two sperm whale calves of similar size which appeared to be suckling at the same time from the same individual (H. Whitehead, pers. comm.). In sperm whales, births of twins have not been recorded, although whaling data show a proportion of 0.005 of prenatal twins (Gambell, 1972). Whitehead's observation is not likely to have been of twins, although this cannot be excluded. Communal suckling was discussed by Best et al. (1984). Who quoted Schaller (1972) as follows: "communal suckling has an advantage to the offspring that if the mother should have inadequate milk, dry up early or die, its young can still obtain milk from other lactating females in the group. Disadvantages of such behaviour include the deprivation of milk for newborn young as a result of the attentions of older offspring".

4.3.3. Males

The large sperm whales off Galapagos were between 13.7-16.4 m long (Whitehead and Arnbom, in press) and none had a callus on the dorsal fin. There is no record of a female larger than 12.3 m (Clarke, 1956) and large males do not have a callus (Kasuya and Ohsumi, 1966). Thus it was assumed they were large males.

The large males were observed singly, in pairs or, once, in a set of three but always associating with groups of females/immatures. There was no obvious tendency for any particular males, or males of the same size, to be identified together.

The number of large males observed together at the same time off Galapagos is in accordance with a review by Best (1979). However, off the Galapagos large males of different sizes were identified together, while Best (1979) presents material which indicates that males of similar size swim together. The difference between this study and Best's may be that my observations were in tropical waters, presumably on a breeding ground, while Best's were in sub-tropical waters during migration. It may be advantageous for males to swim together during migration, while on the breeding grounds they may compete with one another for females and therefore avoid males of similar size.

Results from Kato (1984) show an increase in the number of scars observed on large males at a length of 14 m, the length at which sperm whale males come into breeding conditin (Best, 1979). All the identified large males off Galapagos were 13.7 m or longer. Thus, the large males identified in this study are likely to be of potential breeding status. No fresh wounds or agonistic behaviour between large males was observed off the Galapagos.

Large bulls of the African elephant have rarely been observed fighting and it has been suggested that resident large bulls know the other bulls and their relative social status (Douglas-Hamilton and Douglas-Hamilton, 1975). The ability of large sperm whales to hurt one another in a combat is high. Broken jaws, missing teeth and heavy scarring are frequently found (Best and Gambell, 1968; Kato, 1984). Territorial males of Grevy's zebra (*Equus grevyi*) tolerate other males as long

there is no female in oestrus (Kmgel, 1972). However when an oestrus female is present the resident male chases away the other males from its territory. Fights between large sperm whale males may only occur when a female in oestrus is present.

Water visibility off the Galapagos varied between 1-40 m, so the usefulness of visual displays between large males may have been limited. No lob-tailing or breaching was observed from large males. Sperm whales probably communicate more acoustically than visually. During the rutting season red deer (*Cervus elaphus*) stags use sounds for display and it has been shown that the stags avoid fighting with individuals they are unlikely to beat (Bützler, 1974; Clutton-Brock, Albon, Gibson and Guinness, 1979). The distinct "slow clicks" of large male sperm whales (Weilgart and Whitehead, in prep.) may also be used for assessment. The only observation during the Galapagos study which may support this, was the encounter when 3 large sperm whale males were identified together with approximately 35 females/immatures, but only 1 large male was clicking (section 3.7.2). Best et al. (1984) proposed that medium-sized (12.2-13.7 m) males may also take part in the breeding. The lack of any identification of medium-sized males during the study off Galapagos suggest that such males may not be involved in reproduction in this area.

4.3.4. Proportion of large males to mature females

Whitehead (1986b) used Schnabel mark-recapture census to estimate the number of females/immatures off the Galapagos Islands. However Whitehead cautioned that any immigration into, or migration from, the study area will have considerably biassed his estimate of 272 (standard error 23.6) females/immatures. Using a maximum correction factor of 0.087 from the regression analysis of identifiability to account for the whales that may not be identifiable by the method used in this study (section 3.2.2), a total population estimate for my study area is 272-296 females/immatures.

Best (1979) estimated the ratio of large males to sexually mature females in a population to be 1:2.6, and an estimate of the proportion of mature females in

mixed group is 0.585 (0.78 of the population of mixed groups are females and 0.75 of these are mature, from Best, 1979). Then, the expected proportion of large males to mature females in tropical waters is 0.225 (0.585 x 1/2.6). The observed ratio of large males to mature females, assuming all large males during the study period off Galapagos were identified and that the total estimated population of females/immatures in mixed groups was 272-296, was 0.0404-0.0440 (7/0.585 x 296 or 272).

The proportion of large males to mature females off the Galapagos (0.0404-0.0440) was considerably lower than the expected (0.225). Obsumi (1966) suggested, from theoretical age distributions of sperm whales and North Pacific whaling data, that 75-90% of the large males migrate to high latitudes during summer. Based on Obsumi's (1966) analyses and the distribution of large males from whaling data, Best (1979) suggested that only 10-25% of the large males take part in the breeding each y. Best believed that, every spring, all large males migrate to the low latitudes, and, after a selection process, the medium-sized and large males which were unsuccessful in obtaining access to a mixed group, migrated back to the high latitudes. If the expected number of large males on the breeding grounds (0.225) is corrected for Best's assumption that 10-25% of the large males take part in the breeding the corrected proportion will be 0.0225-0.0560, which is similar to what was observed (0.0404-0.0440) off the Galapagos.

However, the Galapagos data do not concur with the suggestion that all large males migrate to the low latitudes each y. The time of the year and the low proportion of large males to mature females indicates that only a small proportion of the large males migrate to the breeding grounds and take part in reproduction. It is not known whether the large males observed off Galapagos are resident for several consecutive breeding seasons or migrate away after the breeding season is over. However Whitehead and Arnbom (in press) calculated that the proportion of large males to other animals which were sighted less than 300 m from the research vessel increased from 0.0024 in late February to 0.026 in April. They suggested immigration of large males into the area might have occurred during

the study period. The peak of the breeding season for the northern hemisphere stock of sperm whales is thought to be from March to May (Ohsumi, 1965; Berzin, 1971). Thus the increase of large males seems to coincide with the breeding season for the northern hemisphere stock.

4.3.5. Associations between large males and mixed groups

By using the sound of the "*slow click*" as an indication of the presence of males (Weilgart and Whitehead, in prep.), Whitehead and Arnbom (in press) estimated that 16% of the time that groups of females/immatures were followed, they were attended by 1 or more large males. The 21 encounters with large males varied in duration from 5 min to over 19 h, although it was often difficult to tell when a male joined or left a group (Whitehead and Arnbom, in press). During 15 encounters with males, the association between the male and the group was clear (only 1 group was identified before, during and after the encounter). These encounters had a mean duration of 5 h and 52 min.

Identified large males were observed with different mixed groups, and, different large males were associated with the same mixed groups. The data did not suggest that some mixed groups associated more with large males more than other mixed groups. These findings do not support the general belief that 1 large male holds a harem during the breeding season (e.g. Berzin, 1971).

From a simple model, Whitehead and Arnbom (in press) suggest that as long as the time between encountering groups of females for a large male is less than the period of oestrus, a "searching strategy", as observed off the Galapagos, should be favoured over a "harem holding strategy". Whitehead and Arnbom stress that the model is simplistic and various factors could modify or invalidate its conclusions: females might eject males from the group, "resident" males might possess an advantage during encounters with other males, or a female might show signs of approaching oestrus which could be monitored by males.

The Galapagos study confirms Best's (1979) suggestion, from his analysis of the different species of ecto-parasites found on large males and females, that the interaction between females and large males may only be brief, a matter of a few

days. The study supports Best et al. (1984) speculation that sperm whales may have a behaviour which resembles the "searching strategy" of bull elephants suggested by (Barnes, 1982).

4.4. CARE-GIVING AND PREDATION

When the killer whales attacked the sperm whales, the sperm whales bunched together with the calf positioned in the middle of the group. The killer whales tried to approach the sperm whales, from behind or the flank. The sperm whales tried to position themselves so their heads always pointed towards the attackers. Sperm whales are known to dive to a depth of more than 1,500 m (Heezen, 1957) and killer whales to approximately 300 m (Bowers, 1975). The attacked sperm whales did not dive out of reach of the killer whales. This may be attributed to the limited diving ability of the calf, or the need to return to the surface for breath. No sperm whale was killed and only a few gashes were seen. No pieces of blubber or flesh were noticed. The whales showed a coordinated behaviour during the flight.

Sperm whales have been seen to bunch around calves during a killer whale attack and just after a birth (Gambell, 1968; Best et al., 1984; Weilgart and Whitehead, 1986). This bunching behaviour may have evolved as a mean of protecting calves from predators such as killer whales and sharks (Best et al., 1984). Other mammals known to protect calves from predators by bunching around calves include African elephant and muskox, *Ovibos moschatus*, (Hone, 1934; Douglas-Hamilton and Douglas-Hamilton, 1975). Jarman (1974) suggests that a group may successfully defend itself against a predator in a concerted action, where a single animal could not.

The killer whales were not successful in attacking the sperm whales, which seemed to defend themselves with their jaws and flukes. The number of sperm whales surrounding the calf, coordination between these individuals, and the power of the sperm whale jaw are probably efficient ways to protect calves from killer whales. However Best et al. (1984) found stranded and net-entangled sperm whale calves which had tooth mark scars from killer whales.

Both killer whales and sperm whales leave parallel tooth mark scars on their victims (Best et al., 1984). Other likely sources for the tooth mark scars on the whale flukes off the Galapagos are cephalopods, sharks and false killer whales (*Pseudorca crassidens*). However, it seems impossible for cephalopods to make parallel lines in the free edge of the tail, as the cuts are too close together (F.A. Aldrich, pers. commn.).

Killer whales have erupted teeth in both upper and lower jaw while sperm whales have erupted teeth in the lower jaw but rarely any erupted teeth in the upper jaw. Thus if it had been possible to see the ventral and the dorsal side of the flukes it might have been possible to tell if the tooth mark scars were from sperm or killer whales. However this was not possible from the photographs. No flukes with 2 parallel rows of tooth mark scars were found, which could have been used for comparing the shape between the 2 jaw rows: sperm whales have straight jaws, while killer whales have curved jaws.

There are differences in tooth mark scars on the flukes of sperm and humpback whales. The information on humpback whales comes from photographs in the catalogues of humpback flukes in the northwest Atlantic (Katona, Harcourt, Perkins and Kraus, 1980) and of the southern gulf of Maine (Mayo, Carlson, Clapham and Mattila, 1985). The entire surface area of some humpback flukes is covered with tooth mark scars, while on sperm whale flukes these were only found along the trailing edges. Most tooth mark scars on the flukes of humpbacks are from killer whales (Katona et al., 1980). This suggests that most of the tooth mark scars on the sperm whale flukes are either from a different species or, less likely, from killer whales but that they only bite along the edge of the flukes. A photograph of possible tooth mark scars from a shark on a sperm whale calf (in Best et al., 1984), shows similar tooth mark scars found on 8 of the flukes photographed off Galapagos.

A comparison of the scallop shapes on the flukes with photographs (in Lineaweaver III and Backus, 1970) of a blue shark (*Prionace glauca*) attacking a dead dolphin, suggests that scallops are made by sharks. The results from the Galapagos seem to strengthen the assumption that sharks attack sperm whales.

There is a description of *Moby-Dick's* fluke in Melville (1851) "his broad fins are bored, scalloped out like a lost sheep's ear". Sharks have been present at birth of sperm whales (Gambell, 1968) and have also been noted to follow groups (Best, 1979). Off Sri Lanka, the number of natural marks on the trailing edges of the flukes was lower than off Galapagos Islands (J. Gordon, pers. comm.). This may be because of a better ability of the sperm whales off Sri Lanka to defend themselves against predators or there may be less predators. However, this would imply that the method of individual photographic identification relying on uniquely marked flukes may be less successful in other areas.

4.5. CONCLUSIONS

Individual sperm whales such as *Mocha Dick*, *Timor Tim* and *Newfoundland Tom* were well known to whalers by their distinctive natural marks (Reynolds, 1839; Slijper, 1962). However, not until recently have scientists started to use the method of individual photographic identification on sperm whales.

The results presented in this thesis confirm that females/immatures live in discrete groups, at least for several weeks. However the results do not support the general belief that male sperm whales hold a harem, rather it seems like they adopted a searching strategy for female groups. The lack of observations of medium-sized males suggests that they do not migrate to the breeding ground and take part in the reproduction and the ratio of the number of large males to mature females indicates that there is only a small proportion of the large males are available for breeding every y.

The non-intrusive methods developed for studying living sperm whales by Hal Whitehead and Jonathan Gordon and their colleagues have brought us over a threshold in the understanding of the social system of these animals. Previously it was thought to be almost impracticable technically and economically (Ohsumi, 1971) to obtain systematic and protracted observations of sperm whales in the wild (Best, 1979). The results in this thesis are just a first step in our understanding of the true nature of the *Leviathan* which has more books devoted to him than any other marine animal.

4.6. SUMMARY

1. Focus and distance between the photographer and the whale were the most important factors when taking photographs useful for the identification of individual sperm whales.

2. The median distance between the photographer and the whale for photographs of individual with certain identification was about 70 m.

3. Photographed flukes with a deviation of less than 30-35 degrees from being perpendicular to the camera axis were useful for identification.

4. Reasonable variations of the relative lightness and darkness on the negative did not change the identifiability of flukes.

5. It was possible to identify individuals as long as the trailing edge of the fluke was visible.

6. It was easier to identify individuals from the natural marks on flukes than dorsal fins.

7. Natural marks used for individual identification were nicks, distinct nicks, waves, scallops, holes, missing portions, tooth mark scars, barnacles, the shape of fluke and the type of fluke notch. Additionally, on dorsal fins, skin shedding patterns and the presence and form of a callus were useful.

8. No changes of natural marks were noticed during the study period, although the trailing edge of the flukes may change with time.

9. Fluking behaviour was similar for individual sperm whales, although calves rarely raised their flukes in the air before a dive.

10. It was estimated that up to 8.7% of the photographed female/immature sperm whales off the Galapagos were not possible to identify using the method of individual photographic identification.

11. Two hundred and ten females/immatures were individually identified with certainty from fluke patterns.

12. Sixty-three females/immatures, 4 large males and 3 calves were identified on 2 or more days.

13. The geographical positions of re-identifications of known individuals suggest that the sperm whales preferred a rich upwelling area.

14. Re-identification of individuals showed that many stayed in the area for at least the duration of the study period, which suggests that the sperm whales off the Galapagos have at least a temporary home range.

15. The mean speed over the bottom for individuals identified on consecutive days was 2.5 km/h.

16. Females/immatures always occured in groups.

17. Individually identified females/immatures were clustered into 23 discrete groups. Thirteen of these groups contained more than 6 associated individuals.

18. Ten of the 13 groups were observed on 2 or more days.

19. The estimated median size for these 10 groups was 19.5 animals per group.

20. Observations of calves, the high frequency of dorsal fins with a callus, and the predominance of whales 7-11 m in length suggested that most sperm whales off Galapagos belonged to mixed groups of mature females, immatures and calves.

21. Mixed groups associated on several occasions, and 2 of the groups associated more than others.

22. There was an overall difference between groups when comparing the shape of the fluke notch.

23. The estimated number of identified calves per mixed group varied from 0 to 2. This was lower than the expected number.

24. All whales scored as escorting a calf and from which it was possible to tell if a callus was present or not, had a callus. This indicates that they were females.

25. Different females/immatures were observed to escort the same calf. Further, particular females/immatures were observed with several calves.

26. Seven large males with lengths of 13.7-16.4 m were individually identified with certainty.

27. None of the large males had a callus on the dorsal fin.

28. The large males were observed either as singles, pairs or a set of three.

29. There was no preference for particular large males, or large males of similar size, to be identified together.

30. The large males are likely to be of potential breeding status.

31. No fresh wounds or agonistic behaviour between large males was observed.

32. The lack of sightings of medium-sized (12.0-13.7 m) males suggests that they do not take part in reproduction in this area.

33. The proportion of large males to mature females suggests that all large males do not migrate to breeding grounds and therefore do not take part in reproduction every year.

34. Identified large males were observed with different mixed groups.

35. Different large males were associated with the same mixed group.

36. There was no indication that some mixed groups associated more with large males, more than others.

37. The large males seemed to follow a strategy of searching for mixed groups, instead of holding harems.

38. During an attack by killer whales on sperm whales a high degree of coordination of the sperm whales was noted. For instance: larger animals bunched around a calf and thus protected it.

39. Twenty-one percent of the flukes had tooth mark scars of which a majority were probably derived from sharks attacks, but some may also be from sperm, killer or false killer whales.

40. Scallops on the trailing edge of the flukes are probably caused by sharks.

41. A difference in the number of unique marks on the flukes between different geographical areas suggests that the method of photographic identification relying on uniquely marked flukes may be less successful in other areas.

LITERATURE CITED

Arnbom, T, Papastavrou, V, Weilgart, L. and Whitehead, H. In press. Sperm whales react to an attack from killer whales. *J. Mammal.*

Ash, C. 1962. *Whaler's Eye.* Mamillan, New York, 245 pp.

Backus, R.H. and Schevill, W.E. 1966. Physeter clicks. pp. 510-528. *In*: K.S. Norris (ed.). *Whales, Dolphins and Porpoises,* University of California Press, Berkely, 789 pp.

Bannister, J. and Mitchell, E. 1980. North Pacific sperm whales from Maury and Townsend charts. *Rep. int. Whal. Commn. (special issue 2)*: 219-230.

Barnes, R.F.W. 1982. Mate searching behaviour of elephant bulls in semi-arid environment. *Anim. Behav.* 30: 1217-1223.

Beale, T. 1835. *A Few Observations on the Natural History of the Sperm Whale.* Effingham Wilson, London, 1976, 58 pp.

Beale, T. 1839. *Natural History of the Sperm Whale.* Holland Press, London, 1973, 394 pp.

Bennet, F.D. 1840. *Narrative of a Whaling Voyage Around the Globe from the Year 1833 to 1836.* Richard Bentley, London, 2 vol.

Berzin, A.A. 1971. *The Sperm Whale.* Pishchevaya Promyshlennost, Moscow; translation by Israel Program for Translations, 1972, 394 pp.

Berzin, A.A. and Veinger, G.M. 1981. Investigations into the population morphology of sperm whales, *Physeter macrocephalus* L. 1758, of the Pacific Ocean. *FAO Fish. Ser. 5* [Mammals in the seas] 3: 259-268.

Best, P.B. 1968. The sperm whale (*Physeter catodon*) off the west coast of South Africa 2. Reproduction in the female. *S. Afr. Div. Sea. Fish. Invest. Rep* 66: 1-32.

Best, P.B. 1970. The sperm whale (*Physeter catodon*) off the west coast of South Africa 5. Age, growth and mortality. *S. Afr. Div. Sea. Fish. Invest. Rep.* 79: 1-27.

Best, P.B. 1974. Biology of the sperm whale as it relates to stock management. pp. 257-293. *In* W.E. Schevill (ed.). *The Whale Problem.* Harvard University Press, Cambridge, Mass., 419 pp.

Best, P.B. 1979. Social organization in sperm whales, *Physeter macrocephalus*. pp. 227-289. *In*: H.E. Winn and B.L. Olla (eds). *Behavior of Marine Animals. Current perspectives in research 3.* Plenum Press, New York-London, 438 pp.

Best, P.B. and Butterworth, D.S. 1980. Timing of oestrus within sperm whale schools. *Rep. int. Whal. Commn.* (special issue 2): 137-140.

Best, P.B., Canham, P.A.S. and Macleod N. 1984. Patterns of reproductions in sperm whales, *Physeter macrocephalus. Rep. int. Whal. Commn.* (special issue 6): 51-80.

Best, P.B. and Gambell, R. 1968. A comparison of the external characters of sperm whales off South Africa. *Nor. Hvalfangst-tid.* 57: 146-164.

Bigg, M.A. 1982. An assessment of killer whales (*Orcinus orca*) stocks off Vancouver Island, British Columbia. *Rep. int. Whal. Commn.* 32: 655-666.

Bigg, M.A., Ellis, G.M. and Balcomb, K.C. 1986. The photographic identification of individual cetaceans. *Whalewatcher* (J. Amer. Cetacean Soc.) 20: 10-12.

Bower, C.A. 1975. Deep object recovery with pilot and killer whales. *Abstract I Biennial Conference on the biology of marine mammals*, Santa Cruz, Califonia.

Bullen, F.T. 1899. *The Cruise of the "Cachalot"*. Smith, Elder and Co., London, 379 pp.

Bützler, W. 1974. *Kamp- und Paarungsverhalten, soziale Rangordnung und Aktivitätsperiodik beim Rothirsch (Cervus elaphus L.).* Verlag Paul Parey, Belin, 80 pp.

Caldwell, M.C. and Caldwell, D.K. 1966. Epimelectic (care-giving) behavior in *Cetacea*. pp. 755-788. *In* K.S. Norris (ed.). *Whales, Dolphins and Porpoises*. University of Califonia Press, Berkely, 789 pp.

Caldwell, D.K., Caldwell, M.C. and Rice, D.W. 1966. Behavior of the sperm whale, *Physeter catodon L.*. pp. 677-717. *In* K.S. Norris (ed.). *Whales, Dolphins and Porpoises*. University of califonia Press, Berkely, 789 pp.

Christensen, A.F. 1926. Hvalfeltet paa Ecuador. *Nor. Hvalfangst-tid.* 15: 111-112. (In Norwegian)

Clarke, M.C. 1980. Cephalopoda in the diet of sperm whales of the Southern Hemisphere and their bearing on sperm whale biology. *Discovery Rep.* 37: 1-324.

Clarke, R. 1956. Sperm whales off the Azores. *Discovery Rep.* 28: 237-298.

Clarke, R. 1962. Whale observation and whale marking off the coast of Chile in 1958 and from Ecuador towards and beyond the Galapagos Islands in 1959. *Nor. Hvalfangst-tid.* 51: 265-287.

Clarke, R., Aguayo, A. and Paliza, O. 1968. Sperm whales of the Southeast Pacific. *Hvalradets Skrifter* 51: 1-80.

Clarke, R., Aguayo, A. and Paliza, O. 1980. Pregnancy rates of sperm whales in the southest Pacific between 1959 and 1962 and a comparison with those from Paita, Peru between 1975 and 1977. *Rep. int. Whal. Commn.* (special issue 2): 151-158.

Clutton-Brock, T.H., Albon, S.D., Gibson, R.M. and Guinness, F.E. 1979. The logical stag: adaptive aspects of fighting in red deer (*Cervus elaphus L.*). *Anim. Behav.* 27: 211-225.

Colnett, J. 1798. *A Voyage to the South Atlantic and Round Cape Horn Into the Pacific Ocean for the Purpose of Extending the Spermaceti Whale Fisheries.* W. Bennet, London, 179 pp.

Darling, J.D. and Jurasz, C. 1983. Migratory destinations of North Pacific humpback whales. pp. 359-368. *In* R. Payne (ed.). *Communication and Behaviour of Whales.* AAAS Selected Symposium 76, Westview Press, Boulder, Co., pp. 643.

Dorsey, E.M. 1983. Exclusive adjoining ranges in individually identified minke whales (*Balaenoptera acutorostrata*) in Washington state. *Can. J. Zool.* 61: 174-181.

Douglas-Hamilton, I and Douglas-Hamilton, O. 1975. *Among the Elephants.* Collins and Harvill Press, London, 285 pp.

Edwards, A.E. 1979. *Multiple Regression and the Analysis of Variance and Covariance.* Freeman W.H. and Company, New York, 212 pp.

Everitt, B. 1974. *Cluster Analysis.* Henemann, London, 122 pp.

Firing, E., Lukas, R., Sadler, J. and Wyrtki, K. 1983. Equatorial undercurrent disappears during 1982-83 *El Nino. Science* 222: 1121-1123.

Ford, J.K.B. and Fisher, N.D. 1983. Group-specific dialects of killer whales (*Orcinus orca*) in British Columbia. pp. 129-162. *In* R. Payne (ed.). *Communication and behavior of whales.* AAAS Selected Symposium 76, Westview Press, Boulder, Co., 643 pp.

Gambell, R. 1968. Aerial observations of sperm whale behaviour. *Nor. Hvalfangst-tid.* 57: 126-138.

Gambell, R. 1972. Sperm whales off Durban. *Discovery Rep.* 35: 199-358.

Gaskin, D.E. 1970. Composition of schools of sperm whales, *Physeter catodon, L.* east of New Zealand. *N.Z.J. Mar. Freshwater Res.* 4: 456-471.

Gaskin, D.E. 1976. The evolution, zoogeography and ecology of Cetacea. *Oceanogr. Mar. Biol. Ann. Rev.* 14: 247-346.

Gaskin, D.E. and Cawthorn, M.W. 1973. Sperm whales (*Physeter catodon* L.) in the Cook Strait Region of New Zealand: Some data on age, growth and mortality. *Norw. J. Zool.* 21: 45-50.

Gordon, J.C.D. 1986. Sperm whale groups and social behaviour observed off Sri Lanka. *Rep. int. Whal. Commn.* Doc. SC/38/Sp7, 16 pp.

Hammond, P.S. 1986. Estimating the size of naturally marked whale populations using capture-recapture techniques. *Rep. int. Whal. Commn.* (special issue 8): 253-282.

Heezen, B.C. 1957. Whales entangled in deep sea cables. *Nor.-Hvalfangst-tid.* 46: 665-681.

Hone, E. 1934. The present status of the muskox in Artic North America and Greenland. *Spec. Publ. Amer. Comm. Int. Wild Life Protect.* 5: 1-87.

Houvenhagel, O.T. 1978. Oceanographic conditions in the Galapagos Archipelago and their relationships with life on the islands. pp. 181-202. *In* R. Boje and M. Tomczak (eds). *Upwelling Ecosystems.* Springer-Verlag, New-York, 303 pp.

Husson, A.M. and Holthuis, L.B. 1974. *Physeter macrocephalus Linnaeus, 1758,* the valid name for the sperm whale. *Zoologische Mededelingen,* Leiden 48: 205-217.

Ivashin, M.V. 1977. Soviet investigations of Cetacea June 1976 to May 1977. *Rep. int. Whal. Commn.* 28: 119-122.

Ivashin, M.V. 1981. Some results of the marking of sperm whales (*Physeter macrocephalus*) in the Southern Hemisphere under the Soviet marking program. *Rep. int. Whal. Commn.* 31: 707-718.

International Whaling Commisssion. 1983. Report of the sub-committee on sperm whales. *Rep. int. Whal. Commn.* 33: 74-90.

International Whaling Commission. In press. Report of the sub-committee on Northern Hemisphere minke and other baleen whales. *Report int. Whal. Commn.*

Jarman, P.J. 1974. The social organization of antelope in relation to their ecology. *Behaviour* 48: 215-267.

Jonsgard, A. 1962. Tre funn av sverd fra sverdfish (*Xiphias gladius*) i antarktisk finnhval. *Nor. Hvalfangst-tid.* 51: 287-293.

Kasuya, T. and Ohsumi, S. 1966. A secondary sexual character of the sperm whale. *Sci. Rep. Whales Res. Inst.* 20: 89-95.

Kato, H. 1981. Trial-firing of .410 marks at a minke whale carcase on the factory ship, 1979/80 Antarctic season. *Rep. int. Whal. Commn.* 31: 367-370.

Kato, H. 1984. Observation of tooth scars on the head of male sperm whales, as an indication of intra-sexual fightings. *Sci. Rep. Whales Res. Inst.* 35: 39-46.

Katona, S.K., Harcourt, P., Perkins, J.S. and Krauss, S.D. 1980. *Humpback Whales: A Catalogue of Individuals Identified by the Fluke Photographs.* Publ. College of the Atlantic, Bar Harbour, Maine.

Katona, S.K. and Whitehead, H.P. 1981. Identifying humpback whales using their natural markings. *Polar Record* 20: 439-444.

Klingel, H. 1972. Das Verhalten der Pferde (Equidae). *Handbuch der Zoologie, Bd VIII: Mammalia* 10(24): 1-68.

Laws, R.M., Parker, I.S.C. and Johnstone, R.C.B. 1975. *Elephants and Their Habitats.* Clarendon Press, Oxford, 376 pp.

Lineaweaver III, T.H. and Backus, R.H. 1970. *The Natural History of Sharks.* Lippincott, New York, 256 pp.

Lockyer, C. 1977. Observations on diving behaviour of the sperm whale. pp. 591-609. *In* M. Angel (ed.). *A Voyage of Discovery.* Pergamon Press, Oxford, 696 pp.

Lockyer, C. 1981. Estimates of growth and energy budgets for the sperm whale, *Physeter catodon. FAO Fish, Ser. 5* [Mammals in the seas] 3: 489-504.

Mate, B. 1985. A mass stranding of sperm whales: all was not lost. *Whalewatcher* (J. Amer. Cetacean Soc.) 19(2): 18-20.

Matthews, L.H. 1938. The sperm whale, *Physeter catodon*. *Discovery Rep.* 17: 93-168.

Mayo, C., Carlson, C., Clapham, P., and Mattila, D. 1985. *Humpback Whales of the Southern Gulf of Maine.* Publ. Center for Coastal Studies.

Melville, H. 1851. *Moby Dick: or, the Whale.* Penguin Books, Aylesbury, England, 1981, 1012 pp.

Melville, H. 1854. *The Encantadas or the Enchanted Isles.* pp. 157-226. *In*: *Shorter Novels of Herman Melville.* Liveright Publishing Co., New York, 1942.

Mitchell, E.D. 1975. Preliminary report on Nova Scotia fishery for sperm whales (*Physeter catodon*). *Rep. int. Whal. Comm.* 25: 226-235.

Mitchell, E.D. 1977. Sperm whale maximum length limit: Proposed protection of harem masters. *Rep. int. Whal. Commn.* 27: 224-225.

Nemoto, T. and Nasu, K 1963. Stones and other aliens in the stomachs of sperm whales in the Bering Sea. *Sci. Rep. Whales Res. Inst.* 17: 83-91.

Nishiwaki, M. 1962. Aerial photographs show sperm whales interesting habits. *Nor. Hvalfangst-tid.* 51: 395-398.

Nishiwaki, M, Ohsumi, S. and Maeda, Y. 1963. Change of form in the sperm whale accompanied with growth. *Sci. Rep. Whales Res. Inst.* 17: 1-14.

Norusis, M.J. 1985. *SPSS^x Advanced Statistics Guide.* McGraw-Hill Book Company, New York, 505 pp.

Ohsumi, S. 1965. Reproduction of the sperm whale in the northwest Pacific. *Sci. Rep. Whales Res. Inst.* 19: 1-35.

Ohsumi, S. 1966. Sexual segregation of the sperm whale in the North Pacific. *Sci. Rep. Whales Res. Inst.* 20: 1-16.

Ohsumi, S. 1971. Some investigations on the school structure of sperm whales. *Sci. Rep. Whales Res. Inst.* 23: 1-25.

Ohsumi, S. 1977. Age-length key of the male sperm whale in the North Pacific and comparison of growth curves. *Rep. int. Whal. Commn.* 27: 295-300.

Papastavrou, V. 1986. Diet and Feeding Ecology. pp. 34-35. *In* H. Whitehead (ed.). *Sperm Whales off the Galapagos Islands, February-April 1985.* Unpublished report to Green Island Foundation, Marion, Mass., 50 pp.

Payne, R., Brazier, O., Dorsey, E.M., Perkins, J.S., Rowntree, V.J. and Titus, A. 1983. External features in southern right whales (*Eubalaena australis* and their use in identifying individuals. pp. 371-445. *In* R. Payne (ed.). *Communication and Behaviour of Whales.* AAAS Selected Symposium 76. Westview Press, Boulder, Co., 643 pp.

Perkins, J. and Whitehead, H. 1983. The legend of the swordfish and the thresher. *Whalewatcher* (J. Amer. Cetacean Soc.) 17(1): 10-15.

Reynolds, J.N. 1839. Mocha Dick: or the white whale of the Pacific: a leaf from a manuscript journal. pp. 991-1011. *In* H. Beaver (ed.). *Moby Dick.* Penguin Books Ltd, Harmondsworth, Middlesex, England, 1981. 1012 pp.

Rice, D. 1975. Sperm whales in the equatorial eastern Pacific: population size and social organization. *Rep. int. Whal. Commn.* 25: 333-336.

Rice, D. and Caldwell, D.K. 1961. Observations of the habits of the whalesucker *(Remilegia australis). Nor. Hvalfangst-tid.* 50: 181-187.

Robson, F.D. and van Bree, P.J.H. 1971. Some remarks on a mass stranding of sperm whales, *Physeter macrocephalus, L. 1758* near Gisborne, New Zealand, on March 18, 1970. *Zeits. f. Saugetierk.* 36: 55-60.

Schaller, G.B. 1972. *The Serengeti Lion.* Univ. of Chicago Press, 480 pp.

Schevill, W.E. 1986. The International Code of Zoological Nomenclature and a paradigm: The *Physeter catodon*, Linnaeus 1758. *Mar. Mammal Sci.*, 2: 153-157.

Sears, R. 1984. Photo-identification of individual blue whales. *Whalewatcher* (J. Amer. Cetacean Soc.) 18(3): 10-12.

Shevchenko, V.I. 1975. Kharakter vzaimootnoshenii kasatok i drugikh kitoobraznykh. *Morskie Mlekopitayushchie* Chast'2: 173-175. Naukova Dumka, Kiev. Translated by the Translation Bureau (WRI) Multilingual Services Division, 1976.

Shuster, G.W. 1983. The Galapagos Islands: a preliminary study of the effects of sperm whaling on a specific whaling ground. *Rep. int. Whal. Commn.* (special issue 5): 81-82.

Slijper, E.J. 1958. *Whales.* Hutchinson, 1962, 475 pp.

SPSS Inc. 1983. *SPSS^x User's Guide.* McGraw-Hill Book Company, 806 pp.

Stephenson, A.B. 1975. Sperm whales stranded at Muriwai Beach, New Zealand. *N.Z.J. Mar. Freshw. Res.* 9: 299-304.

Tormosov, D.D. 1977. Ecological aspect of differential distribution of sperm whales. *Rep. int. Whal. Commn.* 27: 361-362.

Townsend, C.H. 1935. The distribution of certain whales as shown by logbook records of American whaleships. *Zoologica* 19: 3-50.

Veinger, G.N. 1980. Intra species structural data of sperm whales in the North Pacific. *Rep. int. Whal. Commn.* (special issue 2): 103-105.

Volkov, A.F. and Meroz, I.F. 1977. Oceanological conditions of the distribution of cetacea in the eastern tropical part of the Pacific Ocean. *Rep. int. Whal. Commn.* 27: 186-188.

Weilgart, L.S. and Whitehead, H. 1986. Observation of a sperm whale (*Physeter catodon*) birth. *J. Mamm.* 67: 399-401.

Whitehead, H. 1982. Populations of humpback whales in the northwest Atlantic. *Rep. int. Whal. Commn.* 32: 345-353.

Whitehead, H. 1985. Humpback whale breaching. *In* G. Pilleri (ed.). *Investigations on Cetacea* 17: 117-155.

Whitehead, H. (ed.). 1986a. *Sperm whales off the Galapagos Islands, February-April 1985.* Unpublished report to Green Island Foundation, Marion, Mass. 50 pp.

Whitehead, H. 1986b. Sperm whale groupings. pp.13-22. *In* H. Whitehead (ed.). *Sperm Whales off the Galapagos Islands, February-April 1985.* Unpublished report to Green Island Foundation, Marion, Mass., 50 pp.

Whitehead, H. 1986c. General behaviour of Sperm whales. pp. 31-33. *In* H. Whitehead, (ed.). *Sperm Whales off the Galapagos Islands, February-April 1985.* Unpublished report to Green Island Foundation, Marion, Mass., 50 pp.

Whitehead, H. and Arnbom, T. In press. Social organization of Galapagos sperm whales. *Can. J. Zool.*

Whitehead, H. and Gordon, J. 1986. Methods of obtaining data for assessing and modeling populations of sperm whales which do not depend on catches. *Rep. int. Whal. Commn.* (special issue 8): 149-166.

Yukhov, V.L., Vinogradova, E.K. and Medvedev, L.P. 1975. Ob"ekty pitaniya kosatok (*Orcinus orca* L.) v Antaktike is sopredel'nykh vodakh. *Morskie Mlekopitayushchie* Chast'2: 183-185. Naukova Dumka, Kiev. Translation by the Translation Bureau (WRI) Multilingual Services Division, 1976.

APPENDIX 1

FORMULA FOR CONVERTING THE PERCENTAGE AREA OF A NEGATIVE OCCUPIED BY A FLUKE INTO DISTANCE FROM PHOTOGRAPHER TO PHOTOGRAPHED WHALE

The relationship in Figure 1 makes it possible to convert the percentage area of a negative occupied by a fluke into the distance (R) between the photographer and the photographed whale. The photo quality measures (X2, X3, X5 and X6) are described in more detail on page 28 in Table 2-1.

Figure 1.

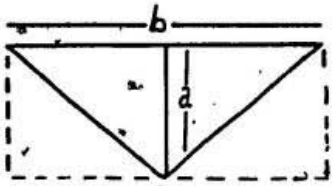
$$w/W = f_0/R \quad [1]$$

w = Width of fluke on negative.
W = Actual width of fluke (2.95 m). This fluke width is from two female sperm whales which were 10 m in length and had fluke widths of 2.90 m and 3.00 m, respectively (from tables in Fujino, 1956).
f_0 = Focal length of lens (0.300 m)
R = Distance between photographer and photographed whale in metres

Actual area of fluke visible n negative = X2/100·NArea
X2 = Percentage area the individual fluke occupied relative to the total area of the negative.
NArea = Total area of negative (0.036·0.024 m).

The corrected area of the fluke is $a/b \cdot w^2/2$, where a/b is the ratio of the width to the depth of the fluke (Figure 2). The ratio a/b was measured on ten selected fluke photographs (flukes almost perpendicular to the camera axis). The mean for a/b from these ten prints was 0.392 (s.d. 0.0097).

Figure 2.



Other correction factors necessary to estimate the width of the fluke on the negative were:

- Deviations of the fluke surface from being perpendicular to the axis of the camera, measures X3 and X5 (Cos (X3) and Cos (X5)).
- Percentage of the fluke out of the water (X6/100).

The following formula makes it possible to estimate the width of the fluke on the negative:

$$w = \sqrt{\frac{X2(0.036 \cdot 0.024)}{((a/b)/2)X6Cos(X3)Cos(X5)}} \quad [2]$$

Formula [2] is inserted in formula [1]; to give the range, R:

$$R = \frac{f_0 W}{\sqrt{(X2(0.036 \cdot 0.024))/((a/b)/2)X6Cos(X3)Cos(X5)}}$$

Literature cited

Fujino, K. 1956. On the body proportions of the sperm whale (*Physeter catodon*). *Sci. Rep. Whales Res. Inst.* 11: 47-83.